Dynamic coding of body-related and spatial information during tactile sensorimotor processing and continuous bimanual coordination

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Abbreviations

2AFC	2-alternative-forced choice
aIPS	anterior intraparietal sulcus
BOLD	blood-oxygen-level-dependent
CI	confidence interval
DGPs	German Psychological Society
DST	Dynamic Systems Theory
EEG	electroencephalography
EMG	electromyography
EOG	electrooculography
EPI	echo planar imaging
ERP	event-related potential
ESS	effective sample size
fANOVA	functional analysis of variance
fMRI	functional Magnetic Resonance Imaging
FWE	family-wise error correction
GLM	General Linear Model
HDI	highest density interval
hLIP	human homolog of non-human primate lateral intraparietal area
hVIP	human homolog of non-human primate ventral intraparietal area
ins	insula
IPL	inferior parietal lobule
IPS	intraparietal sulcus
IR	infrared
LED	light emitting diode
LH	left hemisphere
LIP	lateral intraparietal area
LL	lower limit
LSM	least square mean
M1	primary motor cortex
M1h	hand area of primary motor cortex
MCMC	Markov Chain Monte Carlo
MEG	magnetoencephalography
mIPS	medial intraparietal sulcus
MPRAGE	Magnetization Prepared Rapid Gradient Echo
MVPA	multi-voxel pattern analysis
OFC	Optimal Feedback Control
PC	personal computer
pIPS/ cIPS	posterior or caudal intraparietal sulcus
PMC	premotor cortex
PMd	dorsal premotor cortex
PMv	ventral premotor cortex
POS	parietal occipital sulcus
PPC	posterior parietal cortex
PPS	peripersonal space

preSMA	pre-supplementary motor area
PRR	parietal reach region
RF	receptive field
RH	right hemisphere
ROI	region of interest
RT	reaction time
s.d.	standard deviation
S1	primary somatosensory cortex
S1f	foot area of primary somatosensory cortex
S1h	hand area of primary somatosensory cortex
S2	secondary somatosensory cortex
SMA	supplementary motor area
SOA	stimulus onset asynchrony
SPL	superior parietal lobule
SPOC	superior parieto-occipital cortex
SVM	support vector machine
TE	echo time
TMS	transcranial magnetic stimulation
TOJ	temporal order judgment
TR	repetition time
UL	upper limit
V5	visual area 5
VIP	ventral intraparietal area
vIPS	ventral intraparietal sulcus

There is really nothing ordinary about our most ordinary movements.

(Shadmehr & Mussa-Ivaldi, 2012)

Abstract

Flexible interaction with the external world, as squatting a mosquito or applauding at a concert for example, depends on processing information about the body and the environment. This information is sampled through different senses that code it relative to native anchors, such as the retina in vision or the skin in touch. Some body-related and spatial aspects are redundantly coded in multiple senses, as body posture or movement direction in vision and proprioception for instance. Others are uniquely coded in one sense, such as color in vision or tickling in touch. Successful interaction with the environment relies on combining redundant and complementary information across the senses. The three studies of the present thesis investigate the organizing principles of this process for different kinds of action. The first two studies examined how body-related information is processed in 3D space. For instance, to squat a mosquito, a tactile stimulus, natively coded relative to the skin, has to be recoded into an external movement target by integrating multisensory information about body posture. This process presumably encompasses coordinate transformation from skin-based into external coordinates and subsequent integration of both location codes. The first study investigated how both of these processes contribute to goal-directed action toward a touch using motion tracking of hand movements during a sensorimotor decision task (Chapter 2). The results showed that flexibly weighted integration of skin-based and spatial coordinates, as well as prior probabilities signaling previous movement goal locations, is the prime computational mechanism underlying touch localization for action. The second study investigated the neural implementation of this process using functional Magnetic Resonance Imaging (fMRI; Chapter 3). The results revealed that dynamically employed body-related and spatial codes differ depending on the stage of movement planning and are implemented in posterior parietal cortex (PPC). Other kinds of action, as applauding at a concert for example, also rely on processing body-related and spatial information. The third study examined how both aspects are coded across vision and proprioception using motion tracking of bimanual index finger adduction and abduction movements (Chapter 4). The results showed that coordinative movements are most stable if homologous muscles were used in both hands. Moreover, vision exclusively contributed to spatial (i.e., movement direction), but not to body-related (i.e., posture, muscle) movement coding. Taken together, the results of the present thesis show that body-related and spatial coding is flexibly employed according to the task context across

different kinds of action. On a neural level, PPC appears to play a key role for spatial processing of body-related information. More generally, sensorimotor processing and continuous bimanual coordination have been investigated in two largely separate research fields to date, in part because studies on these different kinds of actions were motivated by distinct theoretical concepts. Building on the results of the present thesis, future investigations of tactile sensorimotor processing and continuous bimanual coordination could further characterize unique and shared processing principles against a common theoretical background, such as Optimal Feedback Control (OFC). Collectively, the present thesis advances our understanding of how perceptual and motor aspects of behavior interact during seemingly ordinary movements, such as squatting a mosquito or applauding at a concert.

1 | General introduction

Interaction with the environment requires flexible processing of body-related and spatial information derived through different sensory channels. For instance, both vision and proprioception may convey information about posture or the movement direction. Relying on multiple senses is beneficial for behavior, as they also complement each other. Color, for instance, is uniquely coded in vision, whereas tickling is uniquely coded in touch. Together, coding redundant and complementary information across the senses reveals more about the environment than could be conveyed by each sense in isolation. Each sensory channel codes information relative to a different spatial anchor, such as the retina in vision or the skin in touch. As a consequence, information has to be matched across the senses so it can be used to interact with the environment. For instance, the skin-based location of a tactile stimulus alone is not sufficient for goal-directed action, because the body can be moved in space. Thus, to squat a mosquito for example, body-related tactile information has to be recoded spatially, that is, independent of its original skin-based anchor. Native skin-based coding must therefore be complemented by other senses that code space relative to different, skin-independent anchors, if the body is both the target and the effector of an action. Vision might be a prime candidate for spatial coding of skin-based information for action, because it generalizes across the body and the external world by coding both relative to the retina. The contribution of visual information to native body-centered coding may be a general organizing principle that is relevant for different kinds of actions. Naturally, we interact with the environment using a combination of unimanual goal-directed movements toward our body or external targets. Moreover, we effortlessly coordinate movements of both hands, such as applauding at a concert. Motionless start and end points characterize the goal-directed movements (Huys, 2010), whereas the rhythmic repetition of a particular "movement event" characterizes continuous bimanual coordination (Hogan & Sternad, 2007; Huys, Studenka, Rheaume, Zelaznik, & Jirsa, 2008). In the context of continuous bimanual coordination, proprioceptive body-related movement coding too has been shown to be complemented by other sensory channels, in particular by vision (Buckingham & Carey, 2008; Heed & Röder, 2014). For instance, visual movement information, possibly related to the movement direction, influences coordination stability (Buckingham & Carey, 2008). Thus, movement information as coded by vision impacts behavior, although the same information is simultaneously coded by proprioception in a body-centered code. Thus, despite fundamental differences between tactile sensorimotor processing and continuous bimanual coordination, both kinds of movements potentially share processes related to the coding of redundant and complementary body-related and spatial information derived through different sensory channels. Hence, the principles that determine how the brain translates and combines body-related and spatial information for action across distinct movement types may inform about how we achieve dynamic interaction with the external world more generally.

The present thesis investigated the organizing principles of processing body-related and spatial information for action. Three studies approached this topic from different viewpoints. The first two studies examined how body-related information is spatially processed when recoding a tactile stimulus, natively coded relative to the skin, into an external movement target. The first study focused on the computational mechanisms of this process (Chapter 2), whereas the second study investigated its neural implementation (Chapter 3). The third study examined how body-related and spatial aspects are coded across vision and proprioception during continuous bimanual coordination (Chapter 4). In particular, this study investigated whether vision contributes to coding body-related aspects, such as posture and the muscles that are used, in addition to proprioception. Or whether, alternatively, vision exclusively contributes to coding spatial aspects, such as movement direction. In the following, I review the concepts and empirical findings that build the background for the three studies of the present thesis. First, I give an overview over research that has investigated how the brain processes multisensory body-related and spatial information for action. Second, I summarize research that has investigated how the brain chooses appropriate motor commands and translates body-related and spatial information coded across different senses into suitable muscle patterns. Finally, I recapitulate previous research on tactile sensorimotor processing and continuous bimanual coordination as two types of action that both rely on multisensory coding of body-related and spatial information.

1.1 Multisensory processing for action

The complexity of seemingly simple actions is in part due to the density of constantly changing information around us, necessitating flexible and fast movement adaptation. For instance, we effortlessly adapt our initial reach path to squat a mosquito if it flies to a different location on the body, for example to the leg. Motor control of such goal-directed reaching movements involves processing of information related to the body part that executes the action, that is, the so-called effector, and to the target. Naturally, information about either, here, the hand and the mosquito on the leg, arrives at the brain through a combination of sensory channels. With regard to the effector, we see and feel our hand moving toward the leg, as well as the fingers opening up in preparation of squatting. Thus, vision and proprioception inform about effector position, that is, where the hand is located in space, and about effector posture, that is, how the wrist and finger joints are configured. Similarly, with regard to the movement goal, we see the mosquito and we feel it on the body. Thus, vision and somatosensation inform about the characteristics of the movement goal. In this situation, somatosensation codes the movement goal through proprioception, signaling leg position and posture, and through touch, informing about the goal location on the skin surface. Thus, information arriving in the brain contains information that is redundantly coded across multiple sensory channels, such as hand position signaled by vision and proprioception, and information that is uniquely coded in one sensory modality, such as tickling signaled by touch (Spence, 2012). Thus, the basic code that represents common and unique features differs across sensory modalities. That is, this code may be related to the body as in somatosensation or it may generalize across the body and the environment, as in vision. Redundant and at the same time complementary coding across the senses is beneficial, as it increases the likelihood of detecting a feature of interest fast and accurately (Stein & Stanford, 2008). Additionally, it reveals more about the body and the environment than could be extracted from each sensory channel alone (Stein & Stanford, 2008). In correspondence, multisensory processing leads to faster response times and more accurate responses than unisensory processing (Stein, Huneycutt, & Meredith, 1988; e.g., Stein, Meredith, Huneycutt, & McDade, 1989). Nonetheless, employing distinct body-related or spatial codes across different senses requires that redundant and complementary information is matched and integrated for successful interaction with the environment.

The following section reviews the principles that determine how we construct coherent percepts of the body and the environment from multisensory information. First, I outline how information is coded across the senses with a focus on vision and somatosensation. Second, I describe the computational principles of how multisensory information is combined for action at the single neuron level and beyond. Finally, I discuss the neural networks mediating these computations in non-human primates and humans. Collectively, the first section discusses the sensorimotor principles underlying the coding of body-related and spatial information for both types of action investigated in the empirical studies of the present thesis: tactile sensorimotor processing and continuous bimanual coordination.

1.1.1 Coding information about the body and the environment across the senses

In each sensory channel, the majority of neurons code information in a modality-specific reference frame. To illustrate the concept of a reference frame, picture a person driving a car and another person observing the car (Soechting & Flanders, 1992). Two reference frames, one fixed to the car and another fixed to the earth, could be used to describe this situation. In earth coordinates, the driver is moving, whereas he/she is stationary in car coordinates. The observer in turn is stationary in earth coordinates, but is moving in car coordinates. An object dropped out of the cars' window follows a straight path in car coordinates and a curved one in earth coordinates while falling down. Thus, the anchor of the coordinate system determines the description of events (Soechting & Flanders, 1992). In a similar vein, neurons code information about the body and the environment relative to different, modality-specific anchors. A receptive field (RF) describes a specific part of visual space which optimally activates a neuron (Batista & Newsome, 2000). RFs are typically fixed to the retina in vision, fixed to the head in audition, fixed to the skin in touch, and fixed to joints and muscles in proprioception (Batista & Newsome, 2000). Thus, when we reach to squat a mosquito, for example, information about the mosquito is coded in eye-centered reference frames in vision and in different body-centered reference frames, anchored to the skin, joints, and muscles, across touch and proprioception. Similarly, when we applaud at a concert, for example, information about our hands as effectors is coded in eye-centered reference frames in vision and in different body-centered reference frames anchored to joints and muscles in proprioception.

In touch, cutaneous receptors signal the position of the tactile stimulus on the skin surface (cf. Gallace & Spence, 2014). In proprioception, afferent information is derived through mechanoreceptors in joints, muscles, muscle tendons, and stretch-sensitive receptors in the skin (cf. Longo, Azañón, & Haggard, 2010) that signal body posture with regard to the degree of flexion or extension of each joint (Burgess, Wei, Clark, & Simon, 1982). To derive how and where in external space the body is positioned, proprioceptive information has to be combined with information about the length and width of the body segments linking the joints (cf. Longo et al., 2010). This information may be derived through vision. However, visual information of the effector is not always available. For instance, as we reach for the mosquito at the leg, we might divert the eyes to look at a person next to us. Moreover, it may be dark in the concert hall, or, we might fixate the stage, while we applaud. Crucially, we are not only passive observers of action but also their generator. Therefore, information about the effector can additionally be extracted from motor commands send to the periphery. Specifically, so-called efference copy signals of motor commands are thought to inform about anticipated hand position and posture, that is, they function as forward models of the state of the body (cf. Scott, 2012). Similarly, information about the length and width of the body segments linking the joints can be constructed from efference motor signals (cf. Longo et al., 2010). Visual, proprioception, and efference copy signals are complemented by predictions based on prior knowledge about the regularities of sensory and motor signals (Crevecoeur & Scott, 2013; O'Regan & Noë, 2001; Rincon-Gonzalez, Buneo, & Helms Tillery, 2011). For instance, we have experience with squatting mosquitos, or, put differently, with the co-occurrence of tactile, proprioceptive, and movement information, in this situation. Proprioception drifts over time, which can be prevented by visual feedback of the limb, or, by moving the limb (Wann & Ibrahim, 1992). This phenomenon exemplifies the reliance of proprioception on complementary information derived from vision and forward models of the body. Conversely, forward models of the body are also complemented by proprioception. That is, they are continuously updated as we move and sample sensorimotor signals. More generally, the interaction of forward body models and proprioception illustrates how multisensory information is effortlessly combined for successful interaction with the external world. The three empirical studies of the present thesis delineate how information sampled through different combinations of sensory channels are processed for action. Our first and second study focus on how tactile and proprioceptive information related to the target is processed for goal-directed action (Chapters 2, 3), whereas our third study scrutinizes how visual and proprioceptive information is processed for continuous bimanual coordination (Chapter 4). Building on the results of our empirical studies, I develop experiments that could investigate the principles of how the brain constructs forward models of the body during these different types of movements in the future in the general discussion of the present thesis (Chapter 5). Collectively, the brain has to translate and combine information that is initially coded in reference frames that are native to each sensory channel for successful interaction with the environment. Specific rules at the single neuron level and across neuronal assemblies have been identified that mediate the combination of redundant and complementary multisensory information about the body and the environment.

1.1.2 Organizing principles of multisensory integration for action

Specialized frontal, parietal, temporal, and subcortical structures have been shown to respond to information coded in more than one modality (cf. Stein & Stanford, 2008). At the extreme, the entire neocortex has been suggested to be multisensory (Ghazanfar & Schroeder, 2006), as even coding in primary sensory cortices, traditionally viewed as unisensory, was found to be modulated by information from other modalities (Murray et al., 2016; Schroeder & Foxe, 2005). Thus, multisensory neurons responding to information coded in more than one modality, can be found across the processing hierarchy. They receive input from ascending sensory pathways as well as descending cortical projections (cf. Stein & Stanford, 2008). Their RFs are spatially overlapping. For example, in ventral intraparietal area (VIP) in posterior parietal cortex (PPC) of non-human primates, bimodal visuo-tactile neurons have been identified that respond to tactile stimulation of the arm and to visual stimuli presented in the space directly surrounding the arm (Duhamel, Colby, & Goldberg, 1998). However, each sensory organ can be moved independently, complicating the alignment of RFs. For instance, the eyes can be moved without changing the spatial position of the arm. Thus, depending on eye position, different parts of the retina correspond to the location of the arm, so that a change in eye position requires realigning visual and tactile RFs. As a solution, some bimodal neurons have been shown to compensate for eye or arm movements, coding multisensory information in an eye- or body-centered reference frame, respectively (e.g., Batista, Buneo, Snyder, & Andersen, 1999; Duhamel et al., 1998). Such RF alignment is a prerequisite for multisensory integration, that is, the combination of unisensory signals into a unified percept (cf. Stein et al., 2010). More generally, PPC has been suggested as an interface where multisensory information converges for action. Within PPC, VIP is of particular interest for the present study, because it has been assigned a central role in realigning tactile with visual maps (e.g., Duhamel et al., 1998). Functions of VIP in non-human primates and potential human homologs (hVIP) will be discussed in detail in the next section.

The integration of multisensory information at the single-neuron level and across neuronal assemblies is guided by distinct principles. Temporal and spatial constraints act as filters that select favor appropriate stimulus configurations for multisensory integration (Meredith, 2002; Meredith & Stein, 1983). In particular, stimuli are most likely to be integrated when they coincide spatially and temporally (cf. Stein & Stanford, 2008). That is, to be integrated, stimuli have to be within the space covered by the overlapping RFs and fall within a time window of about 100 ms (Meredith, Nemitz, & Stein, 1987; Meredith & Stein, 1986). Such a margin of tolerance makes sense due to the properties inherent in the different sensory organs and the environment. For example, sound is transduced faster than light in the brain; however, within the environment, sound travels slower than light. Properties of the environment also determine whether information conveyed through one sensory channel or another is more useful for behavior. For example, relying more on visual than auditory signals might be useful at a loud party, whereas the opposite would be helpful when navigating through a dark movie theater. Computational models have been put forward that formalize how the brain integrates multisensory information beyond single neurons and why it relies more on one sensory channel than another in a given situation. These models assume that multisensory information is integrated in a statistically optimal way, that is, reliability determines how each channel is weighted during integration (Alais & Burr, 2004; Ernst & Banks, 2002; Hillis, Ernst, Banks, & Landy, 2002; Knill & Saunders, 2003). Consistent with intuition, this conceptualization predicts that vision would outweigh audition at a loud party, whereas audition would outweigh vision in a dark movie theater. The percept resulting from integration, then, is more reliable than each of its parts in isolation (Ernst, 2012). Prior knowledge and expectations about the probability of stimuli co-occurrence are thought to additionally modulate integration (Ernst, 2012). For example, if you hear laughter and see a dog opening its snout at the same time, you will probably not attribute the laughter to the dog despite perfect temporal co-occurrence, as a laughing dog would be highly unexpected. These computational models of multisensory integration formalize how we perceive our body and the environment. However, they do not account for the fact that, when interacting with the external world, perception is intrinsically linked to action. That is, we do not only perceive to act, but also act to perceive. Put differently, the relation of perception and action may be bilateral: action may influence perception just as perception influences action.

In line with this view, computational models that characterize how multisensory information is integrated for action have been proposed (McGuire & Sabes, 2009; Pouget, Deneve, & Duhamel, 2002; Sober & Sabes, 2003, 2005; Tagliabue & McIntyre, 2014; Tramper & Medendorp, 2015; van Beers, Sittig, & Denier van der Gon, 1999). These models assume that target- and effector-related information is maintained in multiple reference frames at the same time. Each piece of information is thought to be weighted according to task demands, target modality, and reliability for optimal integration. Furthermore, it has been suggested that reference frame integration depends on how sensory information is going to be used, that is, action is thought to modulate perception (Sober & Sabes, 2003, 2005). For instance, the relative weighting of visual and proprioceptive signals is thought to differ according to the stage in motor planning. Visual information appears to be central when inferring external spatial movement parameters, whereas mainly proprioceptive feedback is used when deducing muscular-based, position-related information, as is the case when motor commands are send to the periphery (Sober & Sabes, 2003, 2005). Our third study explores whether the contributions of vision and proprioception to spatial and body-related aspects follow similar principles when coordinating continuous movements with both hands (Chapter 4).Collectively, the neural implementation of the computational principles of multisensory processing for action have been the topic of extensive research. Parallel to the development of computational models of multisensory processing, neurophysiological research too has traditionally either focused on sensory processing or motor control. However, many findings, especially related to PPC, indicate that both might be only theoretically separable concepts.

1.1.3 Neuronal networks mediating multisensory processing for action

Multisensory information about the environment and the body converges in PPC (Gallivan & Culham, 2015). In general, processing in PPC has been related to the transformation from sensory into motor-related references frames (Culham, Cavina-Pratesi, & Singhal, 2006; Gallivan & Culham, 2015; Scott, 2012; Vesia & Crawford, 2012). More specifically, a central role in processing multisensory information related to the target and the effector of an action has been assigned to areas around the intraparietal sulcus (IPS) located in PPC (Crawford, Henriques, &

Medendorp, 2011; Culham et al., 2006; Filimon, 2010; Gallivan & Culham, 2015; Grefkes & Fink, 2005; Medendorp, Buchholz, Van Der Werf, & Leoné, 2011; Vesia & Crawford, 2012). For instance, in humans, a central role in visuomotor control has been assigned to an area in the superior parieto-occipital cortex (SPOC), bordering the precuneus (Astafiev et al., 2003; Beurze, Lange, Toni, & Medendorp, 2007; Connolly, Andersen, & Goodale, 2003; Fernandez-Ruiz, Goltz, DeSouza, Vilis, & Crawford, 2007; Vesia & Crawford, 2012). SPOC has been shown to process target and visual effector information (Fernandez-Ruiz et al., 2007; Filimon, Nelson, Huang, & Sereno, 2009), possibly suggesting that it calculates the movement goal from sensory target information, while more medial IPS regions have been suggested to incorporate proprioceptive effector information to finalize the reach plan (Vesia & Crawford, 2012). However, this specialization appears to be relative and not absolute, as the coding of motor goal information in SPOC is modulated by the target modality, that is, in specific task contexts, it codes proprioceptive targets in body-centered coordinates (Bernier & Grafton, 2010). Taken together, SPOC in human PPC is thought to play a central role in processing body-related and spatial target and effector information for action, and as such, may be of central relevance for controlling tactile sensorimotor processing and continuous bimanual coordination.

In non-human primates, a region with similar properties has been described. In particular, the parietal reach region (PRR) has been related to the preparation of hand movements (Batista et al., 1999; Y. E. Cohen & Andersen, 2000, 2002), whereas a lateral intraparietal area (LIP) has been related to the preparation of eye movements (Snyder, Batista, & Andersen, 1997). In humans, however, regions related to eye movement planning appear to be located medially, instead of laterally as in non-human primates (Grefkes & Fink, 2005; Medendorp et al., 2011; Sereno, Pitzalis, & Martinez, 2001; Silver & Kastner, 2009), emphasizing that anatomical differences between species translate to differences in functional localization (Caminiti, Innocenti, & Battaglia-Mayer, 2015; Kastner, Chen, Jeong, & Mruczek, 2017). Nevertheless, It has been suggested that effector-specific modules also exist for motor control in human PPC in correspondence to non-human primate neurophysiology (e.g., Connolly, Goodale, Cant, & Munoz, 2007). For instance, consistent with a reach-specific computational function, Transcranial Magnetic Stimulation (TMS) over SPOC perturbs reach, but not saccadic, movements to contralateral targets (Vesia, Prime, Yan, Sergio, & Crawford, 2010). Alternatively, recent results suggest that human PPC is organized functionally and not effector-specifically efe(Heed, Beurze, Toni, Röder, & Medendorp, 2011; Heed, Leoné, Toni, & Medendorp, 2016; Leoné, Heed, Toni, & Medendorp, 2014). In a similar vein, VIP has been well defined with regard to function and anatomical location in non-human primates, whereas it is not resolved whether and where hVIP exists. In non-human primates, VIP has been associated to spatial coding of touch in particular, and to the alignment of multisensory maps, more generally (Bremmer, Duhamel, Ben Hamed, & Graf, 2002; Bremmer, Klam, Duhamel, Ben Hamed, & Graf, 2002; Colby, Duhamel, & Goldberg, 1993; Duhamel et al., 1998; Grefkes & Fink, 2005; Klam & Graf, 2003). Here, multisensory integration has been demonstrated in bimodal visuo-tactile neurons (Avillac, Ben Hamed, & Duhamel, 2007). With regard to somatosensation, VIP is sensitive to tactile, but not to proprioceptive, stimulation (Colby et al., 1993; Duhamel et al., 1998). Visuo-tactile RFs for example are mainly anchored to the head or face, but the upper limbs (shoulders, arms, hands) are represented, too (Duhamel et al., 1998). The majority of these neurons code space in body-centered coordinates, that is, their firing is unaffected by changes in eye position (Duhamel et al., 1998). Such neuronal properties have been suggested to serve spatial sensorimotor transformations for goal-directed action (Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981b, 1981a). In contrast to the well-defined functions and anatomical location of VIP in non-human primates, there is no consensus concerning functions and exact spatial location of putative hVIP; instead, across various studies, hVIP has been suggested to lie along the IPS, anterior to posterior and also along the superior parietal lobule (SPL). Our second study discusses the functions and locations of hVIPs in detail in the context of tactile sensorimotor processing (Chapter 3). Thus, even though neurophysiological research in non-human primates provides a model for understanding how multisensory processing for action is neurally implemented in humans (Grefkes & Fink, 2005; Medendorp et al., 2011; Vesia & Crawford, 2012), neither the functional nor the anatomical correspondence between sensorimotor regions of non-human primate and human PPC has been conclusively resolved yet.

Collectively, invasive neurophysiological recordings in non-human primates have revealed a modular organization of areas around the IPS, which appear to be specialized according to the actions and functions they are involved in. In contrast, the organization of function in human PPC appears to be more distributed and it has been a matter of debate whether similar dimensions are relevant for the organization of human and non-human primate PPC. However, even in non-human primates, the specializations along the IPS are relative and not absolute (cf.

Andersen & Cui, 2009). For instance, it has recently even been questioned whether the motor system is strictly hierarchically organized (Gardner, 2017; Rathelot, Dum, & Strick, 2017). In particular, traditionally, frontal cortex has been thought to exclusively send descending motor commands to the periphery. However, a recent neuroanatomical tracing study suggests that PPC might directly issue motor commands for goal-directed actions of the hand and arm to the spinal cord, circumventing frontal cortex (Gardner, 2017; Rathelot et al., 2017). These results are in line with earlier reports of electrical stimulation in VIP eliciting complex movements (e.g., Cooke, Taylor, Moore, & Graziano, 2003). Therefore, these results favor a view of motor control, also in non-human primates, whose organization is not strictly hierarchical and modular, but instead, is characterized by a combination of hierarchical and parallel computations. In this view, PPC is the knob of the motor control network that is central for multisensory processing for direct and indirect relay of information to the periphery. Our second study characterizes the role of human PPC in processing tactile and motor reference frames for action (Chapter 3). In the general discussion of the present thesis, I consider potential overarching functions of human PPC and develop experiments related to tactile sensorimotor planning that may advance our understanding of PPC function more generally (Chapter 5).

So far, this general introduction focused on the principles that determine how multisensory information about the body and the environment is structured for action, computationally and neurophysiologically. These are the neural principles and structures that determine body-related and spatial processing across different types of actions. In the following, the focus is shifted to the principles that determine output generation, that is, the next section reviews how multisensory information about the body and the environment is transformed into suitable motor commands and muscle patterns.

1.2 Organizing principles of goal-directed motor control

Beyond constantly changing external inputs, successful interaction with the environment is complicated by the mechanics of the body. Across more than 200 joints and 600 muscles many different combinations of muscle patterns can lead to the same movement (Franklin & Wolpert, 2011). Thus, a simple reaching movement toward a mosquito on the leg can be implemented in many different ways. Nonetheless, goal-directed movements are highly stereotypical across individuals (Morasso, 1981). Theories of motor control differ as to whether they attribute this phenomenon to inherited control mechanisms shared across individuals, or alternatively, whether they attribute it to common properties of the task (Haith & Krakauer, 2013). Correspondingly, ideas on how the nervous system accomplishes motor control in light of the complexity of the environment and the redundancy within the motor system can be broadly classified into three major perspectives. One class of models assumes that motor control relies on hierarchical transformations of an actions' movement goal into an appropriate muscle pattern (Batista et al., 1999; Y. E. Cohen & Andersen, 2002; Pouget, Ducom, Torri, & Bavelier, 2002; Soechting & Flanders, 1989, 1992). Alternatively, another class of models assumes that motor commands are selected by optimizing a task-specific cost function (Scott, 2004, 2012, 2016; Todorov, 2004). A third view suggests that motor control is closely linked to decision making, defined as the "[…] deliberative process that results in the commitment to a categorical proposition" (Gold & Shadlen, 2007; p.536). Each movement could be viewed as a decision outcome chosen among many possibilities. The following section gives an overview over these three different perspectives on motor control of goal-directed actions. These have mainly motivated investigations of how body-related and spatial information is processed for goal-directed action toward visual targets.

1.2.1 Hierarchical transformation of motor plans into actions

One influential model of motor control has suggested that movement goal, hand path, direction, distance, and speed of an action are "pre-planned" for hierarchical transformation into muscle patterns (Batista et al., 1999; Y. E. Cohen & Andersen, 2002; Pouget, Ducom, et al., 2002; Soechting & Flanders, 1989, 1992). The resulting movement parameters are then presumably transformed sequentially: first into the necessary joint rotations to move the hand, then into joint torques to produce joint rotations, and finally into muscle signals acting upon each joint (Kalaska, 2009). Thus, motor control is thought to rely on an inverse relation of planning and execution stages of motor control (Haith & Krakauer, 2013). Although such inverse models of motor control have been superseded, they have been influential in characterizing central computational concepts of motor control (Haith & Krakauer, 2013; Kalaska, 2009). For instance, sensorimotor transformations involve multisensory spatial information about the environment or the body coded in different reference frames. Any point in a reference frame can be described with a vector of a specific direction and amplitude, relative to a given origin (Soechting & Flanders, 1992). Correspondingly, the notation of a movement vector is frequently used to describe the trajectory from effector position to an external target (e.g., Vesia & Crawford, 2012). In this context, it has been suggested that the calculation of a movement vector requires that external movement goal and current effector position are transformed into a common, presumably eye-centered, reference frame (Batista et al., 1999; Y. E. Cohen & Andersen, 2002; Henriques, Klier, Smith, Lowy, & Crawford, 1998; Medendorp, Goltz, Vilis, & Crawford, 2003; Soechting & Flanders, 1989). This view thus predicts that a limited number of reference frames code motor representations during movement guidance (Scott, 2003). Inconsistently, primary motor cortex (M1) for example, has been shown to code a large number of features, that is, it potentially adds to many different representations (cf. Scott, 2003). This realization has led to the emergence of an alternative perspective that views the task demands as the factor that determines flexible motor control in multiple reference frames at the same time.

1.2.2 Optimal control of movements based on task demands

Motor control theories in the tradition of optimal control assume that perceptual and cognitive systems choose a configuration of motor commands among the abundant possibilities by optimizing a task-specific cost function (Scott, 2016; Todorov & Jordan, 2002). Whereas inverse models of motor control typically describe the properties of goal-directed actions, OFC formalizes how the brain deals with redundancy in the motor system (Haith & Krakauer, 2013). Task-specific cost functions are related to movement features such as variability and more general aspects, such as effort or satisfaction of task goals (Flash & Hogan, 1985; Todorov & Jordan, 2002; Uno, Kawato, & Suzuki, 1989). Thus, according to this view and in contrast to inverse models of motor control, movement parameters are not explicitly planned, but instead, the consequences of motor commands on the body are predicted and optimized (cf. Scott, 2004, 2012). A so-called feedforward control policy then specifies how to achieve the target, i.e. achieve the task goal, by changing the current state of the body (cf. Haith & Krakauer, 2013). Early formulations of OFC were solely based on feedforward control policies (e.g., Flash & Hogan, 1985; Uno et al., 1989). Thus, they specified how the brain arrives at an optimal control policy for a given task that can be released during execution. However, they did not incorporate how movements are constantly revised when interacting with the environment. For instance, we smoothly adapt the reach path toward a mosquito if it flies to a different location on the body. To realize continuous movement adaptations the brain is thought to instantiate a feedback control policy that specifies rules that determine the motor commands necessary to achieve a desired body configuration at each point in time (Todorov & Jordan, 2002). It follows that there is no qualitative difference between planning and execution stages of motor control, because forward and feedback control rely on optimizing the current state of the body to achieve the task goal (state estimation; Todorov & Jordan, 2002).

As discussed earlier, reliability of sensory information is expressed in differential noise levels as well as temporal delays between the senses and determines multisensory integration (Alais & Burr, 2004; Ernst & Banks, 2002; Hillis et al., 2002; Knill & Saunders, 2003). Reliability of multisensory information also determines state estimation for motor control (Franklin & Wolpert, 2011). For instance, task-dependent corrective motor responses have been observed as early as 50-105 ms after a mechanical perturbation (Pruszynski & Scott, 2012), while sensory delays are known to be in the magnitude of tens of milliseconds (Scott, 2012). In other words, the fastest volitional movement corrections are measurable in behavior before sensory feedback even arrives in the brain. As a solution to this discrepancy, forward models estimating the current state of the body have long been suggested as a prerequisite for timely movement adaptation (Desmurget & Grafton, 2000; Wolpert & Ghahramani, 2000). Nonetheless, state estimation is thought to be computed on the basis of all available information, that is, sensory feedback as well as internal forward models of the limb based on efference copies of prior motor commands and sensory predictions (Todorov & Jordan, 2002). For instance, in support of sensory predictions significantly contributing to state estimation, trial-by-trial corrective responses to mechanical perturbations have been shown to be influenced by internal models of the perturbation load (Crevecoeur & Scott, 2013). These models are likely based on sensory predictions, because the perturbations occurred too early during the reach, that is within the first 50 ms, to be influenced by efference copy signals (Crevecoeur & Scott, 2013). In sum, feedback control policies have provided a framework of how fast and flexible interaction with the environment is achieved on a millisecond time scale, thereby effectively circumventing sensory feedback delays inherent in the nervous system. Against the background of the results of the present thesis, I develop experiments that could investigate how sensory predictions contribute to state estimation during tactile sensorimotor processing in the general discussion of the present thesis (Chapter 5).

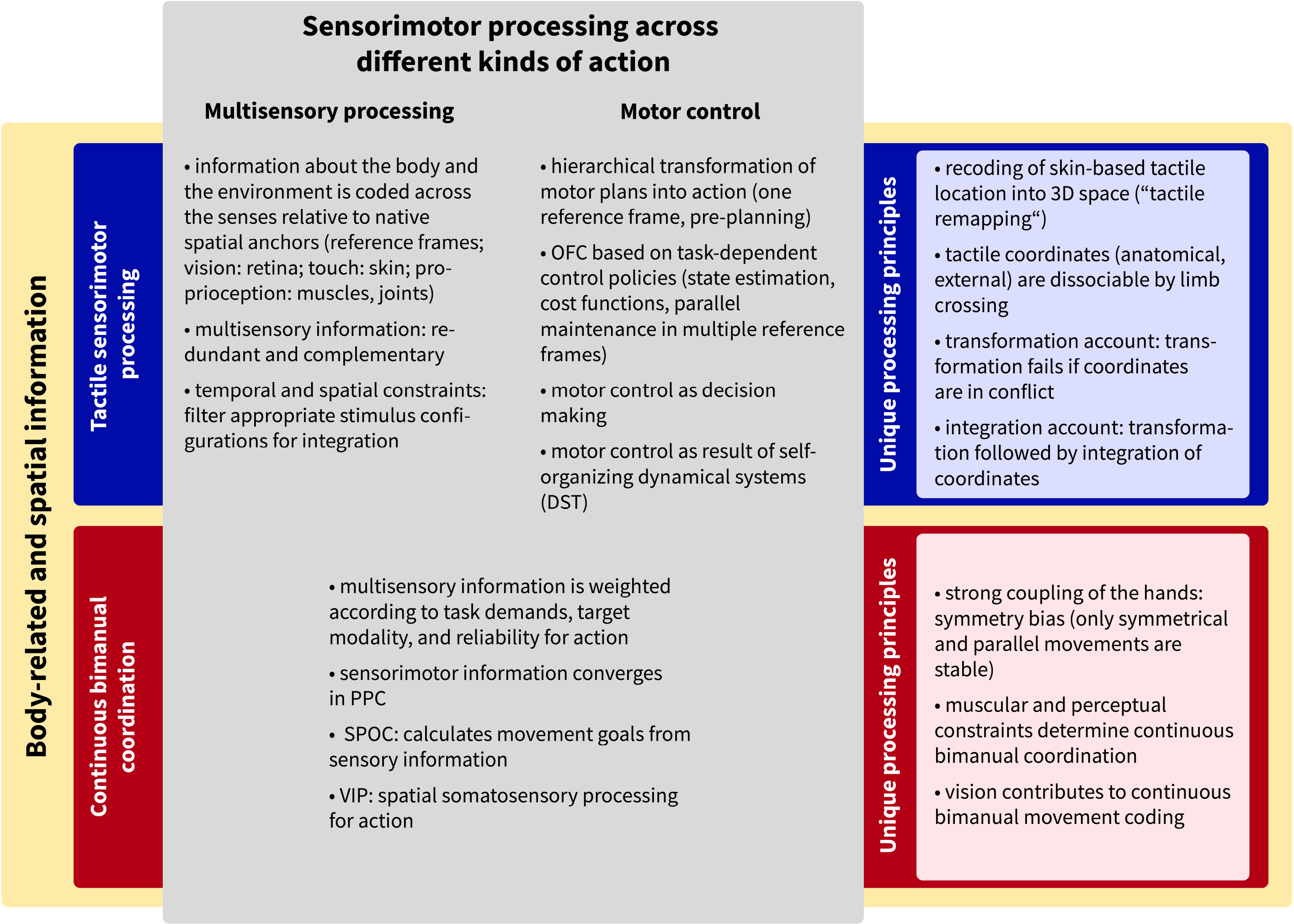
As a key feature of OFC, it has been shown using mechanical perturbations that the brain does not adapt to all perturbations, but only to those that are relevant for achieving the task goal (minimum intervention principle; Todorov & Jordan, 2002). For example, corrective responses after a mechanical perturbation depend on the size of the target that has to be reached (Nashed, Crevecoeur, & Scott, 2012). If the target is small, reach perturbations in the direction orthogonal to the direction of the reach are corrected, returning the hand to its initial path to reach the goal. In contrast, if the target is large, such perturbations are not corrected because the goal can be reached without returning to the original path (Nashed et al., 2012). Next to artificial or natural movement perturbations, variance can stem from noise in the sensory and motor systems. In either case and in line with the idea that task requirements determine the motor control policy, variance is thought to be accepted as long it does not impact task performance (Todorov & Jordan, 2002). Common neural circuits have been suggested to underlie optimal feedforward and feedback control, as they share similar sophistication (Nashed et al., 2012; Pruszynski et al., 2011; Scott, 2004, 2016). For instance, feedback responses in M1 are modulated by task constraints, that is, they account for the mechanical properties of the effector (Pruszynski et al., 2011), just as feedforward control does (Scott, 2003). Against the background of the results of the present thesis, I develop experiments that could investigate whether tactile sensorimotor processing and continuous bimanual coordination similarly rely on task-dependent control policies in the general discussion (Chapter 5). The framework of OFC has superseded mechanistic views on motor control, as it successfully explains flexible behavior with task-specific cost functions. Crucially, according to OFC, both perceptual and cognitive processes determine volitional motor control on a millisecond time scale (Scott, 2016). In that respect, it conceptually overlaps with more cognitive theories of behavior, such as decision making.

1.2.3 Motor control as decision making

Motor control has been framed in the context of decision making, as in principle, the actor has to “decide” on an appropriate action from many possibilities to attain a given goal (Cisek, 2012; Cisek & Kalaska, 2010; Wolpert & Landy, 2012). Or, framed in the context of OFC, the actor has to “choose” an appropriate control policy from many possibilities to solve a given task (Scott, 2016). Although decision making and motor control have traditionally been viewed as distinct processes (Scott, 2016), a close link between both has been suggested by seminal research in non-human primates (Gold & Shadlen, 2000, 2007; Shadlen & Kiani, 2013; Shadlen & Newsome, 1996, 2001). Here, it has been shown that areas in PPC typically associated with movement planning, such as LIP and PRR, carry signals indexing the evolving decision, too. Decision signals are conceptualized as reflecting the combination of all accumulated sensory evidence, prior knowledge and expectations about the probability of stimuli co-occurrence s, as well as costs and benefits associated with each choice and are the basis for choosing one alternative over another (Gold & Shadlen, 2007).

In support of the idea that a close relation between motor control and decision making exists in humans too, it was shown that the computations involved in OFC are closely related to decision processes in classical decision making tasks (Cisek, 2012; Resulaj, Kiani, Wolpert, & Shadlen, 2009; Wolpert & Landy, 2012). For instance, in one study (Selen, Shadlen, & Wolpert, 2012), participants had to decide whether the majority of random dots on a visual display were moving to the left or right by moving a handle to one of two targets. At different times during decision making, the arm holding the handle was mechanically perturbed. The gains of the muscular stretch reflex in response to the perturbations were modulated by the strength as well as by the time point at which the perturbation occurred. Reflex responses were larger when more motion evidence was available, and the more time for integrating this evidence had passed. This finding suggests that reflex gains track an evolving decision variable which progressively accumulates sensory evidence (Selen et al., 2012). Thus, this study tested whether decision signals were evident in motor behavior before the voluntary motor response, reporting the decision, was initiated. Other studies have shown that decision signals are also evident during a motor response. For instance, hand reach trajectories reflect cognitive processing in spatial biases and in the timing of trajectory corrections (Gallivan & Chapman, 2014; Song & Nakayama, 2009). In particular, cognitive biases toward one of several choice alternatives translate into spatial biases in reach trajectories toward target locations associated with the chosen alternative (Chapman et al., 2010a, 2010b; Spivey, Grosjean, & Knoblich, 2005). Chapman and colleagues (2010a) showed that reach trajectories are spatially biased by the number of visual targets and their location if reaches are initiated before the final target is known. Thus, trajectories reflect probabilistically weighted averages during online motor control (Chapman et al., 2010a). Consequently, it has been suggested that they are suitable to probe decision making in real time (Chapman et al., 2010a; Gallivan & Chapman, 2014). From the perspective of OFC, trajectories may thus reflect control policies that are optimally tuned to the task and flexibly adapted as soon as the final target is known. However, it is under debate whether decision signals are continuously passed on to the motor system, or alternatively, whether they are even generated here (e.g., Gold & Shadlen, 2001; Heekeren, Marrett, Bandettini, & Ungerleider, 2004). Despite such central yet open questions, re-framing questions of decision making in the context of motor control and conversely, re-framing questions of motor control in the context of decision making, has proven valuable for both fields. Our first study (Chapter 2) conceptualizes motor control of goal-directed actions toward tactile locations as a question of decision making. In particular, the computational principles of touch localization for sensorimotor decisions are characterized by investigating the timing and spatial profile of hand reach trajectories.

So far, in this general introduction, I recapitulated how multisensory information is coded in different native reference frames across the senses and how map alignment and integration is achieved on a single neuron level. Moreover, I outlined ideas on how multisensory information is structured for action. Then, I reviewed how sensorimotor functions are implemented in non-human primate and human PPC, which acts as an interface, where sensory and motor information converges. Here, I specifically focused on the functions of VIP and SPOC, because the former has been related to tactile spatial perception, whereas the latter plays a central role in combining body-related and spatial information about the target and effector of an action. Next, I summarized different theoretical views on how the brain chooses appropriate motor commands and translates multisensory body-related and spatial information into muscle patterns. In this context, I gave an overview of hierarchical transformation accounts of motor control, OFC, and perspectives that have emphasized the close link of motor control and decision making. *Figure 1.1* summarizes the key concepts outlined so far (grey box). Against this background, in the following, I discuss tactile sensorimotor processing. Planning movements toward tactile targets posits a special situation for the brain, as the body is both the goal and the effector of the action. It relies on the processing of multisensory information coded in different reference frames, because body-related tactile information has to be recoded spatially, that is, independent of its original skin-based anchor, to act toward a touch. Thus, successfully squatting a mosquito relies on the sensorimotor principles and neural circuity outlined to this point.



Multisensory processing

- information about the body and the environment is coded across the senses relative to native spatial anchors (reference frames; vision: retina; touch: skin; proprioception: muscles, joints)
- multisensory information: redundant and complementary
- temporal and spatial constraints: filter appropriate stimulus configurations for integration

Motor control

- hierarchical transformation of motor plans into action (one reference frame, pre-planning)
- OFC based on task-dependent control policies (state estimation, cost functions, parallel maintenance in multiple reference frames)
- motor control as decision making
- motor control as result of self-organizing dynamical systems (DST)

Tactile sensorimotor processing – Unique processing principles

- recoding of skin-based tactile location into 3D space (“tactile remapping“)
- tactile coordinates (anatomical, external) are dissociable by limb crossing
- transformation account: transformation fails if coordinates are in conflict
- integration account: transformation followed by integration of coordinates

Continuous bimanual coordination

- multisensory information is weighted according to task demands, target modality, and reliability for action
- sensorimotor information converges in PPC
- SPOC: calculates movement goals from sensory information
- VIP: spatial somatosensory processing for action

Continuous bimanual coordination – Unique processing principles

- strong coupling of the hands: symmetry bias (only symmetrical and parallel movements are stable)
- muscular and perceptual constraints determine continuous bimanual coordination
- vision contributes to continuous bimanual movement coding

Figure 1.1. Overview of the key concepts that build the background for the three studies of the present thesis. DST, Dynamic Systems Theory; OFC, Optimal Feedback Control; PPC, posterior parietal cortex; SPOC, superior parieto-occipital cortex; VIP, ventral intraparietal area.

1.3 Beyond visuomotor control: moving toward tactile targets

The modality of the sensory target matters for the multisensory computations involved in motor control, as every information is initially coded in reference frames that are native to each sense. Most previous studies have investigated visuomotor processing, that is, action planning toward visual targets (for reviews see: Gallivan & Chapman, 2014; Gallivan & Culham, 2015; Vesia & Crawford, 2012), whereas fewer studies have assessed how somatosensory targets, that is, proprioceptive and tactile targets, are processed for action (Bernier, Gauthier, & Blouin, 2007; Bernier & Grafton, 2010; Blangero, Rossetti, Honoré, & Pisella, 2005; Jones & Henriques, 2010; Macaluso, Frith, & Driver, 2007; Müller & Fiehler, 2014a, 2014b, 2016). How movements toward proprioceptive targets are controlled has been investigated using the fingers of one hand positioned at different spatial locations as targets that have to be reached with the other hand (e.g., Blangero et al., 2005). Tactile sensorimotor processing has been investigated using mechanical stimulation of the fingers as reach targets (e.g., Buchholz, Jensen, & Medendorp, 2011). Irrespective of whether the movement goal is proprioceptive or tactile, planning a movement toward a somatosensory target involves body-related coding of both the effector and the target. Information about either is derived in body-centered reference frames, but may be corroborated by visual information coded in eye-centered coordinates. Thus, in theory, movements toward somatosensory targets could be controlled entirely in body-centered coordinates. Yet, proprioceptive movement targets have been shown to be coded in eye-centered (Blangero et al., 2005; Jones & Henriques, 2010; Müller & Fiehler, 2014a, 2016; Pouget, Ducom, et al., 2002) or body-centered coordinates (Bernier et al., 2007; Bernier & Grafton, 2010). Similarly, tactile movement targets have recently been shown to be coded in both eye- and body-centered coordinates (Müller & Fiehler, 2016). Thus, compared to visuomotor control that is characterized by native eye-centered coding of the target, planning movements to somatosensory targets appears to be guided by unique principles that involve eye-and body-centered reference frames.

The following section scrutinizes tactile sensorimotor processing as a unique case of motor control due to the native skin-centered coding of the target. First, I review the principles of localizing a touch for binary sensorimotor decisions. Second, I outline computational principles of touch localization that have been identified in previous studies. Finally, I discuss the neural networks that mediate touch localization.

1.3.1 Touch localization for sensorimotor processing

Tactile localization is a prime example of how motor decisions must rely on multisensory signals and their integration. For recoding of a tactile stimulus into a movement goal, multisensory processing of the body in external space is essential. If the target of an action is tactile, such as a mosquito landing on the hand, its location is first coded relative to the skin surface in addition to proprioception signaling body position. Each movement changes the relation of tactile skin location and body position in space. For example, the anatomical location of the mosquito is defined by the body part on which it landed, here, the hand. In external spatial coordinates, the mosquito may be anywhere in space where the hand can be located. It follows that anatomical and external touch locations can implicate incongruent locations, as for example, when the hands are crossed over the body midline. More generally, when touched limbs are uncrossed, anatomical and external reference frames indicate corresponding locations. However, when the touched limbs are crossed, anatomical and external reference frames indicate different locations, because the right limb lies in left space and the left limb lies in right space. Limb crossing has been frequently used to experimentally dissociate tactile location codes (Heed, Buchholz, Engel, & Röder, 2015; Shore, Spry, & Spence, 2002; Yamamoto & Kitazawa, 2001). Thus, planning a movement toward an initially anatomically coded tactile stimulus requires its exact localization in external space, independent of the skin surface, a process which has also been termed “tactile remapping” (Driver & Spence, 1998). A touch is remapped into external space by integrating multisensory signals originating from proprioception, the vestibular system and, if available, vision (Driver & Spence, 1998; Heed, Buchholz, et al., 2015; N. P. Holmes & Spence, 2004).

Target-related computations that involve skin-based, also termed anatomical, and external reference frames are unique to the tactile system and distinguish tactile sensorimotor from proprioceptive- and visuomotor processing. For instance, a study by Müller and Fiehler (2016) showed that reference frames for reaching toward tactile targets are flexibly determined. In this study, touches applied to the fingers of the left hand served as reach targets. Two conditions were implemented. In the stationary condition, the left hand did not move before and after a tactile target was applied to one finger. Subsequently, participants had to use their right hand to reach to the remembered location of the touch at the left hand. Alternatively, in the dynamic condition, the left hand was moved from a start to a target location, then a touch was applied to one finger, and finally the left hand was moved back to the start position. Subsequently, participants had to reach to the remembered tactile location. This location was thus neither defined by proprioception nor by tactile information at the time of reaching but only by the remembered touch location. In the stationary condition, reach endpoints were best described by a body-centered reference frame. In contrast, in the moved condition, reach endpoints were best described by a combination of body- and eye-centered reference frames (Müller & Fiehler, 2016). Consequently, the authors suggested that the task context, precisely, whether or not a movement intervenes target presentation and response, determines which reference frame outweighs the other when reaching toward a tactile target (Müller & Fiehler, 2016). Thus, planning movements to somatosensory targets seems to involve the flexible weighting of eye- and body-centered reference frames.

An functional Magnetic Resonance Imaging (fMRI) study directly compared visuomotor and tactile sensorimotor processing in a paradigm that parsed target presentation/ movement preparation and movement execution into two separate delays (Macaluso et al., 2007). Specifically, visual or tactile stimuli were presented to the left or right index finger on a trial-by-trial basis. The effector varied block-wisely. That is, participants either had to plan a saccade toward the exact stimulus location or respond by pressing a button with the thumb of the stimulated hand, that is, they had to choose where of two possible locations the touch occurred. Across movement effectors, visual and tactile target processing, as well as movement preparation were confined to distinct networks, spanning occipital and somatosensory networks, respectively, which partially overlapped in PPC. Movement execution in response to either target modality recruited similar networks. These latter activations instead depended on whether a saccade or a button press was executed with principal involvement of M1 during button presses and principal involvement of the occipital cortex during saccades. These results have been suggested to indicate that target processing is modality-specific, whereas the brain abstracts goal information from the sensory information for execution (Macaluso et al., 2007). Although the task in this investigation required a sensorimotor action in response to a tactile stimulus, the conclusions that can be drawn about the mechanisms and implementation of tactile sensorimotor processing are limited. The binary sensorimotor responses (button presses) employed in this set-up did not require exact localization of the target; instead participants had to decide which of two possible locations was stimulated. In principle, the task thus corresponded to a 2-alternative-forced choice (2AFC) single touch localization task. Nonetheless, targets had to be precisely localized when participants had to execute saccades toward them. However, saccades are functionally different from limb movements, as they are closely connected to visual perception (Heed et al., 2011). Moreover, the authors did not report any analysis of the target presentation/ movement preparation delay that probed whether processing a tactile target for a saccade differs from processing a tactile target for a button press. Such differences would hint at potential distinction between binary and exact localization; although, in this set-up, these differences would be confounded with eye vs. finger movement planning. Finally, this study did not dissociate between anatomical and external tactile reference frames by hand crossing for example. Thus, the neural implementation of exact touch localization in anatomical and external space for action remain unclear.

Whereas research on tactile sensorimotor processing is scarce, touch localization in anatomical and external space has been extensively investigated using perceptual tasks, such as temporal order judgments (TOJ) of two successive stimuli applied to different limbs (Shore et al., 2002; Yamamoto & Kitazawa, 2001). In these tasks, participants indicate which limb was touched first in a 2AFC setting, usually by depressing a button with the corresponding hand (Heed & Azañón, 2014). Thus, similar to the study by Macaluso and colleagues (2007), TOJ tasks require binary instead of exact touch localization. In these tasks, limb crossing behaviorally leads to so-called “crossing effects”. These are characterized by localization performance deficits, such as prolonged processing times and increased error rates (Heed & Azañón, 2014). Localization performance at crossed limbs has proven to be a reliable index of the encoding of touch in external space, although in principle, the task could be solved by relying on anatomical information alone (Heed & Azañón, 2014). Collectively, extensive research on touch localization using perceptual tasks such as TOJ suggests that touch is remapped into external space, even though external coding is detrimental to task performance. Different models that can potentially account for this phenomenon have been proposed.

1.3.2 Computational principles of touch localization

Over the past 15 years, two principal views on how a tactile stimulus is localized have been discussed: the transformation and the integration account (for a complete overview see: Heed, Buchholz, et al., 2015). According to the transformation account, touch localization has been suggested to proceed as an automatic and sequential transformation from anatomical to external space (Gallace, Soto-Faraco, Dalton, Kreukniet, & Spence, 2008; Yamamoto & Kitazawa, 2001). In this view, crossing effects emerge because the coordinate transformation fails, or at least, because it takes much longer due to the unusual limb posture (Gallace et al., 2008; Yamamoto & Kitazawa, 2001). In contrast, according to the integration account, tactile remapping proceeds as a two-staged process (Badde & Heed, 2016; Badde, Heed, & Röder, 2015; Badde, Röder, & Heed, 2015). In this view, a tactile stimulus is first automatically and instantly recoded into external coordinates. Second, all available tactile information, that is, anatomical and external coordinates maintained at the same time, are integrated. Coordinates are flexibly top-down weighted during integration depending on the task context. According to this view, the transformation from anatomical to external space is unaffected by limb crossing, but the prolonged integration of conflicting information causes behavioral crossing effects (Badde & Heed, 2016). Probabilistic modeling has favored the integration over the transformation account across different task contexts (Badde, Heed, et al., 2015). Moreover, consistent with the integration account, a number of studies have shown an influence of both anatomical and external coordinates on behavior, which would not be predicted by the transformation account (Badde, Röder, et al., 2015; Heed & Röder, 2010; Müller & Fiehler, 2016). However, whether the processing principles identified in binary perceptual touch localization generalize to a task context that requires exact localization for action remains unclear. Our first study addresses this gap by characterizing the computational principles of tactile sensorimotor processing (Chapter 2). In particular, the transformation and integration account of touch localization are contrasted in the context of a tactile sensorimotor decision task.

1.3.3 Neuronal networks mediating touch localization

On the cortical level, anatomical coding of touch has been associated with the primary somatosensory cortex (S1; e.g., Azañón, Radulova, Haggard, & Longo, 2016; Tame, Moles, & Holmes, 2014), which is organized according to an orderly map of the body surface (sensory humunculus; Penfield & Boldrey, 1937). Other areas of the somatosensory hierarchy including PPC have also been shown to contain somatotopic maps, however, these appear to be less fine-grained than in S1 (Huang, Chen, Tran, Holstein, & Sereno, 2012; Ruben et al., 2001). Previous studies have suggested that the brain codes the external location of a touch in an eye-centered reference frame (Buchholz et al., 2011; Buchholz, Jensen, & Medendorp, 2013; Heed, Backhaus, Röder, & Badde, 2016; Müller & Fiehler, 2014a, 2014b, 2016). Moreover, external tactile coordinates seem to be independent of the body part that was stimulated, as crossing similarly impairs TOJs in all limb combinations, for example, hands, feet, or one hand and one foot (Schicke & Röder, 2006). Previous fMRI and electroencephalography (EEG) studies suggested that PPC is involved in coding somatosensory space (Brozzoli, Gentile, Petkova, & Ehrsson, 2011; Driver & Noesselt, 2008; Gentile, Petkova, & Ehrsson, 2011; Huang et al., 2012; Macaluso et al., 2007; T. R. Makin, Holmes, & Zohary, 2007; Pasalar, Ro, & Beauchamp, 2010; Pellijeff, Bonilha, Morgan, McKenzie, & Jackson, 2006; Schubert et al., 2015; Soto-Faraco & Azañón, 2013; Tal & Amedi, 2009), consistent with the pivotal role PPC generally plays in spatial reference frame transformations. This view was corroborated by three TMS studies, which have specifically related the coding of tactile external reference frames to a region in medial intraparietal sulcus (mIPS; Azañón, Longo, Soto-Faraco, & Haggard, 2010; Bolognini & Maravita, 2007; Ruzzoli & Soto-Faraco, 2014). However, previous studies did not investigate different reference frames involved in the localization of a tactile stimulus in conjunction, that is, they have not specified how the brain codes anatomical vs. external tactile information. So far, TMS studies on touch localization have selectively disrupted the external coding of touch (e.g., Azañón et al., 2010) and related imaging studies have not manipulated body posture (e.g., Huang et al., 2012) or have exclusively investigated proprioceptive, but not tactile, spatial processing (e.g., Brozzoli, Gentile, & Ehrsson, 2012). Thus, how the brain codes anatomical tactile coordinates, especially in relation to how it codes external tactile coordinates, remains unclear. Our second study fills this gap by scrutinizing how sensory, that is, anatomical and external, as well as motor reference frames are processed for executing a hand pointing movement toward a tactile stimulus (Chapter 3).

So far, this general introduction reviewed the principles that determine how multisensory information about the body and the environment is structured for motor control. Second, I discussed different theoretical perspectives on how the brain chooses appropriate motor commands and translates body-related and spatial information coded across different senses into appropriate muscle patterns (see grey box in *Figure 1.1*). Next, tactile sensorimotor processing was scrutinized as a unique case of motor control that involves multisensory processing of body-related and spatial information related to target localization (see blue box in *Figure 1.1*). In the following, I will address how body-related and spatial information derived through different sensory channels is processed in the context of a different type of action, namely bimanually coordinated hand movements. Thus, as these movements, too, rely on multisensory processing, they are an alternative approach to investigate how we achieve dynamic interaction with the external world more generally.

1.4 Organizing principles of coordinative action

We realize everyday interactions of our body with the environment through a variety of complex actions that are in part composed of unilateral goal-directed movements. Beyond moving unilaterally toward external and body-related targets, we effortlessly coordinate movements of both hands. Applauding at a concert, typing on a keyboard, or unscrewing a lid are examples of such ordinary bimanual coordination. Goal-directed and coordinative action overlap conceptually, because bimanual movements can be continuous or discrete, such as applauding vs. typing, respectively, depending on whether or not they consist of goal-directed actions that are separated in time (Huys, 2010). Furthermore, both kinds of action are generated by the same nervous system and as such, both rely on the same sensory channels processing multisensory information related to the body and the environment for controlling the same motor apparatus. For example, when we applaud at a concert, information about the effectors arrives at the brain through a combination of sensory channels, just as during tactile sensorimotor control for example. We see and feel our hands moving. Thus, vision and proprioception inform about effector position, that is, where the hands are located in space, and about effector posture, that is, how the wrists and finger joints are configured. Vision and proprioception also inform about which muscles are used, that is, in the case of applauding, they signal that homologous muscles are used in both hands. Moreover, vision and proprioception inform about spatial aspects of movement, for example, both inform about movement direction. Although tactile sensorimotor processing and continuous bimanual coordination rely on processing of multisensory body-related and spatial information, research on either type of action has largely developed in isolation.

The following section examines the organizing principles of continuous bimanual coordination, as a type of action that also relies on multisensory processing of body-related and spatial information. Previously discussed tactile sensorimotor processing relies on spatial recoding of skin-based target information. In the context of continuous bimanual coordination, it has been shown that visual information, which redundantly codes movement aspects next to proprioception, determines behavior, too (Buckingham & Carey, 2008) and thus complements body-related movement coding during bimanual coordination. First, I give a general overview of different perspectives on the relation of discrete goal-directed and continuous movements. Second, I outline how bimanual coordination has been conceptualized in the framework of OFC. Then, I discuss how muscular constraints in bimanual coordination have been interpreted as evidence for an alternative framework: Dynamic Systems Theory (DST). Finally, I discuss how perceptual contributions to bimanual coordination have been reconciled within the framework of DST. Across the different theoretical frameworks that have motivated research in this field, evidence suggests that body-related and spatial factors jointly determine continuous bimanual coordination.

1.4.1 On the relation of goal-directed and continuous movements

Different views on how movements are controlled have emerged in the fields of goal-directed movements and (bimanual) coordination. Measured by the extensive theoretical and empirical advances that have been made within each community, there were only few attempts at reconciling these different kinds of action in the past (Diedrichsen, Shadmehr, & Ivry, 2010; Hogan & Sternad, 2007; Ronsse, Sternad, & Lefèvre, 2008). Nonetheless, three different views on the relation of discrete movements and continuous coordination have emerged (Sternad, 2008). The understanding that discrete movements are the essential class, whereas continuous movements merely denote a concatenation of multiple discrete movements, has been principal in the community investigating goal-directed movements (e.g., Diedrichsen et al., 2010). Conversely, the view that continuous movements are the fundamental class, whereas discrete movements merely represent a truncation of continuous movements, has been dominant in the community investigating bimanual coordination (e.g., Miall & Ivry, 2004; Schaal, Sternad, Osu, & Kawato, 2004; Sternad, Saltzman, & Turvey, 1998). Both views advocate a common control mechanism underlying both movement types (Howard, Ingram, & Wolpert, 2011). According to a third view, both discrete and continuous movements have been suggested to be controlled by separable neural mechanisms or motor primitives (e.g., Hogan & Sternad, 2012; Howard et al., 2011; Sternad, Dean, & Schaal, 2000). Dissociating the relation of discrete and continuous movements experimentally has proven difficult. Nonetheless, a number of studies have interpreted their findings in light of these three different perspectives.

Discrete and continuous movements have been compared using unimanual tasks, such as wrist flexion and extension or circle drawing. In the discrete condition, movements are separated by temporal gaps, self-paced or instructed by visual or auditory stimuli. Here, it has been shown that continuous movements activate primary motor areas, such as M1 and the supplementary motor area (SMA), whereas discrete movements additionally recruit higher motor areas, such as PPC (Schaal et al., 2004). Thus, continuous movements engage an approximate neural subset of discrete movements, which has been interpreted as supporting the idea that discrete movements might be a special case of continuous movements. In this view, higher motor areas only recruited during discrete movements might be involved in aborting cyclical, continuous movements after half a cycle (i.e., before a theoretical return to the initial position). Alternatively, the results might reflect that both types of movements are controlled by separate neural systems. However, inconsistent with this idea, there were no areas that solely mediated continuous movements. These results, moreover, have been suggested to be inconsistent with the idea that continuous movements are merely a repetition of multiple discrete movements, as then, the opposite result pattern would have been expected, that is, more neuronal recruitment during continuous as compared to discrete movements (Schaal et al., 2004). Furthermore, discrete movements are more affected than continuous movements in stroke patients and in patients with cerebellar lesions, which has been interpreted in a similar manner (Leconte, Xivry, Stoquart, Lejeune, & Ronsse, 2016; Spencer, Zelaznik, Diedrichsen, & Ivry, 2003). It has been suggested that continuous and discrete movements might differ according to whether they are characterized by automatic or cognitive control, respectively (Leconte et al., 2016; Schaal et al., 2004). In line with this idea, in stroke patients, visually-guided continuous movements are more affected than continuous movements that are only proprioceptively guided (Leconte et al., 2016). This might suggest that continuous movements are exclusively guided by low-level circuity that is unaffected by stroke when they are proprioceptively guided. In correspondence, they might recruit additional, higher-level motor regions that are more likely to be affected by stroke when they are visually guided (Leconte et al., 2016). Collectively, these results indicate that discrete movements might represent a truncation of continuous movements, or, alternatively that both might be mediated by separate neural mechanisms. However, they appear to be inconsistent with the view that continuous movements merely represent a repetition of discrete movements. This suggests that, despite the fact that both kinds of movements, discrete and continuous, rely on processing of multisensory body-related and spatial information, they may be guided by different principles that determine how this information is organized.

1.4.2 Bimanual coordination as a special case of optimal control

Beyond the potential dissociation of (unimanual) discrete and continuous movements, other investigations have focused on how unimanual and bimanual movements might be related. Here, it has been suggested that a common control mechanism mediates both types of actions (Diedrichsen, 2007; Diedrichsen & Dowling, 2009; Diedrichsen et al., 2010; Spencer et al., 2003). Specifically, bimanual coordination has been proposed to be controlled by OFC principles, just as unimanual goal-directed movements are. Hypothetically, both rely on coordination, although to different degrees, that is, unilateral goal-directed movements require coordination between joints and muscles, whereas bimanual movements additionally require coordination of muscles and joints between effectors (Diedrichsen et al., 2010). Thus, according to this framework, bimanual coordination, too, is viewed as a solution of an optimization process elicited by the task demands that the neural system faces (Diedrichsen et al., 2010). It follows that stereotypical bimanual coordination across individuals reflects comparable solutions to the redundancy inherent in the motor system prompted by similar task demands. More generally, this view suggests that the same principles determine how multisensory body-related and spatial information is processed, regardless of whether the executed action is uni-, or bimanual.

The OFC framework has successfully been applied to discrete, bimanual movements (Diedrichsen, 2007; Diedrichsen & Dowling, 2009). Yet, OFC predicts independent control of the hands (Diedrichsen & Dowling, 2009). In contrast, especially continuous bimanual movements are tightly coupled. For instance, a key phenomenon in bimanual coordination is the so-called symmetry bias. Participants are able to perform movements that are symmetrical relative to the body midline with higher precision and at higher speeds than movements that are parallel relative to the body midline (L. Cohen, 1971; Kelso, 1984; Kelso, Scholz, & Schöner, 1986). This effect has been demonstrated for finger abduction and adduction movements for example, that is, sideways movements of the two index fingers with the hands held palm down (e.g., Heed

& Röder, 2014). With the palms down, movement accuracy is high when both fingers are abducted at the same time, resulting in symmetrical finger movements. Accuracy is lower when one finger is abducted while the other one is concurrently adducted, resulting in parallel finger movements (Kelso, 1984). Although OFC may be a framework that unifies multisensory processing of body-related and spatial information across goal-directed and coordinative movements, it struggles to explain the tight coupling between the hands during continuous bimanual coordination as evident in the symmetry bias. However, the symmetry bias has been extensively investigated against the background of an alternative framework, that is, DST.

1.4.3 Bimanual coordination as a non-linear dynamical system

DST has dominated the field of bimanual coordination over the past three decades (e.g., Krampe, Engbert, & Kliegl, 2002; Sternad, 2008). According to this view, behavioral phenomena such as the symmetry bias reflect the self-organization of coupled non-linear oscillators (Haken, Kelso, & Bunz, 1985). These oscillators are thought to be self-sustaining, with regard to action frequency and amplitude, and do not require action segmentation or higher-level control (Haken et al., 1985). For example, self-paced continuous bimanual finger movements return to their initial frequency and amplitude after mechanical perturbation of one finger (Kelso, Holt, Rubin, & Kugler, 1981). Furthermore, non-linear oscillators are thought to be stable at specific states and similar movements should be attracted by such stable states (Huys, 2010). According to this framework and in line with empirical data, symmetrical and parallel movements are the only stable states, while intermediate movements, as 5:3 coordination mode for example, are unstable and therefore extremely difficult to maintain (Shea, Buchanan, & Kennedy, 2016).

The concept of low-level self-organization at the core of DST is diametrical to the idea that motor control is organized in a hierarchical manner (Huys, 2010; Krampe et al., 2002). A hierarchical organization of the motor system, that is, the idea that cognitive representations of the environment are constructed through sensory organs and then translated into motor commands that are sent to the periphery, is often implicitly or explicitly assumed in the field of goal-directed action. For instance, the framework of OFC assumes that high-level task goals under top-down control determine action (Todorov & Jordan, 2002). In contrast, according to DST, self-organization is thought to be constrained by low-level factors inherent in the nervous system (Huys, 2010; Schaal et al., 2004). These factors are thought to act as rules that determine the stability of coordination patterns (Bressler & Kelso, 2016).It follows that redundancy within the motor system is limited by these constraints that make coordination controllable (Huys, 2010). Consequently, a substantial amount of empirical research in this field has focused on the identification of constraints governing the nervous system. Low-level constraints are, for example, expressed in motor synergies, that is, functional units of muscle activation that are stable across tasks and movement types, and that are thought to make up complex behaviors (Tresch, Saltiel, & Bizzi, 1999). Muscle synergies have also been suggested to underlie the symmetry bias (L. Cohen, 1971; Kelso, 1984; Kelso et al., 1986). Specifically, they are thought to arise from the use of homologous muscles when performing symmetrical movements due to efficient integration of motor commands across hemispheres, whereas the use of non-homologous muscles in the parallel condition is thought to cause interference from ipsi- and contralateral muscle commands (Shea et al., 2016). Collectively, DST has been successful in describing key phenomena of bimanual coordination with muscular constraints. However, it has been shown that perceptual factors too influence bimanual coordination.

1.4.4 Visual contributions to bimanual coordination

In line with the idea that other factors than muscular constraints influence bimanual coordination as well, it was shown that the symmetry bias prevails when participants perform finger abduction and adduction movements with the two hands held in opposite orientations, that is, one palm facing up and the other down (Heed & Röder, 2014; Mechsner, Kerzel, Knoblich, & Prinz, 2001). In this set-up, symmetrical movements implicate non-homologous muscles, whereas parallel movements are realized through homologous muscles. However, the persistent advantage of symmetrical over parallel movements despite a reversal of the muscles involved in the bimanual movement is at odds with the idea that muscle synergies alone are responsible for the symmetry bias (Bingham, 2004; Mechsner et al., 2001; Shea et al., 2016). At the extreme, it has even been suggested that the symmetry bias only originates from interactions rooted in perception (Mechsner et al., 2001). However, whereas this finding suggests perceptual contributions to bimanual coordination, it is less clear what kind of perceptual information the symmetry bias is based on. In other words, it is not clear which sensory channels contribute to the coding of body-related and spatial information for bimanual coordination and how these perceptual codes interact.

It has been suggested that the major constraint of bimanual coordination is related to the ability to perceptually detect the phase difference between the two hands (Bingham, 2004; Bingham, Schmidt, & Zaal, 1999; Bingham, Zaal, Shull, & Collins, 2001). This idea was formalized in a model developed in the tradition of DST (perception-action model; Bingham, 2004; Bingham et al., 1999, 2001). In the context of DST, the phase of an oscillator is defined as the position within its cycle (e.g., Haken et al., 1985). Correspondingly, the phase difference denotes the difference in phase between two oscillators, here, between the two hands. Specifically, the action-perception model by Bingham and colleagues postulates that the coupling of two oscillators is determined by their actual relative phase (Bingham, 2004; Bingham et al., 1999, 2001). Thus, the model specifies detecting the relative phase relation of the hands as the key aspect that drives bimanual coordination. It has been demonstrated that relative phase is expressed in relative movement directions (Wilson, Collins, & Bingham, 2005a). Difficulty in reliably detecting relative direction then presumably leads to maladaptive error detection and correction, which, in turn, impedes performance (Wilson et al., 2005a).

In principle, the relative movement direction of the hands can be detected through vision and proprioception. Nonetheless, experimental investigations of the action-perception model by Bingham and colleagues (Bingham, 2004; Bingham et al., 1999, 2001) have largely relied on unimanual coordination with a moving dot on a visual display as a proxy to investigate the perceptual guidance of coordination. This experimental approach discounts influences related to the proprioceptive guidance of bimanual movements, although muscular constraints have been shown to modulate the symmetry besides perceptual factors (Heed & Röder, 2014). Moreover, this experimental approach implicitly presumes that the brain abstracts from all movement parameters and, in particular, that it dismisses other body-related visual information. However, visual information transports not just abstract spatial information, but also information about the body, presumably to contribute to the construction of a body model. For example, muscle homology affects bimanual coordination less in congenitally blind than in sighted individuals (Heed & Röder, 2014). This finding proposes that vision may induce not just a spatial bias, but may, add body-related, such as postural and muscle-related, information for motor coordination. Yet, the contribution of visual information to body-related and spatial aspects have not been delineated in a strictly bimanual task. Study 3 of this thesis

(Chapter 4) fills this gap by investigating the joint contributions of muscular and visual, precisely, body-related and spatial, factors to bimanual coordination.

So far, this general introduction reviewed the principles that determine how multisensory body-related and spatial information is structured for motor control. Subsequently, I outlined different views on how the brain converts multisensory body-related and spatial information into appropriate muscle patterns (see grey box in *Figure 1.1*). Next, I scrutinized tactile sensorimotor processing as a unique case of motor control that involves multisensory processing of body-related and spatial information related to target localization (see blue box in *Figure 1.1*). Finally, I discussed how multisensory body-related and spatial information is processed in the context of a different kind of action, namely bimanually coordinated hand movements (see red box in *Figure 1.1*).

1.5 Thesis overview

Successful interaction with the environment requires the ordered processing of a multitude of multisensory information related to the body and the external world. Although body-related and spatial aspects are intrinsically connected in everyday life, dissociating their contributions in a laboratory setting offers prototypical insights about how perception and action interact to achieve complex behavior. As examples of such dynamic interactions, the present thesis scrutinizes how body-related and spatial aspects are processed across two different types of movements, that is, tactile sensorimotor processing and continuous bimanual coordination. During both types of movements, body-related information is complemented by other sensory channels. In particular, presumably principally visual information contributes to the recoding of skin-based tactile target location into 3D space during tactile sensorimotor processing and to the proprioceptive coding of continuous effector movements during bimanual coordination. The first and second study investigate unilateral movements (Chapters 2 and 3), whereas the third study investigates continuous bimanual coordination (Chapter 4). All three studies examine body-related and spatial information that is either primarily related to the target (Chapters 2 and 3) or to the effector (Chapter 4) of an action.

More specifically, the first study characterizes the mechanisms and timing of localizing a tactile target for action. To do so, I experimentally contrast the transformation and integration account as theoretical models of touch localization that were developed in the context of perceptual tasks. Thus, I test whether predictions derived from binary localization generalize to a sensorimotor decision task that requires the processing of anatomical and external reference frames for precise localization (Chapter 2). The second study investigates the neural implementation of tactile sensorimotor processing using fMRI. Planning a movement toward a tactile stimulus involves processing of tactile coordinates signaling the sensory target location, and movement coordinates, translating tactile coordinates into a movement. Both the coding of tactile space and movement planning have been linked to PPC. Here, I characterize how their integration is implemented in this brain region (Chapter 3). The third study assesses whether bimanual coordination relies on visual information about body-related aspects, such as posture and muscles, in addition to spatial aspects, such as movement direction (Chapter 4). In the general discussion, I review unique and shared principles of processing body-related and spatial information across tactile sensorimotor processing and continuous bimanual coordination (Chapter 5). Taking the results of the present thesis as a foundation, I suggest that future experiments could further characterize both kinds of actions against a common theoretical background, such as OFC, and outline open questions and exemplary experiments addressing these questions.

2 | Reach trajectories characterize tactile localization for sensorimotor decision making

2.1 Abstract

Spatial target information for movement planning appears to be coded in a gaze-centered reference frame. In touch, however, location is initially coded with reference to the skin. Therefore, the tactile spatial location must be derived by integrating skin location and posture. It has been suggested that this recoding is impaired when the limb is placed in the opposite hemispace, for example, by limb crossing. Here, human participants reached toward visual and tactile targets located at uncrossed and crossed feet in a sensorimotor decision task. We characterized stimulus recoding by analyzing the timing and spatial profile of hand reaches. For tactile targets at crossed feet, skin-based information implicates the incorrect side, and only recoded information points to the correct location. Participants initiated straight reaches and redirected the hand toward a target presented in midflight. Trajectories to visual targets were unaffected by foot crossing. In contrast, trajectories to tactile targets were redirected later with crossed than uncrossed feet. Reaches to crossed feet usually continued straight until they were directed toward the correct tactile target and were not biased toward the skin-based target location. Occasional, far deflections toward the incorrect target were most likely when this target was implicated by trial history. These results are inconsistent with the suggestion that spatial transformations in touch are impaired by limb crossing, but are consistent with tactile location being recoded rapidly and efficiently, followed by integration of skin-based and external information to specify the reach target. This process may be implemented in a bounded integrator framework.

2.2 Significance statement

How do you touch yourself, for example to scratch an itch? The place you need to reach is defined by sensation in the skin, but our bodies are flexible, so that the location can be anywhere in 3D space. The movement toward the tactile sensation must, therefore, be specified by integrating skin location and body posture. By investigating how humans make hand reaches toward tactile stimuli located at the feet, we show that this is not a serial process. After transformation into space, the skin location lingers, and is integrated with the location in space, probably to optimize the brain's estimate of where the touch is.

2.3 Introduction

It is commonly assumed that the brain uses an eye or gaze-centered reference frame to code the spatial location of movement targets (Batista et al., 1999; Henriques et al., 1998; Medendorp et al., 2003). Whereas a gaze-centered code is native to the visual system and, thus, visually perceived targets (Medendorp et al., 2011), it is less obvious which choice of reference frame the brain might use when a target is defined tactually (Heed, Buchholz, et al., 2015). Tactile location is first represented relative to the skin surface in the primary somatosensory cortex's homunculus (Penfield & Boldrey, 1937). Yet, both saccade and hand reaches to tactile events involve gaze-centered coding (Buchholz et al., 2011, 2013, Müller & Fiehler, 2014a, 2014b), suggesting that action targets in vision and touch are ultimately coded in a common reference frame. Derivation of the recoded location for touch requires the integration of skin location with postural information, a process referred to as tactile remapping (Driver & Spence, 1998).

However, the original, skin-based touch coordinate is retained after transformation (Buchholz et al., 2013; Heed & Röder, 2010). Consequently, conflict can arise when spatial information in the original and the transformed reference frames are incongruent. For example, when the limbs are crossed over the body midline, the right limb lies in left space. Such situations can result in marked performance deficits, evident in increased errors and prolonged processing time (Heed & Azañón, 2014; Shore et al., 2002; Yamamoto & Kitazawa, 2001). These “crossing effects” have frequently been attributed to the tactile remapping process. Yet, reference frame transformations are abundant in sensorimotor processing, and concurrent representation of information in different reference frames appears to be a common coding principle of the brain, without usually leading to noticeable processing deficits (Andersen, Snyder, Li, & Stricanne, 1993; Chen, DeAngelis, & Angelaki, 2013; J. G. Makin, Fellows, & Sabes, 2013; Pesaran, Nelson, & Andersen, 2006; Pouget, Ducom, et al., 2002; Schlack, Sterbing-D’Angelo, Hartung, Hoffmann, & Bremmer, 2005; Snyder, 2000). An alternative explanation of crossing effects is, therefore, that tactile localization comprises two distinct stages (Badde, Heed, & Röder, 2014; Badde, Heed, et al., 2015; Badde, Röder, & Heed, 2014; Heed, Buchholz, et al., 2015). First, touch location is remapped from the anatomical into an external reference frame; second, information from the two reference frames is integrated to derive an optimal touch location estimate. In this framework, coordinate transformation is fast and efficient for all postures, and performance impairments in crossed postures are due to the integration of conflicting information available in different reference frames.

To contrast these two accounts, we characterized the timing and spatial profile of hand reaches toward visual and tactile targets located at uncrossed and crossed feet in a sensorimotor decision task. Reach trajectories are subject to voluntary motor control (Scott, 2004; Todorov & Jordan, 2002), and reflect cognitive processing in spatial trajectory biases and in the timing of trajectory redirection (Gallivan & Chapman, 2014; Song & Nakayama, 2009). In the context of decision making, cognitive biases toward one of several choice alternatives translate into spatial biases in reach trajectories toward target locations associated with the chosen alternative (Chapman et al., 2010a; Spivey et al., 2005). If crossing effects in tactile localization are due to delayed coordinate transformation, reaches toward tactile locations should initially depend exclusively on anatomical coordinates, until the transformation has been performed (Azañón & Soto-Faraco, 2008). Accordingly, when tactile stimuli are presented to crossed feet, reaches should regularly be deflected toward the incorrect foot and be corrected later during the reach. This is because the tactile location coded in an anatomical reference frame points toward the touched limb's body side, not its current position in space. In contrast, if deficits are due to integration of information in different reference frames, then reaches should not regularly be deflected toward the anatomical target location. Instead, they should be delayed by integration of incongruent information, but be guided by the external coordinate once the decision has been made.

2.4 Materials and Methods

2.4.1 Experiment 1

In the main experiment, participants made hand reaches to visual and tactile target stimuli located at uncrossed and crossed feet.

Participants. Fourteen right-handed students (Oldfield, 1971), 8 of them female, aged 25.1 years (range: 20-39 years) took part in Experiment 1. Participants in this and the following experiments all had normal or corrected-to-normal vision and did not report any tactile impairments. They gave written informed consent and received course credit or monetary compensation. The experiments were approved by the ethics committee of the German Psychological Society (DGPs).

Setup. Participants sat on the floor and leaned against a metal bar to support an upright sitting position (*Figure 2.1A*, top row). The bar's height was individually aligned with the lower episternum. A vibrotactile stimulator (Oticon bone-conductor BC 461-0/12, Oticon Ltd., London, UK) was attached to each big toe. Red light emitting diodes (LEDs) were attached just above each tactile stimulator. A central fixation LED was placed on the floor approximately 10 cm in front of the participant’s feet, aligned with the starting position and the body midline. To avoid the impression of apparent motion in visual target conditions, the fixation LED was yellow, and was always illuminated. Tactile stimuli consisted of supra-threshold 200 Hz vibrations of 30 ms duration. For visual stimulation, the red target LEDs were illuminated for 30 ms. Legs and feet were placed such that stimulus locations on both feet were freely accessible by reaches. Location of the stimulators in space was identical across conditions, with a distance of approximately 30 cm between stimulators. Ear plugs, as well as white noise presented through head phones, masked the sound elicited by the tactile stimulators. Experimental protocols were controlled via MATLAB (v7.14, The Mathworks, Natick, MA, USA). Stimuli were controlled by custom-made hardware and triggered with precision of <1 ms through National Instruments PC cards.

A piece of felt on the metal bar, facing away from the participant and aligned with the body midline, marked the reach hand's start position. Reach trajectories were recorded with a sampling rate of 100 Hz using a camera-based motion tracker (Visualeyez II VZ4000v, PTI Phoenix Technologies, Burnaby, Canada). Markers for motion recording were attached to the nail of each index finger as well as near the tactile and visual stimuli on the feet. An additional marker (the “trigger” marker) was placed next to the participant, positioned approximately 15 cm in front of the hand's start position. During reaches, hand and trigger marker positions were read out and compared on-line, so that stimulus presentation could be elicited when the hand marker passed the trigger marker in the depth dimension.

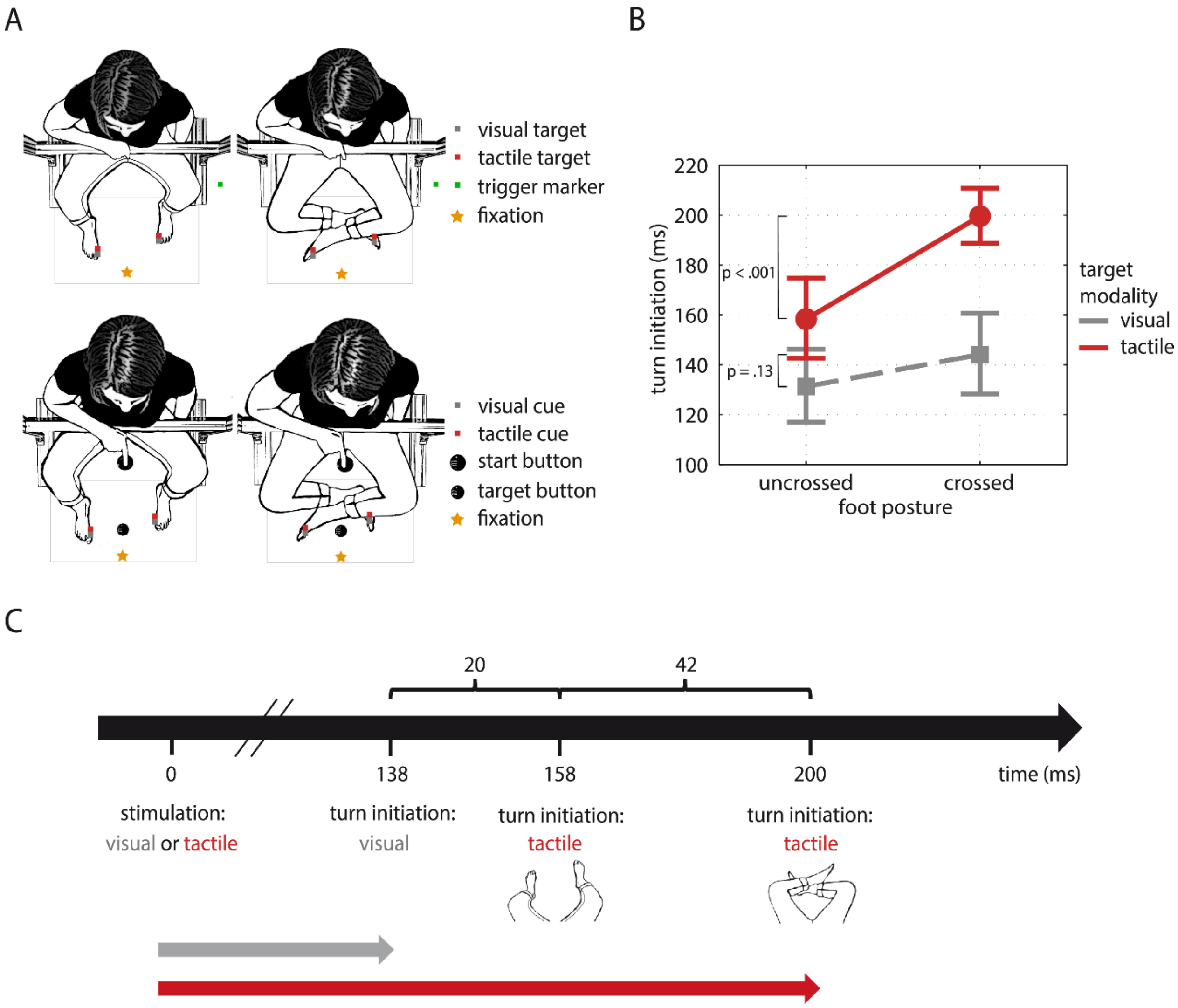


Figure 2.1. Experimental set-up of Experiments 1 and 2 and time-related characteristics of reach trajectories of Experiment 1. *A*. Experimental set-up. Position of tactile and visual stimulators was kept identical in space across foot positions. Top row: Experiment 1. Bottom row: Experiment 2. *B*. Condition estimates from the mixed model analysis of the time of reach turn points. Turns toward tactile targets at crossed feet were initiated later than those at uncrossed feet. Turn point times toward visual targets were not significantly affected by foot posture. Error bars display 95% confidence intervals (CI). *C*. A timeline of tactile remapping depicted in direct comparison to the timing of visual spatial processing, derived from the time analysis of Experiment 1.

Experimental paradigm. Participants made reaches with the right and left hands toward tactile and visual target stimuli located at uncrossed and crossed feet. A trial started when the reaching hand had been still at the start position for 500 ms. After an additional interval of 1000-1400 ms, a tone instructed a straight index finger movement toward the fixation LED. The target was presented in-flight when the finger passed the trigger marker. Participants had to change course and steer the hand toward the target as quickly as possible, and then remain still at the target for 500 ms. A tone then indicated that the hand should return to the start position for the next trial. The task was practiced extensively before running the experiment, so that movements were smooth, continuous, and started out straight at the beginning of the movement.

Experimental design. There were four experimental factors. Factors Foot Posture (uncrossed vs. crossed) and Reach Hand (left vs. right) varied block-wise in randomized order. Factors Target Modality (visual vs. tactile) and Target Location (left vs. right foot) were varied pseudorandomly within blocks. However, because we did not have any hypotheses about differences in trajectory characteristics for reaches to the left and right foot, we pooled over the two target limbs (see below) and omitted factor Target Location in all analyses. Each of the 16 factor combinations was presented 40 times, distributed across 4 blocks of 160 trials. Each block was preceded by 12 practice trials that were not analyzed. Participants had to maintain fixation continuously. They rested and stretched out their limbs after each block.

2.4.1.1 Trajectory analysis

Movement offset and duration. Reach trajectories were analyzed in MATLAB. Movement offset was identified using a recursive algorithm (Teasdale, Bard, Fleury, Young, & Proteau, 1993) based on 3D tangential velocity. Movement time was defined as the time between target presentation and movement offset.

Functional representation of movement trajectories. Participants made decisions between targets on the left and right foot, therefore further analysis focused on the hand trajectories' right-left component (that is, the x coordinate) over time. For trajectory averaging, individual trajectories were extended to the duration of a participant's slowest movement by filling all sampling points between the movement's last true sampling point and the last sampling point of the longest trajectory with the movement's spatial end point. Trajectories were fitted with 6th-order B-splines, using the functional data analysis toolbox MATLAB implementation “FDAfuns” (Ramsay, Hooker, & Graves, 2009; Ramsay & Silverman, 2005). The fitting criterion lambda that trades off data fit against trajectory smoothness, was determined based on the degrees of freedom of the spline fit by accounting for 20% of data points of each trajectory (Hastie & Tibshirani, 1990). The resulting functional trajectory representations, as well as their first two derivatives, were evaluated with 1 ms resolution for further analysis. Acceleration (i.e., the second derivative) was low-pass filtered with a second order dual pass Butterworth filter with a cutoff frequency of 50 Hz after function evaluation.

Identification of trajectory turn points. Because movement duration differed across experimental conditions, it was not possible to normalize reach trajectories over time for trial averaging. Instead, we identified, for each individual trial, the point at which the turn toward the correct target was initiated by decelerating from its current direction, evident in a local extremum in velocity (implying a zero-crossing in acceleration), before the hand turned toward the correct side (Aivar, Brenner, & Smeets, 2008; Day & Lyon, 2000; Oostwoud Wijdenes, Brenner, & Smeets, 2014; Soechting & Lacquaniti, 1983). For brevity, we refer to this point as "turn point". We interpreted the time of this landmark as an indicator that external spatial information had become available for reach planning (Day & Lyon, 2000; Friedman, Brown, & Finkbeiner, 2013; Overvliet, Azañón, & Soto-Faraco, 2011), and its spatial location in the left-right dimension as an indicator of a potential reach bias toward one of the targets. To analyze this bias, trajectories were normalized with respect to start and end point to eliminate spatial variance unrelated to the target decision. Trajectories to the left side were flipped, so that reaches to the left and right could be pooled. Thus, turn points were analyzed in normalized and flipped reach coordinates.

Trial selection. We excluded trials when at least one of five criteria was met: First, the reach ended at the wrong target foot (1.6%). Second, movement duration was slower than the condition's mean +/- 3 standard deviations (1.1%). Third, the trajectory's end point deviated more than +/- 3 standard deviations from a condition's mean (0.6%). Fourth, the hand decelerated, or it was already directed toward the target foot, at time of stimulation, that is, before the movement goal had been specified (4.6%). Fifth, the trajectory comprised a continuous sequence of more than 20% sampling points with missing data (0.8%).The mean number of trials remaining per condition and subject was 36.4 (s.d. 4.0) of 40 possible trials.

2.4.1.2 Statistical inference

General approach. We used R, version 3.2.2 (R Core Team, 2015), and the package lme4 (Bates, Maechler, Bolker, & Walker, 2015) to perform linear mixed effects analyses. Factors were specified with effect coding. Participants were entered as random effects, and the random effect structure comprised random intercepts and slopes for all predictors and interactions (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009), whenever possible. If models did not converge, the maximal random effects structure that was supported by the data was selected. We assessed significance of fixed effects with likelihood ratio tests of the model with the maximal predictor structure and a reduced model without the fixed effect of interest (Pinheiro & Mae, 2000) using the package afex (Singmann, 2015) Fixed effects were considered significant at $p < .05$. For post-hoc analysis of significant interactions, we conducted Tukey tests of the estimated least square means (LSM, package: lsmeans; Lenth, 2015). Condition averages and their confidence intervals (CI) as presented in the figures were calculated based on LSM as well, unless stated otherwise. In order to adhere to the assumption of normality and homoscedasticity, dependent measures were box-cox-transformed prior to setting up the model when appropriate (Box & Cox, 1964).

Time analysis. The time of turn points was analyzed with two related models. The first model comprised factors Reach Hand, Foot Posture, and Target Modality. We included movement time as a centered covariate to control for trivial effects of trajectory duration across conditions; for example, reaches across the midline were slightly longer and, thus, may take longer than reaches within a hemifield. Moreover, we added centered tangential velocity at the time of stimulation as a covariate to the main model to control for differences in hand speed at the time of stimulation.

In the second model, we included Target History as an additional factor to test whether sequential trial dependencies accounted for timing effects (Chapman et al., 2010b). Target History was defined as the number of maximally 4 consecutive previous trials the target had been presented from one side, irrespective of target modality and correct execution of the reach, with left targets coded as negative, and right targets as positive. For example, if in the two trials before the current trial the target had been presented on the left foot, and the target before that had been right, then we coded trial history as -2 for two consecutive left previous targets. For the mixed model, the factor was coded with a normalized linear contrast (Rosenthal, Rosnow, & Rubin, 1999). Model comparison revealed that adding the factor Target History to the main model did not improve data fit ($\chi^2(123)=86.37$, $p>.99$). Therefore, we restrict our report to the first model.

Spatial analysis. The spatial location of turn points, too, was analyzed with two related models. Both models comprised factors Reach Hand, Foot Posture, and Target Modality. In the second model, we included Target History as a fourth factor to test whether spatial biases could be accounted for by sequential trial dependencies (Chapman et al., 2010b). We tested separately whether the occurrence of reach deflections toward the anatomical touch location for reaches to tactile targets at crossed feet could be predicted from target history, using a generalized linear mixed model analysis that comprised only the fixed effects factor Target History and subject-wise intercepts as random effects.

2.4.2 Experiment 2

Experiment 2 tested whether the effects observed in Experiment 1 were truly attributable to stimulus localization. The same stimuli as in Experiment 1 were presented, but served as movement triggers for stereotypical movements rather than as movement targets, eliminating the need for stimulus localization.

Participants. Ten right-handed students (Oldfield, 1971), 8 of them female, aged 23.9 years (range: 20-35 years) took part.

Setup. The setup of this control experiment was largely identical to that of Experiment 1. However, a midline-aligned button, positioned at the distance of the trigger marker used in Experiment 1, served as the start position of the reach hand. A second button, positioned in front of the feet and aligned with the start button, marked the reach goal (*Figure 2.1A*, bottom row). The button release of the start button was recorded as reaction time (RT).

Experimental paradigm. Participants made right and left hand reaches toward the central goal button upon detection of a tactile or visual stimulus that was presented to one of the uncrossed or crossed feet. A trial started when the participant's finger had been still at the start button for 500 ms. The stimulus was presented after an additional random interval of 1000-1800 ms. As quickly as possible, participants had to release the start button and reach toward the pre-defined goal button. Once the goal button was depressed, a tone indicated that the hand should return to the start button for the next trial. If a movement was initiated prematurely, that is, within 100 ms after stimulation, an error tone indicated that the hand should return to the start position, and the trial was repeated at a later time.

Experimental design. We used the same factors as in Experiment 1 for statistical analysis: Foot Posture (uncrossed vs. crossed, varied block-wise), Reach Hand (left vs. right, varied block-wise), and Target Modality (visual vs. tactile, varied within blocks). Each factor combination was presented 18 times, distributed across 4 blocks of 72 trials.

Trial selection. We analyzed RT as dependent measure. Trials were excluded if their RT was greater than the condition's mean +/- 2 standard deviations. The mean number of trials remaining per condition and subject was 17.5 (s.d. 0.1) of 18 possible trials.

2.4.2.1 Statistical inference

General approach. The general statistical analysis approach was identical to that of Experiment 1.

Time analysis. In analogy to Experiment 1, the model for the RT analysis of Experiment 2 comprised factors Reach Hand, Foot Posture, and Target Modality.

2.4.3 Experiment 3

In Experiment 1, reaches were always initiated toward the visual fixation LED. Accordingly, tactile stimulation implied a change of modality for reach planning, whereas visual stimulation did not. We conducted Experiment 3 to eliminate this confound, testing whether reach trajectories were modulated by the modality of the stimulus toward which the reach was initiated.

Participants: Ten right-handed students (Oldfield, 1971), 9 of them female, aged 23 years (range: 20-30 years) took part.

Setup. To provide a tactile fixation location, participants now made reaches with their right hand toward locations on the left arm (*Figure 2.3A)*. They sat at a table, with their left forearm positioned in a 45 degree angle relative to the torso. The yellow fixation LED, as well as a custom-made vibrotactile stimulator, consisting of a cell phone vibration motor glued into a plastic casing, were attached to the center of the left forearm. This central tactile stimulator was driven by electric current to vibrate, but was weaker and clearly distinguishable from the tactile target stimuli. Target stimuli were attached with equal distance toward the left to the left (elbow) and right (wrist) of the central “fixation” stimulators. A piece of felt on the table, positioned 50 cm away from the left arm and aligned in depth with the left arm's central fixation location, marked the right hand's reach start position. Markers for motion tracking were attached to the index finger of the right hand and next to the fixation and target stimuli on the left arm. As in Experiment 1, stimulation was triggered after the movement had been initiated. The trigger marker was placed 10 cm away from the start point in movement direction. All other aspects of the experimental setup were identical to those of Experiment 1.

Experimental paradigm. Participants made right hand reaches toward tactile and visual target stimuli located on the left arm. The course of a trial was identical to that of Experiment 1, with the exception that the fixation stimulus toward which the reach had to be initiated could be either visual or tactile. As the visual fixation stimulus in Experiment 1, visual and tactile stimulation fixation stimuli in Experiment 3 were presented for the entire duration of a trial.

Experimental design. The analysis comprised three factors: Target Modality (visual vs. tactile), Target Location (left vs. right), and Fixation Modality (visual vs. tactile). Fixation Modality varied block-wise in randomized order, whereas Target Modality and Target Location varied pseudorandomly within blocks. Each of the 8 factor combinations was presented 40 times, distributed across 4 blocks of 80 trials. We limit our report to the statistical comparison relevant to control for the potential confound of Experiment 1, that is, reaches to tactile targets that were initially directed toward a congruent (tactile) vs. toward an incongruent (visual) fixation stimulus.

2.4.3.1 Trajectory analysis

Movement offset and duration. Movement offset and duration were computed as in Experiment 1.

Functional representation of movement trajectories. Reach trajectories were converted into functional representations, as in Experiment 1, accounting for 90% of data points per trajectory. The greater restriction during B-spline fitting was chosen because reaches in this experiment were less variable than those of Experiment 1. Because target locations were spaced closer together than in Experiment 1, identification of turn points was not possible in many trials. Instead, we averaged functional trajectory representations after normalizing across movement time by extracting the 3D finger position at 200 equally spaced time points (Gallivan & Chapman, 2014). Normalization across time was adequate, because neither movement time nor hand speed at the time of stimulation differed significantly across conditions in a mixed effects model comprising all experimental factors (Whitwell & Goodale, 2013). Because participants made decisions between left and right targets on the left arm, further analysis focused on the normalized hand trajectories' right-left component (with the arm as the x-coordinate) over time.

Trial selection. We used the same trial selection criteria as in Experiment 1: The reach ended at the wrong target or the fixation (6.0%); movement duration was slower than the condition's mean +/- 3 standard deviations (0.8%); the trajectory's end point deviated more than +/- 3 standard deviations from a condition's mean (0.2%); the hand decelerated, or it was already directed toward the target location, at time of stimulation (that is, before the movement goal had been specified; 2.3%); the trajectory comprised a continuous sequence of more than 20% sampling points with missing data (0.1%). The mean number of trials remaining per condition and subject was 36.3 (s.d. 3.8) of 40 possible trials.

2.4.3.2 Statistical inference

General Approach. We used MATLAB algorithms developed by Chapman and colleagues (2010a) to compare the normalized functional representations of the left-right component of trajectories across experimental conditions and subjects in a functional analysis of variance (fANOVA). Thus, we compared reach trajectories of the different conditions time point by time point. This difference in analysis between Experiments 1 and 3 is owed to the fact that we analyzed turn points in Experiment 1, but could not use this approach in the control experiment. P-values were corrected using the Greenhouse-Geisser approach, whenever necessary due to violations of sphericity.

Time and spatial analysis. The fANOVA for the spatial analysis of the left-right reach component over time comprised factors Fixation Modality and Target Location.

2.5 Results

2.5.1 Time-related characteristics of reach trajectories

Experiment 1 assessed hand reach trajectories to visual and tactile targets located on the feet. Participants initiated a reach directed toward a visual fixation stimulus centrally located between the two feet. Target stimuli were presented in mid-flight, and reaches had to be changed from the initial straight direction toward the new target location. Reaches were usually accurate and rarely ended at the wrong foot. Therefore, we did not analyze error trials. If additional computational effort is required when reaching to tactile as opposed to visual targets, then turn points for tactile reaches should occur later than for visual reaches. In addition, turn points should be delayed even more when tactile targets were presented on crossed rather than uncrossed feet, because the conflict between anatomical and external, eye-centered reference frames has to be resolved. The effect of foot posture should be specific to tactile targets, because coordinates for reaching to visual targets are presumed to be natively eye-centered.

Results of the turn point time analysis are illustrated in *Figure 2.1B,C*. There were main effects of Target Modality ($\chi^2(1)=29.61$, $p<.001$) and Foot Posture ($\chi^2(1)=13.91$, $p<.001$), as well as an interaction of the two ($\chi^2(1)=14.08$, $p<.001$). We observed no further significant effects.

Post-hoc analysis showed that turns toward tactile targets were initiated later than turns toward visual targets. Turn point time differed significantly between modalities when reaching to targets located at both uncrossed ($t(14.86)=7.92$, $p<.001$) and at crossed feet ($t(15.25)=8.78$, $p<.001$). Turn point time was delayed with crossed feet for tactile ($t(15.14)=5.91$, $p<.001$), but not for visual targets ($t(15.07)=2.36$, $p=.13$). The results of the time analysis are summarized in *Figure 2.1C*, and an example subject's single trajectories and turn points are illustrated in *Figure 2.2*.

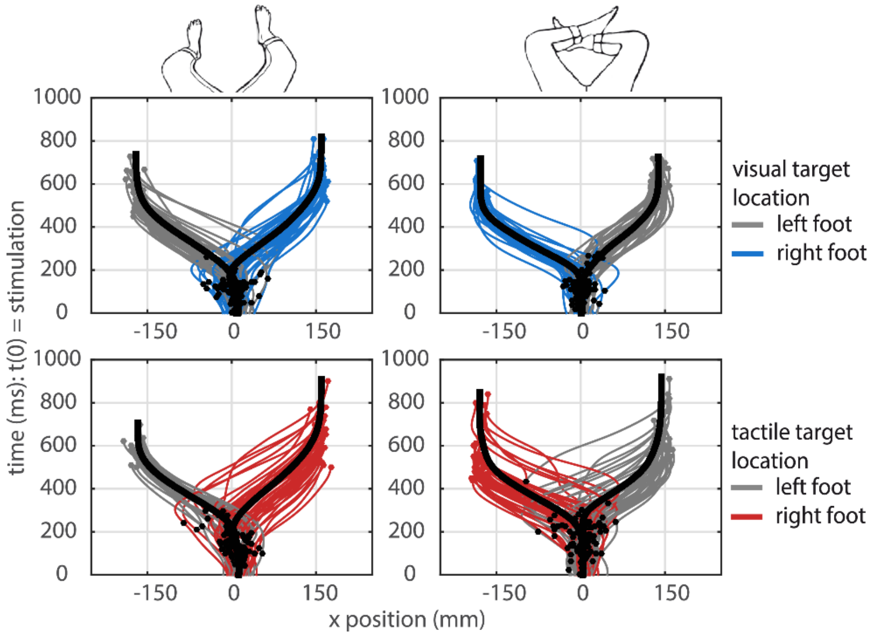


Figure 2.2. Reach trajectories of an example subject in Experiment 1. Turn points to the correct target location are depicted as black dots. Top row: reaches executed with the left hand toward visual targets. Bottom row: reaches toward tactile targets. Left panels: targets located at uncrossed feet. Right panels: targets located at crossed feet.

We conducted two control experiments to scrutinize the results obtained in Experiment 1. First, it was crucial to show that the differences between visual and tactile conditions in our main experiment were due specifically to the process of target localization, and not to more general processing differences between modalities that are unrelated to spatial localization. To dissociate these alternatives, participants made reaches to a single, pre-specified target in all trials. These stereotyped reaches were cued by the same visual and tactile stimuli as in Experiment 1. The important difference between this and our main experiment was that the control experiment did not require stimulus localization. Instead, stimuli merely had to be detected to initiate a stereotyped response. Therefore, if the timing differences between touch and vision observed in Experiment 1 were related specifically to tactile localization, then no difference in RT should be observed in Experiment 2. Note, that the two experiments also differed in that stimuli were presented in mid-flight for Experiment 1, but served as response triggers in Experiment 2. This is because initiation of an in-flight correction would have required target reprogramming, potentially eliciting localization processes and, thus, destroying the purpose of the control experiment. Therefore, we note the caveat that movement initiation probably involves additional processes in comparison to online movement correction (Day & Lyon, 2000).

We observed a trend toward longer RT for the left than the right hand (main effect of Reach Hand, $\chi^2(1)=3.62$, $p=.057$; left hand: LSM=235.87 ms, 95% CI [224.33, 247.41], right hand: LSM=229.57 ms, 95% CI [219.05, 240.09]). Critically, RT did not differ significantly between modalities (main effect of Target Modality, $\chi^2(1)=2.17$, $p=.14$; tactile: LSM=231.81 ms, 95% CI [221.27, 242.36], visual: LSM=233.62 ms, 95% CI [223.11, 244.14]). None of the interactions in the model reached significance. These results suggest that the time difference between turn points in the two modalities observed in Experiment 1 was specifically related to tactile localization.

Second, in the main experiment, participants started moving toward a visual fixation and then corrected reach direction in-flight toward a tactile or visual target. Thus, trials contained a modality switch in tactile, but not in visual target conditions. This switch may take time and, accordingly, confound our experimental results. Our original experimental design, with targets presented at the feet and a visual fixation placed between the two limbs, prevented tactual presentation of the fixation location. In a new experiment, participants made reaches with the right hand toward the left arm. The fixation location was placed on the forearm, midway between elbow and wrist, and could thus be indicated visually or tactually. Results of Experiment 3 are illustrated in *Figure 2.3*. Functional ANOVA of reach trajectories revealed a significant main effect of Target Location, reflecting that reaches to left and right targets differed in the last 29.5% of movement time. Crucially, the congruence of fixation and target modality did not significantly affect trajectories at any point in time, suggesting that the results of Experiment 1 were not due to modality switches in the different experimental conditions.

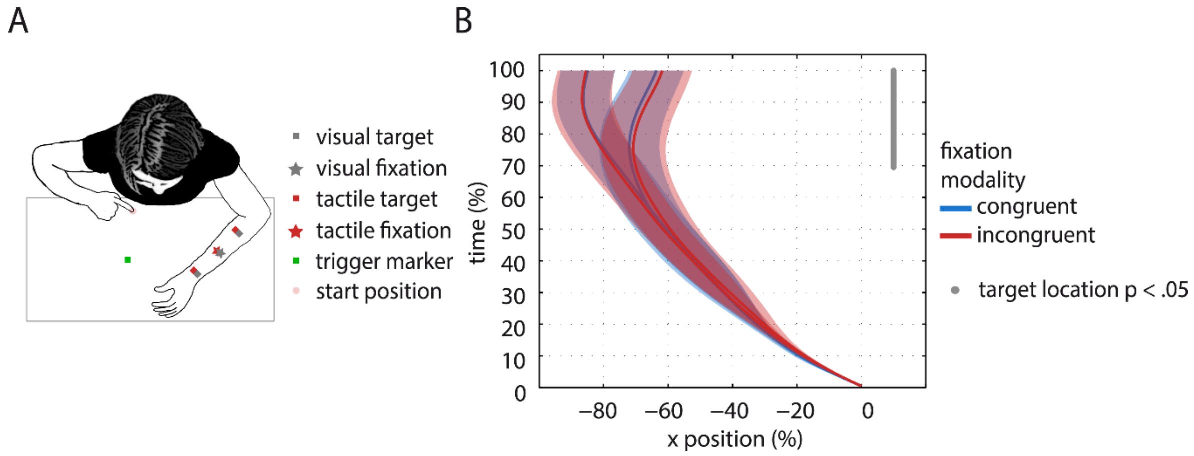


Figure 2.3. Experimental set-up and results of Experiment 3. *A.* Experimental set-up. *B.* Trajectories of reaches to tactile targets were normalized in time and then analyzed point by point with fANOVAs for effects of target side and congruence of fixation and target modality. Movements to left targets differed significantly from movements to right targets during the last third of the movement, but, congruence of fixation and target modality did not significantly affect the movement profile.

2.5.2 Spatial characteristics of reach trajectories

After we had characterized the temporal effects related to tactile remapping, we next analyzed the spatial profile of reach trajectories, with the aim of specifying the mechanism underlying crossing effects in tactile localization. Time delays may be due to impairment of coordinate transformation itself, or due to integration of spatially conflicting information after transformation. During transformation, only the original, anatomical spatial information should be available. Therefore, if delays stemmed from the transformation process, then external, gaze-centered information, too, should become available after considerable delay (Azañón & Soto-Faraco, 2008). Therefore, reach trajectories toward crossed feet should regularly deviate toward the tactile target's anatomical location, and be corrected only once the transformation has been performed. For tactile targets at crossed feet, anatomical and remapped spatial information implicate different sides of space for the movement target. In contrast, with uncrossed feet, both anatomical and external coordinates implicate the same side of space. Thus, the spatial location of turn points for reaches to tactile targets should be consistently biased toward the incorrect side in crossed relative to uncrossed conditions. If, however, time delays stemmed from spatial integration rather than from coordinate transformation, no consistent spatial bias toward the wrong side should emerge when reaching to tactile targets at crossed feet, because information available in both reference frames should be available early and at roughly the same time, but correction of the reach trajectory from a straight path toward the target should be delayed until integration of conflicting information is complete. According to both the transformation and the integration account, foot posture should not affect reaches to visual targets, because the visual system natively provides external spatial coordinates, immediately providing appropriate coordinates of the reach target.

Results of the spatial turn point analysis are illustrated in *Figure 2.4*. We flipped reach trajectories directed to left-side targets (in space) to pool them with those of right target reaches for statistical analysis. A leftward deflection of trajectories displayed in *Figure 2.4* therefore corresponds to a bias toward the anatomical target coordinate when reaching to tactile targets located at crossed feet. Linear mixed model analysis of turn point location revealed a main effect of Target Modality ($\chi^2(1)=13.25$, $p<.001$), as well as a significant interaction of Target Modality and Foot Posture ($\chi^2(1)=4.46$, $p=.035$). Post-hoc analysis of the interaction revealed that, for tactile targets, the location of turn initiation was located 7% further toward the incorrect target when the feet were crossed than when they were uncrossed ($t(14.60)=-2.27$, $p=.039$; *Figure 2.4A*). This difference was exclusive to tactile stimulation (comparison of turn points for visual targets in uncrossed and crossed postures: $t(14.53)=-0.87$, $p=.40$). Inspection of the distribution of tactile turn points (see *Figure 2.4B*, top) revealed that they were not shifted toward the incorrect target in the majority of trials. Instead, for most trials, turn point location was indistinguishable between uncrossed and crossed feet. Thus, the majority of trials did not exhibit a spatial bias toward the anatomical side of tactile stimulation (see *Figure 2.4B*, top, overlap between light and dark red points in x-direction; note that differences in y-direction pertain to time, not space). The large variance observed in the crossed tactile condition was caused by a subset of 17.2% (range: 4-36.5%) of reaches, for which the turn point deviated more than two standard deviations beyond the mean location in uncrossed trials. These trajectories initially digressed far toward the incorrect side and then turned around to the correct side (see *Figure 2.4B*, top, dashed average trajectory). These deviations were mainly observed toward the incorrect target side, and, thus, do not reflect a general tendency for greater trajectory variability in the crossed condition. We term these reaches with deviating reach points turn-around reaches (for a similar effect in saccade trajectories see: Overvliet et al., 2011). When we excluded this subset of trials for illustration purposes, the spatial profile of reaches was visually indistinguishable across conditions (see overlap of turn points in uncrossed and crossed conditions in *Figure 2.4B*, bottom), suggesting that most reaches had similar turn point locations independent of foot posture and target modality. We repeated the mixed model analysis, but excluded all turn-around reaches; consistent with the visual impression, reaches to tactile targets did not exhibit any crossing effects. Correspondingly, turn points of reaches to tactile targets at crossed feet were distributed bimodally, with peaks reflecting regular and turn-around reaches, across participants (not shown). Thus, although the spatial profile of reaches appeared consistent with the hypothesis that crossing effects result from coordinate transformation when considering averaged information, this was not the case when considering behavior on a trial-to-trial basis.

The bias toward the incorrect target was specific for tactile turn points in the crossed condition, but visual turn points were also more variable in the crossed than uncrossed condition (see *Figure 2.4A*). Crucially, for visual targets, variation was centered around zero (see *Figure 2.4B*, top, overlap between light and dark blue points in x-direction and dashed average trajectory of outliers). Recall that Target Modality was varied from trial to trial; therefore, the additional, spatially unbiased variation of reaches to visual targets may reflect uncertainty induced by limb crossing. We note that variance in visual, but not tactile, trials was comparable for uncrossed and crossed postures when we used stricter criteria to select trials for statistical analysis (a strategy that had been criticized and, therefore, abandoned during the review process). Therefore, the high variance in crossed, visual trials appears to be related to deviation in other characteristics of the reach, as for example end location and reach duration.

We next explored whether trajectory profiles conform with the assumption that crossing effects stem from integration-related processing. We reasoned that, if crossing effects are the consequence of an integration process, then other variables might be integrated in the tactile decision as well, and, accordingly, affect the reach trajectories. A popular and well researched class of decision making models are bounded integrator models. These models assume that a decision variable for each choice alternative accumulates toward a bound by integrating evidence over time (Cisek, Puskas, & El-Murr, 2009; Hanes & Carpenter, 1999; Ratcliff & Rouder, 1998). The alternative whose bound is reached first determines the choice. Occasional premature decisions can be triggered when initial sensory evidence in support of a choice alternative is high, and be corrected by continued evidence accumulation (Burk, Ingram, Franklin, Shadlen, & Wolpert, 2014; Resulaj et al., 2009). Furthermore, choices made in prior trials may induce an additive offset to the cumulative decision variable (Gold, Law, Connolly, & Bennur, 2008). Given these previous findings, we reasoned that, if trajectories reflected an integration process, then we should observe an effect of target history in our visual and tactile sensorimotor decision task. In fact, target history effects on the spatial profile of reach trajectories have been previously demonstrated in visual reaching paradigms. Specifically, repetition of target location was shown to bias trajectories toward the repeated side, with the number of repetitions increasing the spatial bias (Chapman et al., 2010b). To explore sequential target effects in the present study, we repeated the analysis of turn points with Target History as an additional predictor. As before, we observed a main effect of Target Modality ($\chi^2(1)=13.33$, $p<.001$), and an interaction of Target Modality and Foot Posture ($\chi^2(1)=4.21$, $p=.040$). There was a significant main effect of Target History ($\chi^2(1)=8.22$, $p=.004$) that did not interact with any other factor, indicating that target history influenced trajectories independent of modality and posture (*Figure 2.4C*). However, the increased number of degrees of freedom in the model with Target History as factor rendered its comparison with the original model non-significant ($\chi^2(2)=0$, $p>.99$).

We therefore used a second approach to assess the potential impact of target history. Consider reaches to tactile stimuli at crossed feet within the bounded integrator framework: when the opposite target than the current one had been presented in previous trials, this would induce a bias toward the anatomically coded target in the current trial and increase the probability that the bound implicating the incorrect choice alternative was reached faster by moving the starting point of the decision variable toward that choice. If the incorrect bound were then reached, the trajectory would be deflected toward the incorrect target, until the decision is eventually corrected. This framework predicts that the probability for turn-around trajectories, that is, reaches that severely deflect toward the incorrect side when the feet are crossed, should increase when the currently incorrect target had been presented in previous trials. In accordance with this prediction, the probability of a turn-around reach was predicted by its target history ($\chi^2(1)=7.14$, $p=.008$), and the proportion of turn-around reaches was twice as high for a target history of four targets at the opposite compared to four targets at the same side as the current trial (percentage of turn-around reaches 23.5% vs. 11.7%).

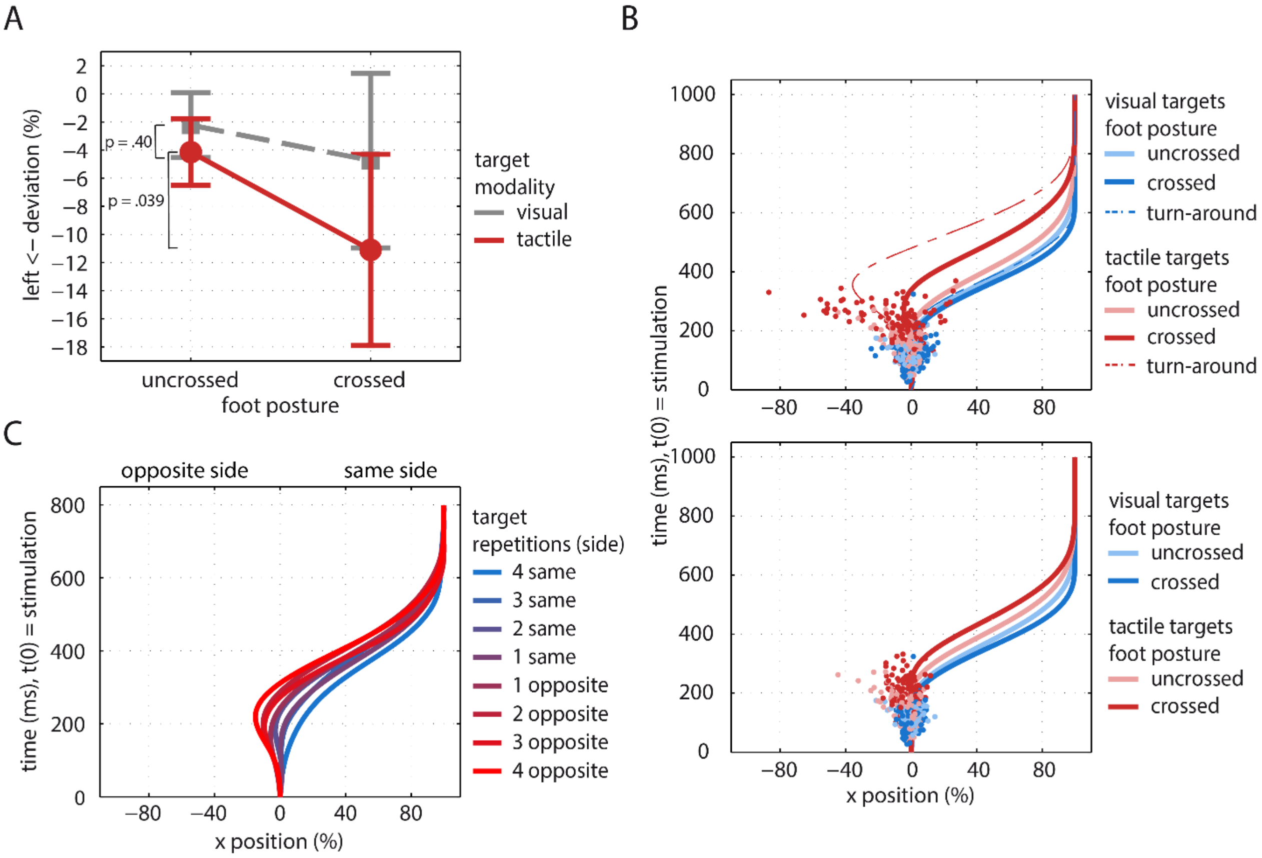


Figure 2.4. Spatial characteristics of reach trajectories. *A*. Model estimates from the mixed model analysis of the spatial location of turn points. The average spatial location of turn points toward tactile targets was slightly biased toward the incorrect side when the feet were crossed. Spatial locations of turn points toward visual targets were not significantly affected by foot posture. Error bars display 95% CIs. *B*. Single subject example of mean trajectories; reaches to the left target were flipped to be analyzed together with reaches to the right target. Start and end position of reaches were normalized. Points display single trial turn points for reaches to visual and tactile targets located at uncrossed (light blue/red) or crossed feet (dark blue/red). Dashed line indicates the mean of turn-around trajectories. Top row includes turn-around reaches, a subset of reaches whose turn point is located left or right of the mean plus two standard deviations of turn points in the uncrossed condition. Bottom row excludes turn-around reaches. *C*. Sequential choice effects in reach trajectories. Mean trajectories of an exemplar subject's reaches toward uncrossed feet of either target modality are ordered according to the number repetitions of left or right targets in the preceding trials.

In sum, the spatial pattern of reach turnpoints is in line with coordinate integration, but not transformation, as the underlying cause of performance deficits in crossed postures. As a last step, we tested whether this conclusion is also warranted by reach timing when turn-around reaches are excluded. Recall, that the transformation account predicts a spatial deviation of reaches due to the prolonged availability of only the anatomical target coordinate in the crossed posture. Accordingly, reaches that do not express such a spatial deviation should not be prolonged as compared to reaches to uncrossed limbs. Contrary to this prediction, a model that excluded turn-around reaches revealed main effects of Target Modality ($\chi^2(1)$= 26.86, p<.001) and Foot Posture ($\chi^2(1)=12.48$, p<.001), as well as an interaction of the two ($\chi^2(1)=9.59$, p<.01), just like the original model that analyzed all trials. The transformation account does not explain why reaches to crossed limbs would be prolonged, but not spatially deviate towards the incorrect side. In contrast, the integration model predicts prolonged, but spatially unbiased reaches, and accounts for occasional deviations towards the anatomical target side.

2.6 Discussion

We aimed at characterizing the processes involved in tactile localization by exploiting the context of a sensorimotor decision making task. Tactile localization has been proposed to involve two separate processes, tactile remapping (that is, coordinate transformation from anatomical into external coordinates), and subsequent integration of anatomically coded information with remapped, externally coded, eye-centered spatial information (Badde, Heed, et al., 2014, 2015; Badde, Röder, et al., 2014; Heed, Buchholz, et al., 2015). To clarify the contribution of these processes to localization behavior, participants executed hand reaches toward visual and tactile targets at uncrossed and crossed feet. We analyzed the timing and location of the point in reach trajectories at which the turn toward the correct target was initiated.

Our study revealed three key results. First, turn points were significantly delayed by foot crossing for tactile, but not for visual reaches. Second, we did not observe a consistent spatial bias toward the stimulus when touch was delivered to crossed feet. Whereas a subset of reaches exhibited pronounced initial deflections toward the incorrect target (termed turn-around reaches) in this situation, the majority of trajectories turned at a horizontal location centered around the start position, just like reaches toward uncrossed feet. Third, target repetition biased trajectories toward the repeated location, and the proportion of turn-around reaches was twice as high when repetition had induced a bias toward the incorrect target than when the bias had been directed toward the correct target.

Our study capitalized on several known features of hand reaches to characterize the processes involved in a tactile localization decision. Reaches are non-ballistic (Jeannerod, 1988) and can be promptly corrected in-flight (Desmurget et al., 1999; Pélisson, Prablanc, Goodale, & Jeannerod, 1986; Scott, 2004; Todorov & Jordan, 2002). They are known to reflect cognitive processing in the context of motor planning and perceptual decision making (Chapman et al., 2010a; Friedman et al., 2013; Körding & Wolpert, 2006; Resulaj et al., 2009; Selen et al., 2012; Trommershäuser, Maloney, & Landy, 2008) on a single trial level (Day & Lyon, 2000). Furthermore, motor correction paradigms reduce motor-related processing unrelated to the cognitive task of interest, because reach initiation is completed before the investigated process begins (Day & Lyon, 2000).

2.6.1 A timeline of tactile remapping

Previous findings concerning the timing of tactile remapping have been heterogeneous, probably owed to the use of divergent paradigms and research methods across studies. A spatially congruent tactile cue can speed up a decision about a subsequent visual stimulus (Azañón & Soto-Faraco, 2008). When the tactile cue led the visual stimulus by 60 ms, spatial congruence was effective in an anatomical reference frame, that is, a right hand stimulus improved the decision about a right-side visual stimulus, independent of where the hand was positioned in space. When the tactile cue led by 180 ms, then spatial congruence was effective in an external reference frame, that is, a hand (whether left or right) positioned on the right side in space improved the decision for a right-side visual stimulus. This result pattern was interpreted to indicate that tactile remapping is completed between 60 and 180 ms after stimulus onset.

In line with this time range, several studies have reported effects of hand posture in event-related potentials (ERPs) evoked by tactile stimulation in the time range of 70-160 ms after stimulation (Heed & Röder, 2010; Rigato et al., 2014; Soto-Faraco & Azañón, 2013). However, it remains unclear whether ERP modulation reflects coordinate transformation or spatial integration of different reference frames, and whether averaged signals truly reflect behavior on a single trial level. Finally, when saccades had to be directed to tactile locations at crossed hands, saccade RT for straight saccades was, on average, 284 ms (Overvliet et al., 2011). Based on estimates for motor preparatory processing in monkey neurophysiology, the authors suggested that remapping was completed after approximately 190 ms.

The current study clarifies previous work in three ways. First, by identifying the time point at which a decision becomes evident in hand reaches, we specified the timing of spatial processing on a continuous time scale. Second, use of an in-flight motor correction paradigm minimized the effects of processes unrelated to stimulus localization. Third, analysis of individual reach trajectories circumvents inferential limitations of trial averaging. *Figure 1.1C* summarizes the timing of stimulus localization revealed by the current experiments. Reaches to visual stimuli were unaffected by posture and were redirected, on average, 138 ms after visual stimulation. This latency is in line with previous response time estimates of about 120-160 ms for in-flight correction of reaches toward a visual target (Day & Lyon, 2000; Scott, 2012). Reaches to tactile targets were redirected 158 ms after stimulation when the feet were uncrossed. Thus, even when anatomical and external reference frames were aligned, decision times for touch were longer than those for vision. In contrast, RT did not differ between modalities in our Experiment 2, which did not require stimulus localization. Thus, the time difference of about 20 ms between tactile and visual choices appears to be specifically related to tactile stimulus localization. It suggests that a tactile decision involves remapping of anatomical into external coordinates also when the feet are uncrossed, and that in-flight correction of the hand movement is not initiated before this process is complete. When anatomical and external reference frames were incongruent, the turn toward the correct tactile target was initiated, on average, after 200 ms. Thus, tactile targets at crossed feet were localized 42 ms later than tactile targets at uncrossed feet, that is, in absence of reference frame conflict. These processing time estimates in the presence of conflict are shorter than previous time estimates of tactile remapping (e.g., saccade RT effects of 190 ms in Overvliet et al., 2011). They indicate that previous experiments may have overestimated the time necessary to localize tactile stimuli in space and demonstrate the feasibility of movement paradigms that involve online movement corrections for the isolation of specific cognitive processes (Day & Lyon, 2000; Gallivan & Chapman, 2014).

2.6.2 Tactile localization as a bounded integrator process

The spatial profile of reach trajectories renders new insight into the origin of the time delays observed in touch localization under reference frame conflict. If prolonged processing time were due to coordinate transformation, then behavior should regularly be affected by the anatomical reference frame, that is, single reaches should usually show an initial spatial bias toward the incorrect target when the feet are crossed. Although average trajectories of reaches to tactile targets were affected by limb crossing, this effect was owed to a minority of trials that were severely deflected toward the incorrect side. In contrast, most trajectories turned at a spatial location that was indistinguishable from turn points of trajectories to uncrossed feet.

Thus, spatial trajectory patterns did not support the notion that anatomical spatial information regularly guided initial reaching behavior.

Instead, the current results suggest that behavior reflected the integration of anatomical and external, gaze-centered spatial information. This account could be implemented, for example, within a bounded integrator framework of decision making (Cisek et al., 2009; Hanes & Carpenter, 1999; Wolpert & Landy, 2012). According to such models, evidence for each alternative relevant for a decision is accumulated until the threshold for one choice is reached and triggers a response associated with the respective alternative (Gold & Shadlen, 2007).

Extending this framework to touch localization implies that spatial information about touch location is available in anatomical and external reference frames, and that both types of information are integrated as sensory evidence toward the two possible target locations (Buchholz, Goonetilleke, Medendorp, & Corneil, 2012; Overvliet et al., 2011). The motor response to turn the reach toward a target is initiated once the bound of either target has been passed. With uncrossed feet, anatomical and external spatial information are congruent, and both contribute to evidence accumulation for the same target foot. Although one might expect that the redundant information from the two reference frames should lead to faster integration compared to reaching to visual targets, formation of the spatial decision took longer for tactile than for visual targets. In two control experiments, we confirmed that this additional processing time was directly related to the process of localization, rather than to unspecific differences between the visual and tactile modalities, and that it was unrelated to modality switch costs inherent in our paradigm. The origin of the posture-independent, localization-specific delay in tactile processing thus appears to be related to the transformation of anatomical into external, eye-centered coordinates.

When anatomical and external information were incongruent, most trajectories toward tactile targets turned later in time, but at a similar spatial location, with respect to left and right, as trajectories to stimuli at uncrossed feet. In the bounded accumulator framework, this result pattern suggests that reach adjustments were initiated only after evidence accumulation had been completed and the decision for a target had been formed. In the crossed posture, the decision was prolonged presumably because evidence accumulation proceeded more slowly due to conflicting input from different reference frames. If, instead, coordinate transformation had been impaired or slowed by limb crossing, anatomical spatial information would nonetheless have been available early on, and should have resulted in a consistent reach bias toward the incorrect target side. This interpretation is in line with the increased probability of turn-around reaches when target history favored the incorrect foot. To summarize, hand reaches indicating tactile decisions about targets defined in incongruent reference frames were regularly delayed, but not consistently biased in space. This result pattern suggests that anatomical spatial information did not dominate early stages of the movement toward tactile targets. Instead, the time delays induced by limb crossing likely originate from integration of incongruent spatial information. These results can be explained by assuming a bounded integrator process that integrates tactile coordinates of anatomical and external reference frames.

3 From touch to movement: flexible coding of sensory and motor information during tactile sensorimotor processing

3.1 Abstract

Planning a movement based on touch information, such as wiping away a mosquito on the hand, entails complex spatial computations. Their bases are tactile coordinates signaling the sensory target location, and movement coordinates, translating tactile coordinates into a movement goal for action. Both the coding of tactile space and movement planning have been linked to posterior parietal cortex; however, how their integration is implemented in this brain region remains unclear. To investigate this question, we recorded BOLD signal changes in the brain using fMRI while participants executed right hand pointing movements toward tactile stimuli at their feet. The legs were either positioned in a regular, uncrossed posture, or crossed over the shin. This manipulation allowed disentangling skin-based and external-spatial tactile coding: With uncrossed limbs (right foot in right space) skin-based and external coordinates are aligned. In contrast, with crossed limbs (right foot in left space) external and anatomical coordinates are misaligned. In addition, we dissociated brain activity related to sensory (tactile) from movement processing by instructing pointing movements either directly towards the touched location (pro-movement), or alternatively, towards its' mirror location (anti-movement). Critically, sensory and movement locations are on opposite spatial sides for anti-movements. Multi voxel pattern decoding of fMRI activation revealed that touch was initially coded in both skin-based and external-spatial coordinates in primary sensory and posterior parietal cortex. However, when the movement goal was specified, sensory spatial information was no longer detectable; instead, a network covering primary motor, premotor and posterior parietal areas now selectively represented information about the movement goal location. This network overlapped partially with areas which previously represented tactile coordinates, indicating that nodes of the identified network progressively change their function. In sum, our results show that the brain dynamically employs different spatial codes depending on the stage of sensorimotor planning.

3.2 Introduction

One of our most basic, but also most important abilities is to perform goal-directed actions towards objects in our environment. Although tasks such as reaching towards a book or a coffee cup appear very easy to perform, the brain's underlying processing of the body and the environment are highly complex. For instance, to plan a movement toward a motor goal, target and effector-related information is thought to be transformed into a common spatial code or “reference frame” (Medendorp et al., 2011). Both, for visual and tactile movement targets this reference frame seems to be eye-centered (Batista et al., 1999; Buchholz et al., 2011, 2013; Henriques et al., 1998; Medendorp et al., 2003; Müller & Fiehler, 2014a, 2014b). However, when reaching towards a touch, that is, towards the own body, deriving an eye- centered target representation requires additional computations that transform spatial information, because touch is initially encoded relative to the skin, unrelated to the eyes (Azañón & Soto-Faraco, 2008; Badde & Heed, 2016; Heed, Buchholz, et al., 2015; Shore et al., 2002; Yamamoto & Kitazawa, 2001). Skin-based coding of touch has been associated with S1, which is organized according to an orderly map of the body surface (“the sensory homunculus”; Penfield & Boldrey, 1937). However, as the body can be moved, anatomical information about where on the skin surface a touch occurred does not sufficiently specify spatial information for acting toward a tactile location. Rather, the brain must integrate visual, proprioceptive, as well as vestibular information to recode where the touched skin is in space (Clemens, De Vrijer, Selen, Van Gisbergen, & Medendorp, 2011). The recoding of tactile coordinates, termed “tactile remapping” (Driver & Spence, 1998), has been linked to IPS located in PPC (Azañón et al., 2010; Ruzzoli & Soto-Faraco, 2014). This structure is thought to process posture, touch, and visual information close to the body (Graziano & Cooke, 2006). Behaviorally, tactile remapping can be investigated by manipulating limb posture to dissociate anatomical and external coordinates, specifically by placing hands or feet either in a uncrossed posture or by crossing them across the midline (for a review see: Heed & Azañón, 2014). Whereas the external spatial location of a touch presented to one of the limbs changes with limb crossing, the anatomical location remains constant. Put differently, crossing changes whether the limb is positioned in the left or right hemispace, while the identical skin location is stimulated across postures. The tactile TOJ task has been frequently used to investigate tactile remapping. This perceptual task does not require an action directed towards the stimulus, but instead requires participants to report which of two (or more) possible locations was tactually stimulated first in a forced choice paradigm (Schicke & Röder, 2006; Shore et al., 2002; Yamamoto & Kitazawa, 2001). Limb crossing in this task leads to prolonged processing times and increased error rates compared to a an uncrossed hands posture (Shore et al., 2002; Yamamoto & Kitazawa, 2001). These so-called "crossing effects" have been related to the integration of conflicting spatial information coded in different reference frames (Badde & Heed, 2016; Badde, Heed, et al., 2015) and have been shown to generalize to task contexts that require a reaching movement toward the exact location estimate (Brandes & Heed, 2015). Thus, planning a goal-directed movement toward a tactile, as opposed to a visual, target requires additional processing related to localizing the target on the body and in space.

Apart from target localization, goal directed action toward a touch entails additional processing concerning the integration of target and effector information to derive a movement goal. As a prerequisite, an internal representation of current hand position is estimated from visual and/or proprioceptive information (Khan et al., 2007; Sober & Sabes, 2003, 2005), presumably in mIPS and angular gyrus (Fernandez-Ruiz et al., 2007; Vesia et al., 2010). Theories that specify visual sensorimotor planning assume that the movement path between target and current hand position is then calculated by optimally integrating the location estimates of the two (Buneo & Andersen, 2006; Sober & Sabes, 2005). Calculating this movement vector has been associated with PRR in non-human primates (Batista et al., 1999; Buneo, Jarvis, Batista, & Andersen, 2002). A homologous region that processes both target and effector information alike, is thought to exist in humans in the posterior occipital cortex, bordering the precuneus (SPOC; Astafiev et al., 2003; Beurze et al., 2007; Connolly et al., 2003; Fernandez-Ruiz et al., 2007; Vesia & Crawford, 2012). To further specify how sensory information is used for action, a number of studies have investigated whether distinct areas are selective for the processing of sensory, usually visual, vs. movement goal locations. Movement goal and sensory information can be dissociated using pro-/anti- movement tasks, which require either a pro- movement directly toward the stimulus, or alternatively, an anti-movement toward its mirror location (Alexander & Crutcher, 1990; Connolly et al., 2000; Crammond & Kalaska, 1994; Gail & Andersen, 2006). Using this manipulation, the role of the putative human homolog of PRR (SPOC) for sensorimotor transformations has been corroborated, as it selectively codes the contralateral movement goal, preferably for the contralateral moving arm (Cappadocia, Monaco, Chen, Blohm, & Crawford, 2016; Gertz & Fiehler, 2015). Furthermore, a transition from sensory to movement selective coding has been shown in a network spanning SPOC, premotor cortex (PMC), anterior and medial intraparietal sulcus (aIPS, mIPS), as well as regions in the superior and inferior occipital gyrus (Cappadocia et al., 2016). This transition has been interpreted as indexing the progression of visuomotor transformations from sensory target processing to derivation of a movement goal (Cappadocia et al., 2016). In sum, a fronto-parietal network including for example SPOC, mIPS and the PMC has been shown to be involved in transforming visual targets into motor goals using pro-/ and anti-movement tasks.

Planning movements to tactile, as opposed to visual, targets presents an additional challenge: Whereas for visual targets sensorimotor transformations reconciling target and effector locations are necessary, tactile target processing for action requires, in addition, the reference frame transformation of anatomical to external tactile coordinates. Moreover, anatomical and external information has to be integrated to arrive at a unified location estimate. Both target-related processing and transforming a sensory into a movement location require the referral to body posture. Specifically, target-related processing depends on the posture of the touched limb, while deriving a movement goal depends on the posture of the effector. Both target-related processing and sensorimotor transformations have been associated with IPS. However, it is currently unknown how integration of these sensorimotor functions is achieved in the case of planning an action towards a touch, both in terms of function and cortical implementation.

The present study aimed to investigate the coding of tactile and movement locations for action toward a touch using fMRI. To this end, participants executed right hand pro- or anti-pointing movements toward tactile stimuli presented to their uncrossed or crossed feet in a delayed movement task. To assess the development of tactile sensorimotor plans from sensation of the target to execution of a movement toward it, touch localization, movement planning, and execution were parsed into separate delays during single trials. Crucially, the movement instruction (pro- vs. anti) was only given after the touch had been presented. Touch and presumably touch location was, thus, initially processed without knowing the movement location. Information is thought to be represented in distributed codes across a network of neural populations, which are natively multivariate (Deneve, Latham, & Pouget, 1999; Ernst & Banks, 2002; Pouget, Dayan, & Zemel, 2000, 2003); a feature which has been extensively studied in the context of spatial processing of the environment and the body in PPC (Buneo & Andersen, 2006; Buneo et al., 2002) Hence, we did not expect spatial coding to be related to global changes in brain states, but rather to be implemented as changes of distributed activity across neuronal populations. Consequently, our analysis focused on the decoding of represented information from multivariate activity patterns (Multi Voxel Pattern Decoding; MVPA). MVPA has been demonstrated to be a sensitive and appropriate approach to quantify how information is coded in the human brain (Haxby, Connolly, & Guntupalli, 2014; Haynes, 2015; Haynes & Rees, 2006; Kaplan, Man, & Greening, 2015; Kriegeskorte, 2009; Kriegeskorte, Goebel, & Bandettini, 2006; Norman, Polyn, Detre, & Haxby, 2006). First, we hypothesized that tactile information, that is, anatomical and external touch locations, would be represented in multivariate activity patterns measured during the touch localization delay. Second, we expected movement goal locations to be represented similarly in multivariate activity patterns measured during the planning delay. Third, we asked whether tactile information, too, would be represented during the planning delay. During visuomotor planning, it has been shown that the preservation of visual codes depends on the function of a specific region and the task demands (Gertz & Fiehler, 2015; Gertz, Lingnau, & Fiehler, 2017). For instance, sensory information theoretically becomes irrelevant once the movement goal has been specified but may nonetheless be preserved (for compatible results from visuomotor planning see: Cappadocia et al., 2016). Alternatively, sensory codes may only be maintained as long as they are relevant (Gertz et al., 2017). To dissociate these alternatives, we tested whether tactile representations are stable and invariant across delays, or whether, alternatively, they are evident in a different format during the planning delay.

Fourth and finally, we hypothesized that the coding of tactile coordinates during touch localization for action reflects a general mechanism, which is also relevant for behavioral performance during a perceptual touch localization task. Consequently, we expected that the representation of tactile coordinates during the touch localization delay would be related to a behavioral efficiency measure of touch localization acquired using a TOJ task (Shore et al., 2002; Yamamoto & Kitazawa, 2001). In TOJ tasks, localization performance at crossed limbs indexes the encoding of touch in external space (Heed & Azañón, 2014). Moreover, crossing equally impairs TOJs in all limb combinations, e.g., hands, feet, or one hand and one foot, suggesting that anatomical information is remapped in a body-part independent, common reference frame (Schicke & Röder, 2006). A common coding mechanism across different tasks may for example be related to the weighting of anatomical and external location codes that determine touch localization (Badde, Heed, et al., 2015). As a result of a common coding mechanism of touch localization across sensorimotor and TOJ tasks, we expected participants who exhibit a strong representation of anatomical touch coordinates during the touch localization delay of the sensorimotor task, as for example reflected in high decoding accuracies obtained from the MVPA, to be better at localizing tactile stimuli in the TOJ task. Likewise, we expected participants who exhibit a strong representation of external touch coordinates during the touch localization delay of the sensorimotor task to be worse at localizing tactile stimuli in the TOJ task.

3.3 Methods

The study consisted of two parts, an fMRI and a behavioral experiment. Behavioral testing was always scheduled a few days before fMRI scanning, to inform participants about the scanning procedure and to practice the sensorimotor task outside the scanner environment. However, the fMRI experiment is outlined first as the behavioral experiment served as a generalization test of the coding delineated in the fMRI experiment.

Participants. Data of 19 participants was acquired. All were students of the University of Hamburg. They were right-handed according to self-report (Oldfield, 1971), had normal or corrected-to-normal vision, and did not report any neurological disorders, movement restrictions, or tactile sensitivity problems. They provided written informed consent and received course credit or € 8/hour for their participation. The experiment was approved by the ethics committee of the DGPs. Data of one participant had to be excluded from the analysis because movements were executed towards the wrong goal in 99.5% of trials with crossed feet in the fMRI experiment. Two further participants had to be excluded, because the slices acquired during scanning did not cover all of the postcentral gyrus and SPL. The final sample, thus, consisted of 16 students, 11 of them female, mean age 23.8 years (range: 19-30 years).

3.3.1 Part 1 | fMRI experiment: tactile sensorimotor planning

Experimental setup and task design. Participants planned and executed right hand movements toward tactile stimuli presented to the feet, while blood oxygenation level dependent (BOLD) signal changes in the brain were recorded using fMRI. To that end, participants lay supine in the scanner with their head stabilized using foam cushions. The right hand was cushioned into a fixed position approximately at body midline above the stomach such that the index finger aimed toward the feet. A cardboard was placed above the right hands' wrist just below the chest to shield the infra-red (IR) LED attached to the finger for movement recording from projector light entering the bore from the head direction. Hands and feet could not be seen by participant throughout scanning, because eyes were directed upward. Experimental instructions were displayed on a monitor, projected onto a translucent screen in the scanner bore. Participants saw the projectors' image through a mirror mounted on the head coil.

We used a delayed movement task to parse brain activity related to touch localization, movement planning and movement execution into separate delays. Similar paradigms have successfully been used to investigate activation (patterns) related to eye or hand movement planning and execution toward visual targets (e.g., Beurze et al., 2007; Gallivan, McLean, Smith, & Culham, 2011; Leoné et al., 2014; Medendorp et al., 2003). Each trial consisted of four separate phases; namely, fixation, tactile localization, planning, and execution delay (*Figure 3.1*). During each trial, a tactile stimulus was applied to the left or right foot after a fixation delay, whose duration was fixed. To ensure precise movement planning instead of rough left-right decisions later on, the tactile stimulus could be located at one of two possible locations, either on the medial or on the lateral foot surface. Crucially, besides the specification of a lateral or medial foot location, the tactile stimulus itself was not informative about the movement that had to be planned. Only after a variable temporal delay (touch localization delay), a visual cue indicated whether a hand pointing movement should be planned directly toward the tactile stimulus (pro-movement), or alternatively, toward its' mirror location (anti-movement). After another variable temporal delay (planning delay), a visual cue prompted movement execution, followed by another delay whose duration was fixed (execution delay). To dissociate anatomical from external touch location, the feet were either positioned in an uncrossed or crossed posture. Participants' feet were moved between runs by the experimenter to minimize head motion. For comfort, the participant chose before scanning which foot would cross over the other in both scanning sessions. The crossed posture was fixed using cushions so that participants could lay comfortably without movement. If necessary for comfort, legs were slightly elevated using additional cushions placed below the knees. Direct skin contact of legs and feet in the crossed posture was prevented using clothing and towels to avoid the generation of conductor loops.

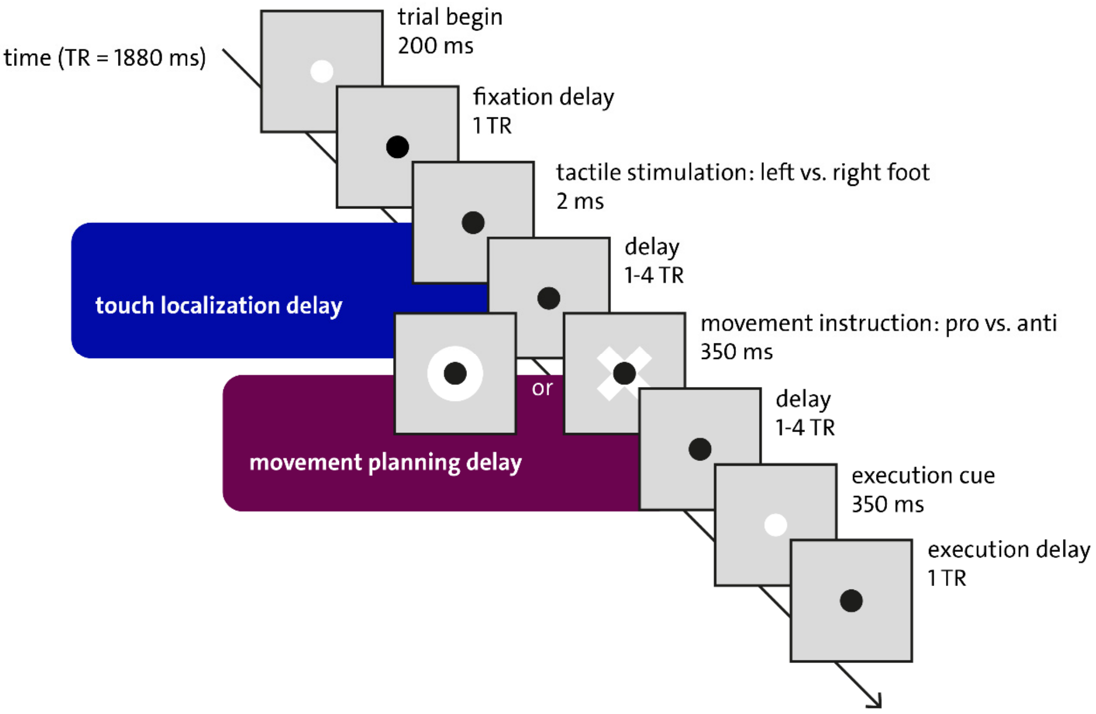


Figure 3.1: Delayed movement task and trial timing. A black fixation dot was presented in the center of the screen throughout scanning. To indicate the beginning of a trial, the fixation dot briefly turned white. A delay with a fixed duration of 1 TR followed. Then, a tactile stimulus was presented to the left or right foot, followed by a variable delay lasting 1-4 TR (touch localization delay). Afterwards, a visual cue indexing the movement instruction that had to be applied to the tactile stimulus (pro: circle, anti: cross) was briefly presented, followed by another variable delay lasting 1-4 TR (movement planning delay). To prompt movement execution, the fixation dot briefly turned white and a delay with a fixed duration of 1 TR to execute the right-hand pointing movement followed.

Experimental protocols were synchronized with volume acquisition (TR=1880 ms) and controlled via the software Presentation, version 17.0 (Neurobehavioral Systems, Albany, USA). The fMRI experiment was conducted in two sessions on separate days. The two scanning sessions were scheduled 3.6 days apart on average (range: 0-21) and lasted approximately 2 hours, including 60 min preparation and 60 min scanning time. If both scanning sessions took place on the same day, a break of 2 hours was scheduled in between. During each scanning session, participants completed 6 runs, each lasting approximately 8 minutes and containing 33 trials plus 2 fixation periods. Participants rested between runs and continued with the next run whenever they were ready. Each run began and ended with longer fixation periods, lasting 11 and 4 TRs respectively. The experiment comprised 3 within-subject factors in total, implemented in a mixed fMRI paradigm, which is characterized by a combination of event-related and blocked manipulation of experimental factors. Foot posture (levels: uncrossed vs. crossed) was maintained for 3 runs in a row, with the starting posture alternated between sessions and counterbalanced across participants. The factors stimulated foot (left vs. right; collapsed across 2 possible locations per foot) and instructed movement (pro vs. anti) varied from trial to trial. Their presentation sequence balanced run-wise such that each condition was followed by every other condition equally often (J. L. Brooks, 2012). Their delay timing optimized to minimize correlations between the predictors of the General Linear Model (GLM) that was fit to the data during analysis. Due to the run-wise balancing procedure, the absolute number of trials across runs and sessions varied from 48-51 trials per condition. Fixation and execution delay durations were fixed and lasted 1 TR. Tactile localization and planning delay durations were jittered between 1 and 4 TRs. In total, we used 4 different randomization protocols across the sample. For statistical analysis, individual stimulus onset protocols were reconstructed from the experimental logfiles offline.

Tactile stimulation. For tactile stimulation, short (2 ms) electrical pulses were applied to one of two possible locations on each foot using a constant current electrical stimulator (DS7A; Digitimer, Hertfordshire, United Kingdom). Stimulation was delivered via custom-built electrodes attached to the lateral and medial surface of each foot, approximately two centimeters below the heads of the metatarsal bones. To ensure that only one electrode was active at a time, a manual switch (DSM367; Digitimer, Hertfordshire, United Kingdom) was operated by the experimenter in the control room. One of four LEDs attached to the switch was illuminated on each trial to indicate where and when to move the switch throughout scanning. To warrant that the electrical stimulation was clearly detectable but not painful, current intensity was adapted individually, starting at 30 mV and increasing in steps of 30 mV until stimuli were reliably detected. The threshold was adapted across stimulus locations at both feet until the stimulation was judged to be equally noticeable at all four possible stimulation sites by the participant. Participants were asked between runs whether tactile stimuli were still clearly detectable and stimulus intensity was adapted whenever necessary. On average, the threshold was 268.33 mV (range: 60-600).

Eye tracking. Participants were instructed to maintain fixation throughout the experiment to avoid confounding effects of saccade planning. To check whether participants kept fixation, right eye movements were recorded using an fMRI-compatible eye tracker (Eye Link; SR Research, Ottawa, Canada) operated at a 250 Hz frame rate. The eye tracker was calibrated using a 9-point fixation procedure before each scanning session. Saccades were detected offline based upon the horizontal or vertical deviation from fixation. Specifically, a saccade was defined by a deviation from fixation that was larger than the mean fixation plus 2 standard deviations and larger than 20 pixels.

Hand movement recording. To check whether movements were performed correctly, hand pointing was recorded through a bore from outside the scanner room using a conventional video camera operated at a 40 Hz frame rate. A custom-build IR LED was attached to the right finger. Additionally, two color LEDs placed directly in front of the camera signaled the location of the tactile stimulus (left vs. right foot) and the instructed movement (pro vs. anti-movement) on each trial to align video with fMRI data offline. They were visible in the upper right corner of the video image to aid analysis. Video data were analyzed using a semi-automated procedure during which video images were first analyzed frame by frame using a custom algorithm based on a combination of cluster detection methods and gradual averaging and subtraction of images to automatically detect the movement of the IR LED across frames. The algorithm failed occasionally when the data quality of the video was bad (e.g., IR LED not visible due to lighting conditions or elevated feet position). The movement direction (left or right) was determined from the output of the algorithm.

Behavioral practice session outside the fMRI scanner. Participants practiced the sensorimotor task outside the scanner environment a few days before the first scanning session. Before/after practice participants performed the TOJ task (see below). To simulate the fMRI set-up as closely as possible, participants lay supine in a reclinable chair and the visual display was mounted above the head. The feet were placed in an uncrossed or crossed posture and vibrotactile stimulators were used for tactile stimulation at the feet (Oticon bone conductors, type BC 461-012, sized about 1.6 x 1 x 0.8 cm). The task completed during the practice session was identical to the task completed during scanning (see *Figure 3.1*). Horizontal and vertical eye movements were monitored online using Electrooculography (EOG). Participants practiced the task until the pointing movement was executed at the correct time during the trial and directed toward the correct location and the hand was still at all other times. Furthermore, participants practiced to fixate a central cross displayed on screen throughout the task and to keep the rest of the body, especially the head, still, while executing the pointing movements. Experimental protocols were controlled via the software Presentation, version 17.0 (Neurobehavioral Systems, Albany, CA, USA).

Data selection. The sample acquired during scanning consisted of 6685 trials in total after one run of one participant had to be excluded due to a technical error. Data quality could not be assessed when hand or eye movement data was not available (19.6% and 18.3% of available trials respectively). This was the case for example when the video camera recording failed or when the right pupil could not be detected through the head coil. Such trials, however, were included in the analysis. Trials were excluded from the analysis if the pointing movement was executed toward the wrong goal (4.1%), when the hand was moved when it had to be still (0.1%), when the eyes were moved (9.9%), or when a combination of either occurred (0.5%). Thus, the analysis was based on 5776 trials, 86.4% of trials originally available. See *Table 3.1* for details on data quality and behavioral performance per run.

Functional MRI acquisition. Functional MRI data was obtained using a 3-tesla MR scanner (Siemens, Erlangen) with an echo planar imaging (EPI) T2*-sensitive sequence, acquiring 32 contiguous axial slices in descending order (3 mm thickness; TR: 1880 ms; TE: 30 ms; flip angle: 70°; FOV: 216 x 216 mm).

Structural MRI acquisition. A high resolution (1 mm thickness) structural MRI image was acquired either during the first or second scanning session of each participant using a T1*-sensitive MPRAGE sequence with 240 slices for coregistration and normalization of functional data.

	1	2	3	4	5	6	7	8	9	10	11	12	mean	total	%
before cleaning	35.00	35.00	35.00	35.00	35.00	35.00	35.00	35.00	35.00	32.81	35.00	35.00	34.82	6685	100.0
after cleaning	29.94	30.00	31.25	29.88	30.88	29.56	29.31	28.75	31.13	28.50	30.25	31.56	30.08	5776	86.4
wrong goal	1.00	1.13	0.75	2.19	1.50	2.25	2.13	2.25	0.63	1.56	1.63	0.19	1.43	275	4.1
hands moved	0.19	0.00	0.00	0.00	0.00	0.06	0.06	0.00	0.06	0.00	0.00	0.00	0.03	6	0.1
eyes moved	4.38	4.13	3.13	3.13	3.00	3.19	3.63	4.19	3.31	2.75	3.19	3.31	3.44	661	9.9
both	0.50	0.25	0.13	0.19	0.38	0.06	0.13	0.19	0.13	0.00	0.06	0.06	0.17	33	0.5
bad quality hand	4.94	7.44	6.88	4.31	7.81	5.94	5.50	8.13	8.13	6.81	5.94	5.94	6.48	1244	18.6
bad quality eyes	0.19	2.00	1.75	0.31	0.38	0.63	0.13	0.13	0.69	2.19	2.81	2.13	1.11	213	3.2
missing hand	7.19	4.88	5.56	4.31	7.06	10.63	14.06	3.25	6.13	8.25	2.25	8.25	6.82	1309	19.6
missing eye	6.56	6.56	6.56	6.56	6.56	6.56	6.56	6.56	6.56	6.56	6.56	4.38	6.38	1225	18.3

Table 3.1: Average (participant-level), total (group-level) and percent number of trials (including 2 fixations per run) before and after data cleaning in the sensorimotor task, grouped according to run (1-12). Trials were excluded if the pointing movement was executed toward the wrong goal, when the hands were moved when they had to be kept still, when the eyes were moved, or when both, hands and eyes were moved. Remaining data is balanced across runs, a prerequisite for run-wise MVPA. Data quality could not be assessed in trials in which data quality was bad or data was missing (included in the analysis). Feet were uncrossed in runs 1-3 and 7-9. Feet were crossed in runs 4-6 and 10-12.

Preprocessing of imaging data. Functional MRI data were preprocessed and analyzed with the software Statistical Parametric Mapping (SPM12, (Statistical Parametric Mapping; http://www.fil.ion.ucl.ac.uk/spm/), running on MATLAB R2015a (The MathWorks, Natick, USA). The first four volumes of each run were discarded to allow for spin saturation. Functional data were corrected for susceptibility artifacts, as well as rigid body motion by unwarping and alignment to the first image of the first session. Then, functional images were corrected for differences in acquisition time and the individual T1 image was co-registered to the mean functional image generated during realignment.

Multivariate imaging analysis. To determine whether multivariate patterns of brain activation allow to differentiate orthogonal tactile and movement locations during touch localization and planning delay, we used a pattern classification approach. To this end, we constructed participant-level GLMs, optimized for subsequent classification. This entailed basing the GLMs on data in participant space; that is, modeling non-normalized and non-smoothed data, as the spatial interpolations inherent in normalization and smoothing might degrade meaningful activation patterns (Hebart, Görgen, & Haynes, 2015). Participant-level GLMs included 23 predictors, which modeled experimentally induced variance. There were 2 baseline predictors (foot posture: uncrossed vs. crossed) modeling fixation delays at the beginning of each trial, as well as before and after each run. The model further included 4 predictors for the touch localization delay (foot posture: uncrossed vs. crossed x stimulated foot: left vs. right), 8 predictors for planning delay and 8 predictors for execution delay (foot posture: uncrossed vs. crossed x stimulated foot: left vs. right x instructed movement: pro vs. anti). Lastly, a predictor for error trials, which were contaminated by saccades or hand movements toward the wrong location was included whenever necessary. We modeled each run separately, resulting in 12 unique predictors per run, because foot posture was alternated between runs. Predictors were modeled with delta functions marking the onsets of the particular delay, which were in turn convolved with the canonical hemodynamic response function. Baseline drifts within a run were accounted for by applying a high-pass filter (128 s). Serial dependency within a run was accounted for by application of an autoregressive autocorrelation model (model order=1).

Run-wise β-images for the different delays and experimental conditions estimated within the GLM and reflecting the voxel-wise amplitude of the hemodynamic response function were used for pattern classification performed with The Decoding Toolbox (Hebart et al., 2015). We used a L2-norm support vector machine (SVM) as classifier in the implementation of LIBSVM (Chang & Lin, 2011), with a fixed cost of c=1. For whole-brain unbiased voxel selection, we applied a spherical searchlight with a radius of 4 voxels (Kriegeskorte et al., 2006). On each classification fold, input patterns from run-wise β-images were extracted and used to train the classifier to differentiate between two classes (e.g., movement goal left vs. movement goal right). Then, the classifiers' performance was validated on patterns of an independent run, that is, a run that had not been used during training. These steps were repeated until data from each run served as a validation test run once, while all other runs were used to train the classifier (11 runs for training, 1 run for testing; leave-one-run-out cross validation design). We implemented a leave-two-run out cross validation design whenever necessary, for example, when classifiers were trained and tested on a subset of conditions (e.g., *Figure 3.2*: classifier 7; 4 runs for training, 2 runs for testing). As a measure of the overall generalization performance of the classifier, the mean decoding accuracy across all classification iterations was stored at the center voxel of the current searchlight. This procedure was repeated for all voxels in the brain, resulting in a whole-brain map of averaged decoding accuracies for both classes across all test runs. Participant-level accuracy maps were normalized to MNI space based on the transformation parameters obtained during segmentation of the T1 image and smoothed with a 6 mm Gaussian kernel for group-level statistical analysis. Across participants and for each classifier, we tested which brain voxels contained accuracy values that differed significantly from zero using a one-sample t-test (Haxby et al., 2001; Haynes et al., 2007). Significance was determined using whole-brain cluster based permutation tests using an initial threshold of $p<.001$ and a secondary family-wise-error correction rate of $p<.05$ (FWE; Nichols & Holmes, 2002). Voxels that survive this correction for multiple comparisons indicate locations where the decoding accuracy of the classifier is significantly better than chance for the differentiation between the two tested classes. Put differently, multivariate patterns surrounding the identified voxels contain information about the differentiation between the two classes of interest, which is interpreted as their feature representation (Haxby et al., 2014; Haynes, 2015; Haynes & Rees, 2006; Kaplan et al., 2015; Kriegeskorte, 2009; Kriegeskorte et al., 2006; Norman et al., 2006).

We implemented two different classification modes, which differed according to whether training and test data came from independent runs of the same delay (within-condition classification), or from independent runs of different delays (cross-condition classification).

During within-condition classification, we tested whether binary classifiers trained to differentiate brain activation patterns related to orthogonal (left and right) tactile and movement locations within a given delay, would be able to decode the correct location in independent test data from the same delay. Successful decoding, that is, above chance prediction of a location in a significant number of voxels during testing, is indicative of information about tactile or movement coordinates being represented in a given activation pattern. If classification within the touch localization delay was successful, we furthermore examined whether the contained information was consistent across touch localization and planning delay (cross-condition classification; Kaplan et al., 2015). Note that successful within-condition classification is a necessary prerequisite for cross-condition classification, as testing for consistency of information is meaningless if information is not detected in the first place (Barany, Della-Maggiore, Viswanathan, Cieslak, & Grafton, 2014). Consistency of information was tested by training classifiers to dissociate tactile coordinates during the touch localization delay and testing their decoding performance in independent data from the planning delay. Above chance cross-condition classification from localization to planning delay is indicative of a stable representation of tactile coordinates, invariant across sequential touch localization and movement planning delays. In contrast, unsuccessful cross-condition classification is indicative of a variable, or alternatively, of a non-existent, representation of tactile coordinates. If the representation is variable, then the pattern during planning cannot be predicted from the activation pattern during the touch localization delay. Crucially, a variable representation would nonetheless entail successful classification of activity patterns separately for touch localization and planning delay as within-condition classification, reflecting that the information is present in both, but that its format changes between trial phases. Alternatively, if tactile coordinates are not represented during the planning delay, this would entail unsuccessful cross-condition classification of tactile coordinates along with unsuccessful within-condition classification within the planning delay.

Classifications and subsumed experimental conditions which aimed to identify multivariate patterns associated with tactile and movement coordinates are illustrated in *Figure 3.2* and *Figure 3.3*. For each participant, 16 classifiers were trained and tested in total, 6 to decode tactile coordinates, 1 to decode movement coordinates, 1 to decode movement instruction representations, and 8 to decode foot posture representations. Visualizations are based on surface-based mapping of 3D activations onto an inflated atlas brain using the Computerized Anatomical Reconstruction and Editing Toolkit (Caret; Van Essen, 2012; Conte-69 atlas; Van Essen, Glasser, Dierker, Harwell, & Coalson, 2012).

Regions of interest (ROI). For visualization of single subject decoding accuracies determined with the MVPA, we extracted accuracies confined to ROIs. This approach acknowledges that there might be anatomical and/or functional variability across individuals regarding the location of representations (adapted from: Ariani et al., 2015; Oosterhof et al., 2012). First, we defined ROIs based on the group-level t-map of significant above chance decoding accuracies. If these clusters were limited to local, separate clusters, ROIs were centered on the peak voxel/s using a sphere with a radius of 6 mm. If clusters were large and spanned multiple, presumably functionally diverse areas, ROIs within clusters were extracted based on theoretical considerations and results reported by previous studies. Second, we extracted single subject decoding accuracies within each ROI and identified the voxel with the highest decoding accuracy. Lastly, we constructed new, participant-specific ROIs around the identified peak voxel, using a sphere with a radius of 6 mm. Some ROIs overlapped partially, and were therefore combined whenever they spanned a similar anatomical location and showed similar means and variances of decoding accuracies across subjects. Single subject means and boot strapped confidence intervals of decoding accuracies within each ROI, as well as their grand mean across participants, were calculated with the Hmisc package (Harrell Jr, 2016) in R (R Core Team, 2016) and visualized using ggplot2 (Wickham, 2009). ROIs were linked to structural brain regions using the anatomy toolbox for SPM (Eickhoff et al., 2005) and labeled based on previous related studies (Gallivan & Culham, 2015).

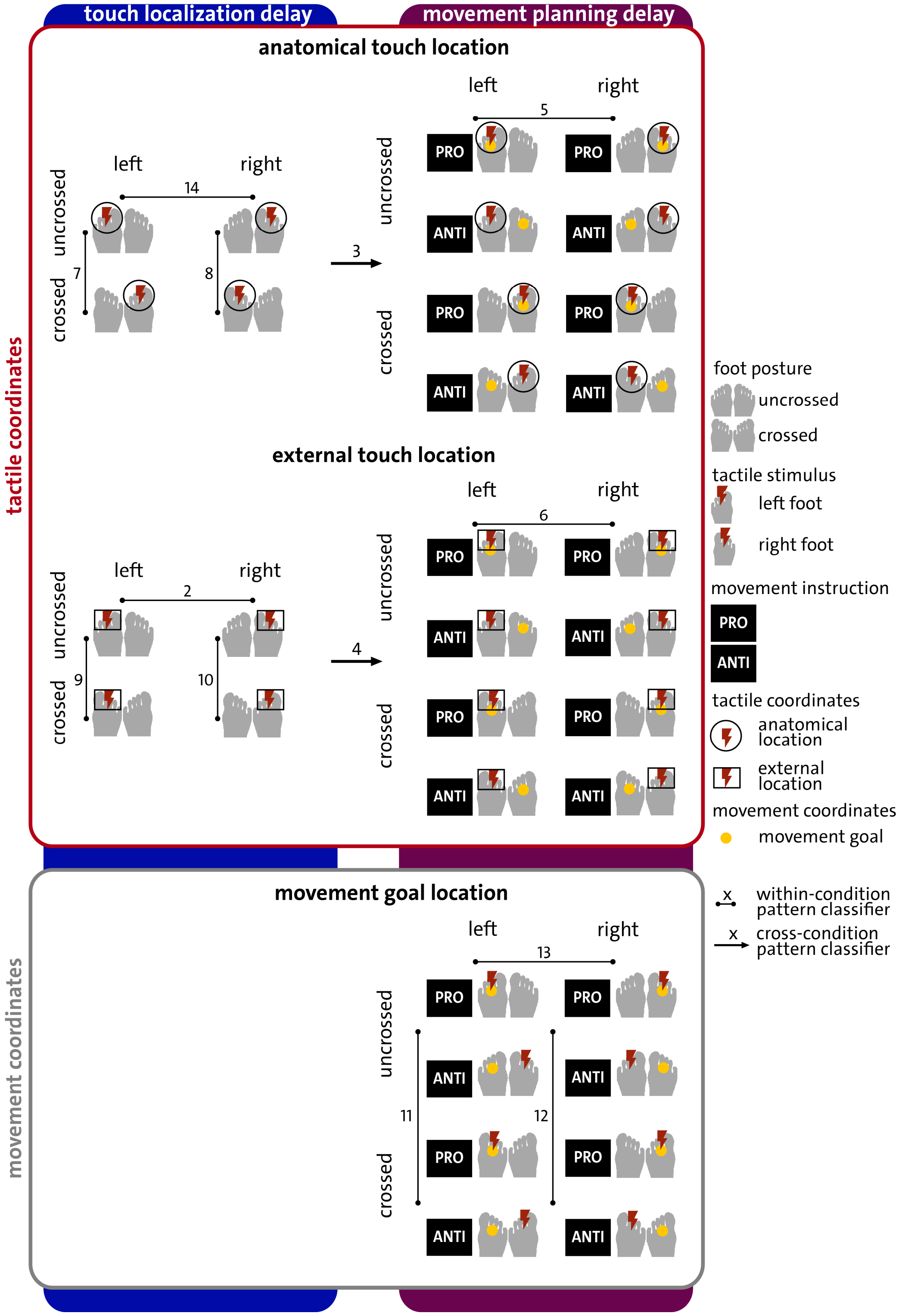


Figure 3.2. Within- and cross-condition classifications and subsumed experimental conditions identifying tactile (top panel: red outlines) and movement coordinates (bottom panel: grey outlines) within the touch localization (left panel: blue background) and planning (right panel: purple background) delay, as implemented in the MVPA.

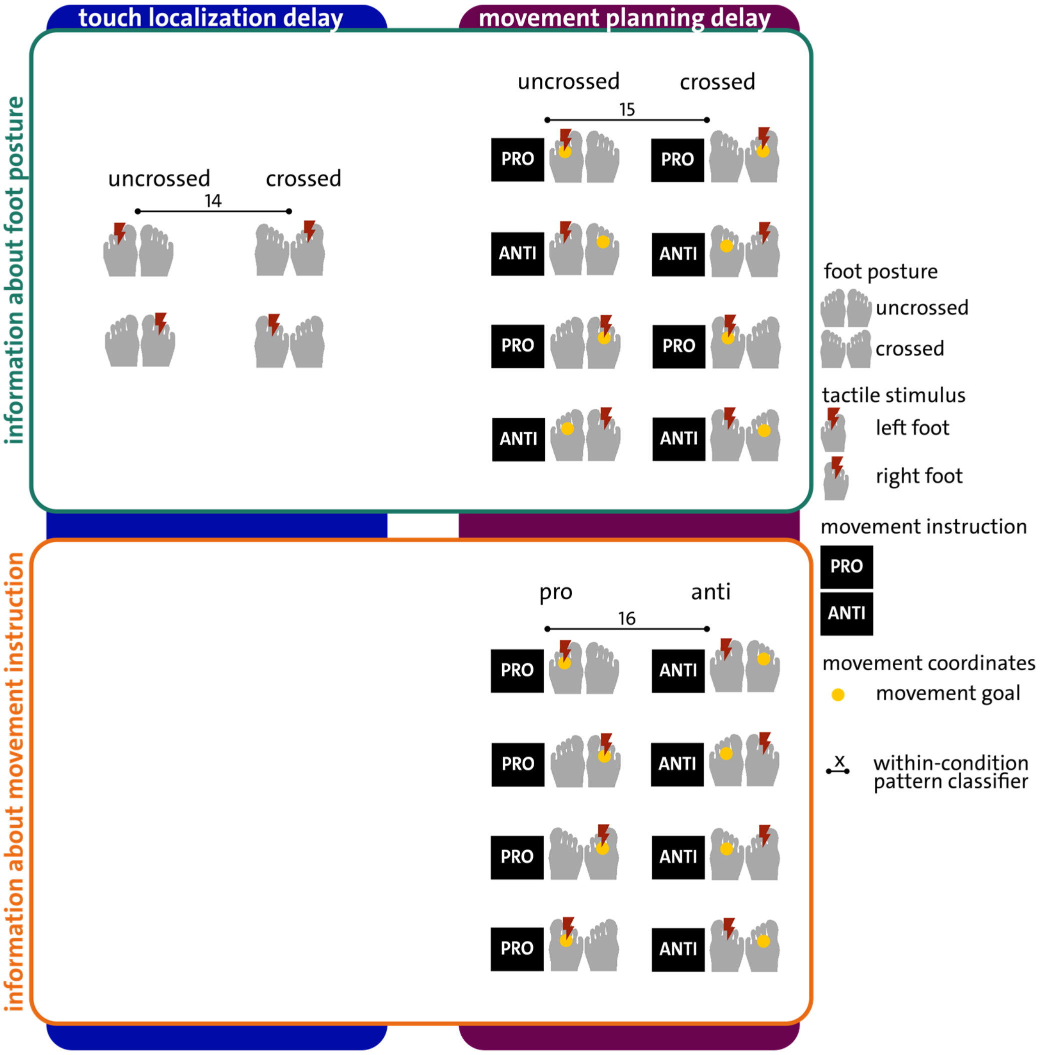


Figure 3.3: Within-condition classifications and subsumed experimental conditions identifying information about foot posture (top panel: turquoise outlines) and the movement instruction (bottom panel: orange outlines) within the touch localization (left panel: blue background) and planning (right panel: purple background) delay, as implemented in the MVPA.

Univariate imaging analysis. Our analysis focused on quantifying multivariate patterns, but to facilitate comparison of results with previous studies, we additionally implemented a classical, univariate analysis. Thus, to determine whether univariate levels of brain activation allow to differentiate orthogonal tactile and movement locations during touch localization and planning delay, we used a GLM approach. To this end, we constructed participant-level GLMs, optimized for subsequent univariate activation analysis. In addition to the preprocessing steps outlined above, T1 images were segmented and the resulting transformation parameters were used to spatially normalize EPI and T1 images to MNI space. EPI images were smoothed with a 6 mm Gaussian kernel. Participant-level GLMs included the same predictors as the GLM optimized for the multivariate analysis, however, here, predictors and functional images of each run were concatenated and 12 run constants were modelled, instead of modeling each run separately. Predictors were fitted with delta functions marking the onsets of the particular delay, which were in turn convolved with the canonical hemodynamic response function. Baseline drifts within a run were accounted for by applying a high-pass filter (128 s). Serial dependency within a run was accounted for by application of an AR (1) autocorrelation model. β-images for the different delays and experimental conditions were used to compute participant-level contrast images. This entailed voxel-wise subtraction of β-images to isolate activation pertaining to tactile and movement coordinates, as well as posture and movement instructions. Across participants and for each contrast, we tested which brain voxels contained values that differed significantly from zero using a one-sample t-test (A. P. Holmes & Friston, 1998). Significance was determined using whole-brain cluster based permutation tests using an initial threshold of $p<.001$ and a secondary FWE correction rate of $p<.05$ (Nichols & Holmes, 2002). Voxels that survived this correction for multiple comparisons indicate significant voxel-wise activation in one tested condition over another.

Contrasts and the subsumed experimental conditions identifying activation associated with tactile and movement coordinates can be deducted from *Figure 3.2*, which illustrates related classifications implemented in the MVPA. For each illustrated within-condition classification, decoding for example the left vs. right movement goal, we computed two related activation contrasts, here, one identifying activation associated with the left movement goal and another contrast identifying activation associated with the right movement goal. Thus, for each participant, we computed 28 contrasts in total, twice as many as there were within-condition classifications. In correspondence to the MVPA, 8 contrasts aimed to isolate activation associated with tactile coordinates, 2 with movement coordinates, 2 with movement instructions, and 16 with foot postures. In addition, we computed 2 contrasts which aimed to identify general activation associated with touch localization and sensorimotor planning.

3.3.2 Part 2 | behavioral experiment: Temporal order judgment (TOJ)

Experimental design. We aimed to link the coding of tactile coordinates to a typical behavioral efficiency measure of touch localization to test whether the neural implementation of touch localization for action identifies a coding mechanisms that generalizes to behavior measured using a perceptual task. A link across sensorimotor planning and perception would indicate that similar mechanisms of touch localization are at play, although the tasks contexts are different. To that aim, participants completed a TOJ (Shore et al., 2002; Yamamoto & Kitazawa,

2001) of two tactile stimuli. Tactile stimuli were presented successively to both index fingers on each trial. Hands were held in either an uncrossed or a crossed posture. Participants responded by pressing the button located below the respective index finger. Thus, the experiment comprised two within-subject factors. The factor hand posture (levels: uncrossed vs. crossed) varied every other block and the start posture was counterbalanced between participants, while the factor stimulated hand varied pseudo-randomly from trial to trial (levels: left vs. right). In addition, stimulus onset asynchrony was varied trial-wise (levels: -300, -200, -110, -80, -50, 50, 80, 110, 200, 300, with negative SOA indicating "left hand first"-stimuli). Each of the 40 combinations of the three experimental factors was presented 12 times during the experiment.

Materials and apparatus. Participants sat at a table with their hands and elbows resting comfortably in front of their body. Hands were positioned 30 cm apart, either in an uncrossed or crossed posture. Tactile stimulators (Oticon bone conductors, type BC 461-012, sized about 1.6 x 1 x 0.8 cm) were attached to the index fingers, just below the fingernails. Stimulators were driven with a frequency of 200 Hz for 15 ms. Both index fingers rested on response buttons. The button located below the finger that had been stimulated first had to be depressed. Responses had to be withheld until the last stimulus had been applied. No feedback was provided during the experiment. To mask sound elicited by the stimulators, participants wore ear plugs and white noise was presented through head phones. Instructions were presented on a monitor located in front of the participants. Eyes were opened throughout testing and participants fixated a cross displayed on screen.

Procedure. The experiment started with 5 practice trials (SOA: 900 ms) to familiarize participants with the task. Posture was varied after 3 Blocks and 5 practice trials in the new posture were completed before testing began. Each trial lasted 5000 ms and the inter-trial interval was set to 1000 ms. Participants were encouraged to rest between blocks. The experiment lasted about 20 minutes in total and was divided into 6 Blocks of 80 trials each.

Data selection and analysis. Trials were excluded from the analysis if the RT was shorter than 150 ms or longer than the mean plus 3 standard deviations (8% of all trials). Responses were transformed into "right hand first"-responses, indexing whether the anatomically right hand was judged to have been stimulated first or not. A probit analysis was conducted, using SOAs from -150 to 150 to adhere to the assumption of normality inherent in the analysis (e.g., Heed, Backhaus, & Röder, 2012; Shore et al., 2002). This analysis resulted in regression slopes per participant and crossing status. Steeper slopes indicate better localization performance. As a measure of the crossing effect, the slope of the regression line from the crossed condition was subtracted from that of the uncrossed condition (slope_{CE}: $\text{slope}_{\text{uncrossed}}$ - $\text{slope}_{\text{crossed}}$). As a second measure of the crossing effect, behavioral accuracies from the crossed condition were subtracted from those of the uncrossed condition ($\text{accuracy}_{\text{CE}}$: $\text{accuracy}_{\text{uncrossed}}$ - $\text{accuracy}_{\text{crossed}}$).

Linking the coding of tactile coordinates to a behavioral efficiency measure of touch localization in the TOJ task. We hypothesized that tactile representations during the sensorimotor task would be linearly related to the behavioral efficiency of perceptual touch localization in the TOJ task. In preparation of the analysis, we operationalized the relative strength of anatomical and external coordinate representations as voxel-wise activation differences, as these have previously been linked to behavioral TOJ performance in another related investigation (Wada et al., 2012) and, more generally, have successfully been linked to behavior in other fMRI studies (e.g., Amedi, Raz, Pianka, Malach, & Zohary, 2003). However, in the present study, the univariate analysis did not reveal global activation differences associated with anatomical or external touch coordinates. Instead, anatomical and external coordinates were reflected in multivariate activation patterns changes. Yet, deriving an equivalent operationalization for the multivariate analysis is not trivial, because it is not obvious how, or if at all, the relative strength of anatomical and external coordinate representations is related to the decoding accuracy derived during classification. We reasoned that a strong or salient representation of anatomical or external information should be reflected in a high proportion of voxels displaying an elevated decoding accuracy. Put differently, we hypothesized that the strength of a representation is reflected in the proportion of voxels with high informational content. Therefore, as a first operationalization, we computed for each participant p and ROI r from the touch localization delay, the percentage of voxels that exhibited a higher decoding accuracy than the mean decoding accuracy across all participants and ROIs representing either anatomical or external information ($\text{decoding}_{\text{percent}}\, p, r$). As an alternative operationalization, we computed the mean decoding accuracy per participant p and ROI r ($\text{decoding}_{\text{mean}}\, p, r$). These two measures may potentially represent the strength of anatomical and external representations, but do not index their relation. To derive a relative measure, decoding accuracies from both classifications could be subtracted or divided. However, it is not obvious how voxels should be selected and organized for such computations that are based on measures derived from all voxels within a

ROI, given that ROIs are of different size and spatially non-overlapping between anatomical and external classifications. The strength of a representation might even be unrelated to measures that are based on all voxels within a ROI, but instead might be best captured by the decoding accuracy of the peak voxel. Accordingly, we extracted for each participant *p* and ROI *r* from the touch localization delay, the peak decoding accuracy ($\text{decoding}_{\text{peak}}\ p, r$). Note that the derived measures depend on the noise evident in the decoding accuracy, which might vary considerably across ROIs and participants. In an exploratory attempt to derive a relative measure of the strength of anatomical and external coordinate representations that is independent of participant-specific noise, we subtracted for each participant *p* the peak decoding accuracy in R-mIPS representing external coordinates from the peak decoding accuracies extracted from all ROIs representing anatomical coordinates r_{anat} ($\text{decoding}_{\text{diff}}\ p, r_{anat}$). Next, for each ROI and measure ($\text{decoding}_{\text{percent}}$, $\text{decoding}_{\text{mean}}$, $\text{decoding}_{\text{peak}}$, $\text{decoding}_{\text{diff}}$), we calculated the Pearson product moment correlation with two behavioral measures of the crossing effect in the TOJ task (slope_{CE}, $\text{accuracy}_{\text{CE}}$). There were 54 correlations in total, namely we correlated 4 saliency measures from 6 anatomical ROIs with 2 behavioral measures and 3 saliency measures from 1 external ROI with 2 behavioral measures. To determine whether correlations were significantly greater or smaller than zero, we calculated two sided t-tests, as Pearson correlation coefficients follow a t-distribution with the number of samples minus 2 degrees of freedom. Significant p-values are reported at an alpha level corrected for multiple comparisons using the Bonferroni method (corrected alpha level at $p<.05/54=.001$). Note that, for this analysis, we collapsed the data from right and left S1 (anatomical ROI), as we had no hypothesis about corresponding functional areas from two hemispheres differing in their association with the behavioral measures from the TOJ task.

3.4 Results

3.4.1 Univariate results

A classical, univariate analysis tests whether voxel-wise subtraction of one class A (e.g., tactile stimulus at the left foot) from another class B (e.g., tactile stimulus at the right foot) of a common condition of interest (e.g. anatomical touch location) results in significant voxel-wise activation. Consistent with previous reports, we interpret significant voxel clusters resulting from this analysis to be involved in general processing of the condition of interest, because the two tested classes differ in the evoked voxel-wise activation level.

3.4.1.1 Activation differences associated with touch localization and tactile sensorimotor planning

Results from the univariate analysis are illustrated in *Figure 3.4*. To identify global activation changes related to touch localization, we added the voxel-wise activation across all predictors from the touch localization delay (foot posture: uncrossed vs. crossed x stimulated foot: left vs. right) and subtracted the sum of the voxel-wise activation across all baseline predictors (foot posture: uncrossed vs. crossed x fixation). Voxels that displayed larger activations during touch localization than baseline are illustrated in *Figure 3.4A*. Voxels displaying significant activation spanned a large bilateral network, covering great portions of the parietal and frontal cortices. Next, to identify global activation changes related to sensorimotor planning, we added the voxel-wise activation across all predictors from the movement planning delay (foot posture: uncrossed vs. crossed x stimulated foot: left vs. right x movement instruction: pro vs. anti) and subtracted the sum of the voxel-wise activation across all baseline predictors (foot posture: uncrossed vs. crossed x fixation). Voxels that displayed larger activations during movement planning than baseline are illustrated in *Figure 3.4B*. This comparison too revealed a large bilateral network, covering M1 and parietal areas. Consistent with right hand movement planning, activation clusters in the left hemisphere were larger than in the right hemisphere.

The previous contrasts identified touch localization- and movement planning-related activation irrespective of touch locations in anatomical and external coordinates and movement goals. Next, we aimed to identify activation changes associated with anatomical and external touch locations, movement goals, foot postures and movement instructions. Of these contrasts only one revealed significant activation changes that were associated with the right as compared to the left movement goal and spanned a small cluster in bilateral SMA (*Figure 3.4*C). In the left hemisphere, the anterior SPL was activated laterally and medially, as well M1 and dorsal premotor cortex (PMd).

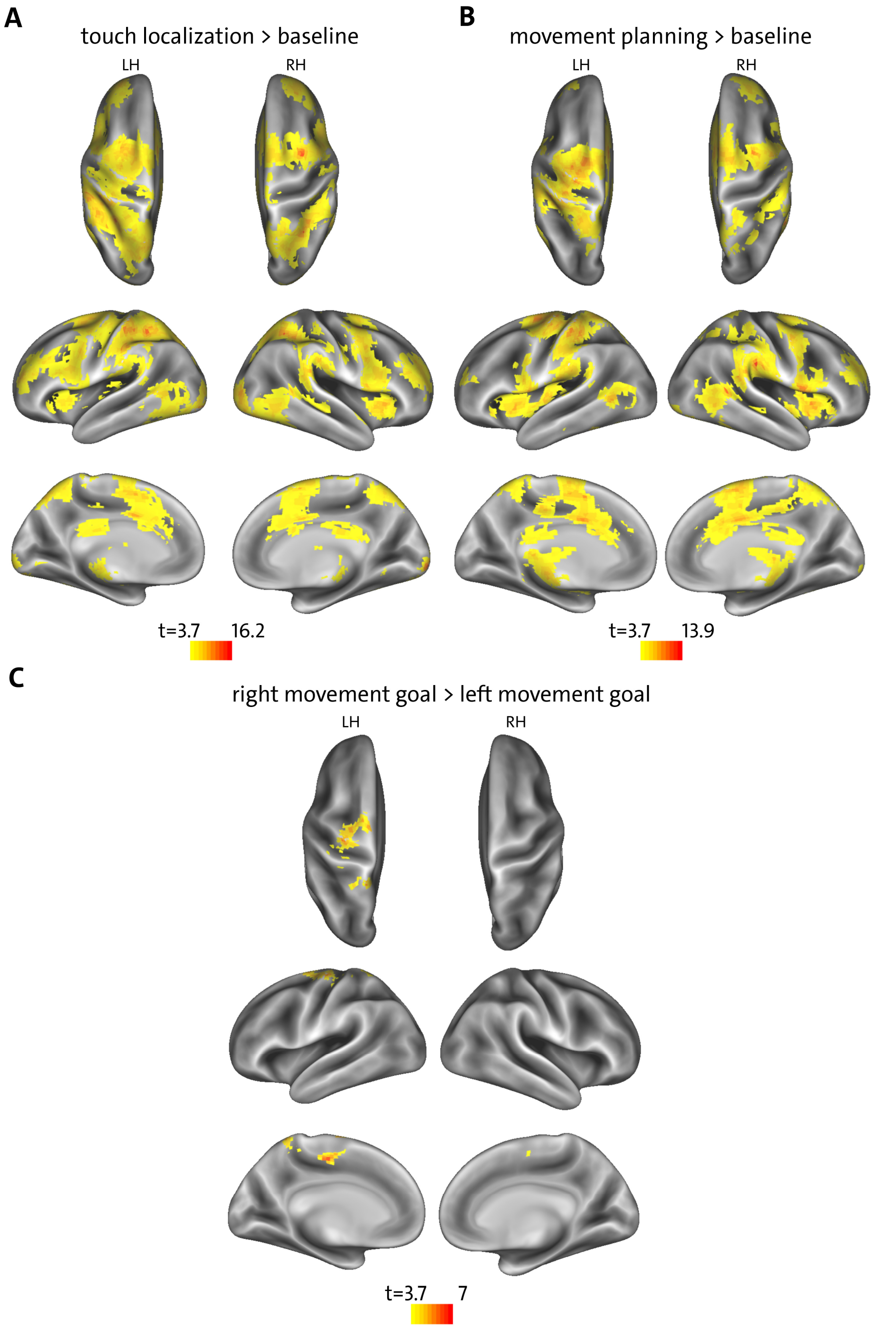


Figure 3.4: Results of the univariate imaging analysis. Statistical maps representing significant group-level activation differences corrected for multiple comparisons using a cluster-based permutation test (FWE, p<.05) are illustrated for three different contrasts. Warmer colors represent higher t-values. LH, left hemisphere; RH, right hemisphere. *A.* Higher relative activation associated with touch localization as compared to baseline. *B.* Higher relative activation associated with movement planning as compared to baseline. *C.* Higher relative activation associated with movement planning toward a right movement goal as compared to movement planning toward a left movement goal (see *Figure 3.2* bottom panel for subsumed experimental conditions).

3.4.2 Multivariate results

In contrast to a univariate analysis approach, MVPA tests whether a classifier trained to dissociate brain activation patterns observed during class A (e.g., tactile stimulus at the left foot) vs. class B (e.g., tactile stimulus at the right foot) of a common condition of interest (e.g., anatomical touch location), is able to significantly predict the correct class label from data patterns which have not been used during classifier training. Consistent with previous reports, we interpret significant voxel clusters resulting from this analysis to represent the condition of interest, because they contain information about the difference between the respective classes.

3.4.2.1 Tactile coordinates are maintained as long as they are relevant

We hypothesized that tactile information, that is, anatomical and external touch locations, is represented in activity patterns measured during the touch localization delay, that is, at a time when sensory information is available, but the movement goal is not yet specified. Results pertaining to the representation of tactile coordinates are illustrated in *Figure 3.5* (anatomical touch location) and *Figure 3.6* (external touch location).

Within-condition classification of anatomical touch location, that is, coding whether the left or right foot was stimulated, during the touch localization delay revealed a network covering the medial bank of bilateral S1, very lateral right inferior parietal lobule (IPL) bordering secondary somatosensory cortex (S2) and spreading into S1 and M1, right PMd, left insula spreading into the superior temporal gyrus (assigned label: L-ins), and left anterior SPL (*Figure 3.2*; classifier 1; *Figure 3.5A*). *Figure 3.5B* shows the identified ROIs within these clusters. Average ROI coordinates across participants are displayed in *Table 3.2*. The grand mean above chance decoding accuracy of anatomical coordinates per ROI ranged from 53.8% to 55.0% with participant-level confidence intervals covering ranges from 0.3% to 2.0% (*Figure 3.5C*). To facilitate comparisons of decoding accuracies across classifications, all figures showing individual decoding accuracies are displayed with the same y axis limits (e.g., *Figure 3.5C*).

Within-condition classification of external touch locations during the touch localization delay revealed a single right-lateralized cluster confined to the mIPS (*Figure 3.2*; classifier 2; *Figure 3.6A*). *Figure 3.6B* shows the identified ROIs within this cluster. Average ROI coordinates across participants are displayed in *Table 3.2*. The grand mean above chance decoding accuracy of external coordinates in mIPS was 54.4% with participant-level confidence intervals covering ranges from 0.4% to 1.4% (*Figure 3.6C*).

As both within-condition classifications revealed significant clusters showing above chance decoding accuracies during the touch localization delay, we next evaluated whether the maintained information about tactile coordinates would be stable and invariant during the planning delay. To this end, classifiers trained to differentiate between anatomical or external locations in the touch localization delay were tested on data from the planning delay (*Figure 3.2*; classifier 3: anatomical, classifier 4: external). Neither of these classifiers revealed significant above chance decoding of left and right anatomical or external touch locations across delays. To scrutinize whether cross-condition classification fails because the format of tactile information changes across delays, or if, alternatively, there is no evidence for maintenance of tactile coordinate once the movement goal is known, we trained two classifiers to differentiate anatomical or external target locations within the planning delay (within-condition classification; *Figure 3.2*; classifier 5: anatomical, classifier 6: external). Again, neither of these classifiers revealed significant multivariate patterns coding the difference between anatomical or external touch locations.

Thus, we did not find any evidence for the maintenance of tactile coordinates in multivariate activation patterns once the movement goal is known. Rather, representations of anatomical and external tactile coordinates appear to be confined to the touch localization delay; each spatial code appears to be prevalent in distinct regions and we did not observe any overlap between the regions coding either reference frame. In sum, it appears that tactile coordinates are maintained as long as they are relevant for tactile localization. In contrast, evidence is scarce that tactile coordinates are maintained as soon as the movement goal is known and tactile coordinates have been transformed to movement coordinates.

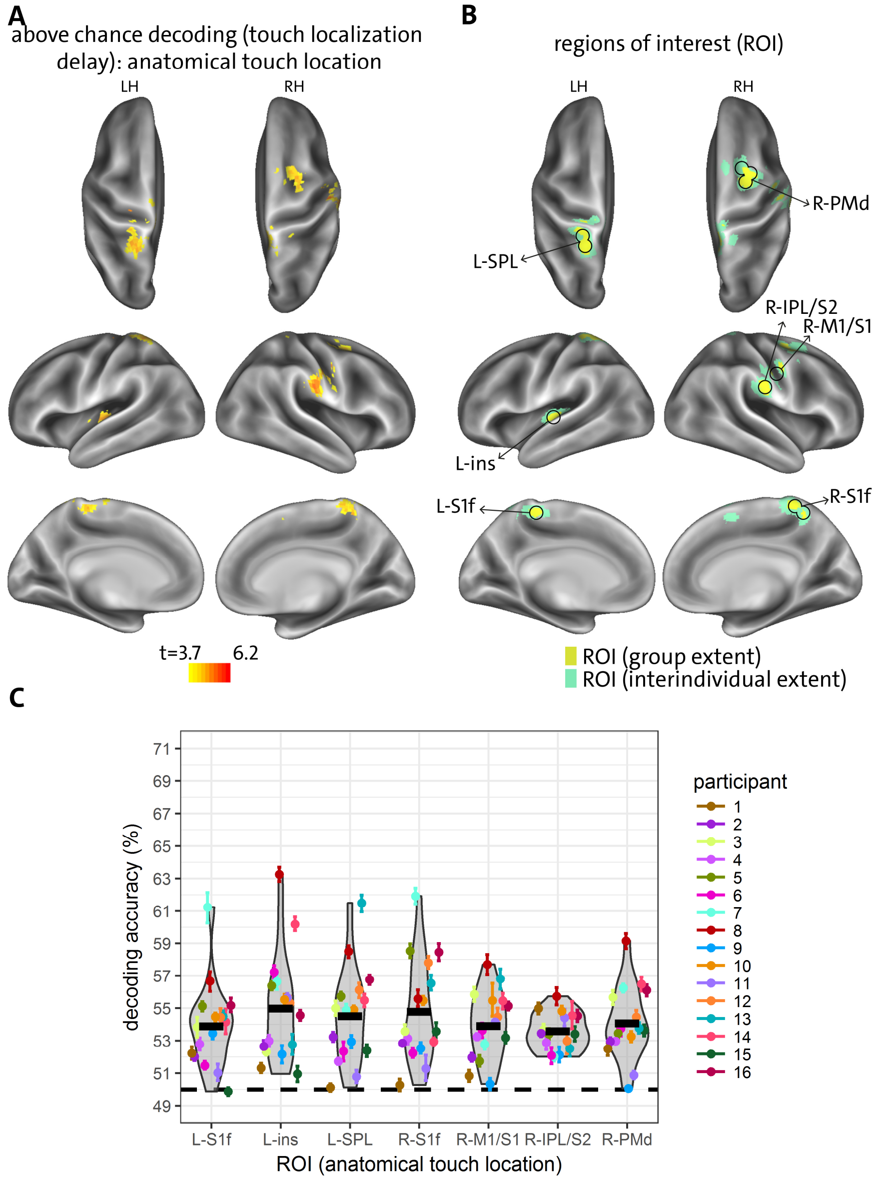


Figure 3.5: Results of the multivariate imaging analysis pertaining to the representation of anatomical touch locations during the touch localization delay. *A.* Statistical maps representing significant group-level above chance decoding accuracies of anatomical touch coordinates corrected for multiple comparisons using a cluster-based permutation test (FWE, p<.05; see *Figure 3.2* top left panel for subsumed experimental conditions). Warmer colors represent higher t-values. LH, left hemisphere; RH, right hemisphere. L-S1f, foot area of left primary somatosensory cortex; L-ins, left insula; L-SPL, left superior parietal lobule; R-S1f, foot area of right primary somatosensory area; R-M1/S1, right primary motor cortex/ primary somatosensory cortex; R-IPL/S2, right inferior parietal lobule/ secondary somatosensory cortex, R-PMd, right dorsal premotor cortex. *B.* Regions of interest identified based on the group-level statistical map shown in A and verified on an individual basis. The extent of the initially identified group ROI is shown in yellow, while the interindividual ROI extent is displayed in green. *C.* Violin plots illustrating the distribution of decoding accuracies across subjects per ROI (grey shading, black outlines). Decoding accuracy at chance (50%) is shown as dashed black line and single subject means and boot strapped confidence intervals of decoding accuracies within each (combined) ROI are shown as color-coded points and error bars. The grand mean decoding accuracy per ROI across participants is shown as black horizontal bar. Axis limits are equal to those in corresponding plots in *Figure 3.6C*, *Figure 3.7C*, and *Figure 3.8C* to facilitate comparisons across different classifications.

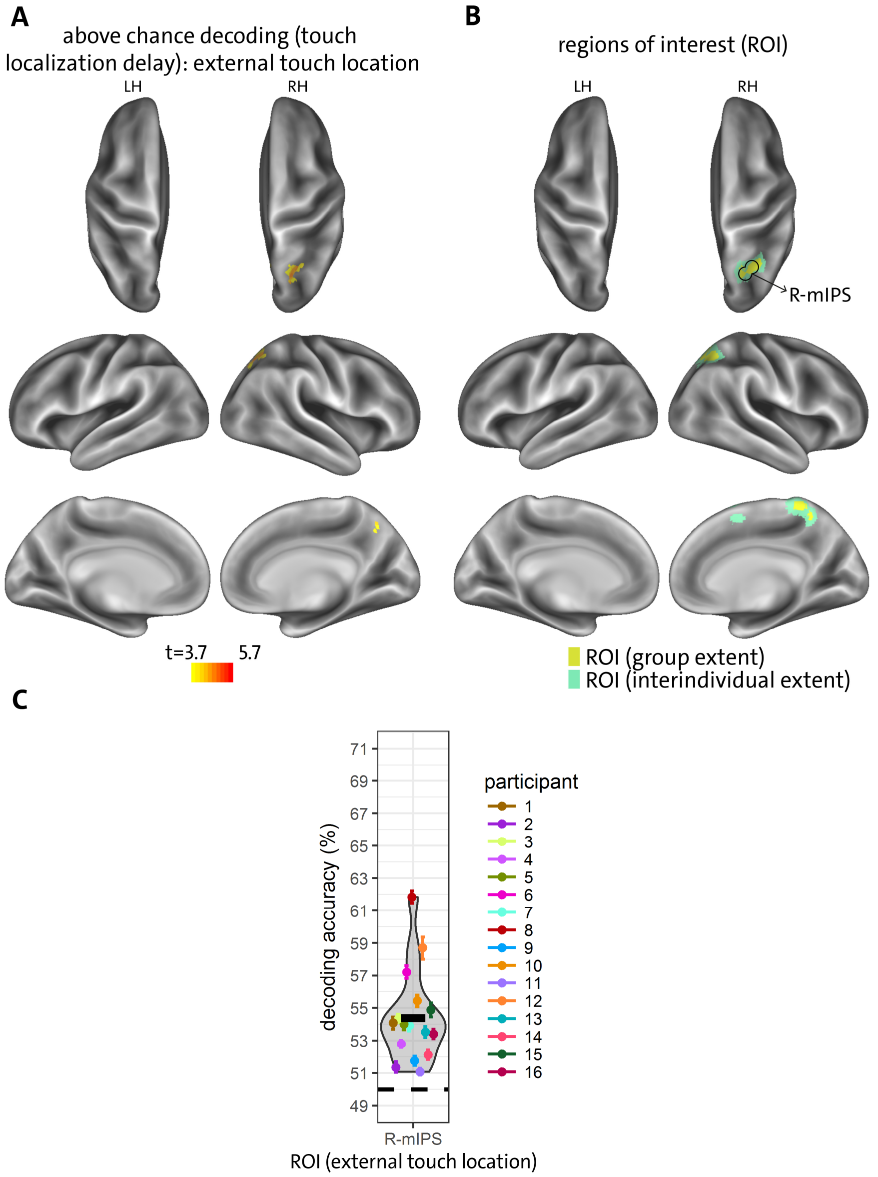


Figure 3.6: Results of the multivariate imaging analysis pertaining to the representation of external touch locations during the touch localization delay. R-mIPS, right medial intraparietal sulcus. All other details are equivalent to those in *Figure 3.5*. *A.* Statistical maps representing significant group-level above chance decoding accuracies of external touch coordinates corrected for multiple comparisons using a cluster-based permutation test (FWE, p<.05; see *Figure 3.2* middle left panel for subsumed experimental conditions). *B.* Regions of interest identified based on the group-level statistical map shown in A and verified on an individual basis. *C.* Violin plot illustrating the distribution of decoding accuracies across subjects in right mIPS.

	Hemisphere-ROI	Mean			Standard Error		
		x	y	z	x	y	z
Anatomical touch locations	L-S1f	-5.6	-37.4	60.3	0.7	0.9	0.5
	L-ins	-35.8	-23.9	5.9	0.7	0.8	0.8
	L-SPL	-21.1	-43.3	64.2	0.4	0.3	0.7
	R-S1f	8.4	-42.2	63.1	0.5	0.4	0.4
	R-M1/S1	58.7	-16.9	28.4	0.7	0.9	0.6
	R-IPL/S2	50.6	-10.9	41.0	0.7	0.9	0.5
	R-PMd	23.9	-0.3	50.6	0.5	0.5	0.3
External touch locations	R-mIPS	24.8	-59.2	51.3	0.5	0.5	0.6
Movement goal	L-M1h	-31.7	-21.6	63.9	0.7	0.9	0.5
	L-S1h	-30.8	-29.3	50.8	0.6	0.9	0.7
	L-S1f	-3.6	-45.8	57.1	0.9	0.6	0.8
	L-PMd	-26.4	-7.8	60.5	0.6	0.8	0.8
	L-SMA	-7.9	-6.8	55.4	0.7	0.8	0.8
	L-preSMA	-10.1	-6.6	46.6	0.7	0.7	0.8
	L-aIPS	-34.9	-35.8	45.9	0.4	0.7	0.6
	L-SPL	-16.7	-53.3	59.0	0.4	0.3	0.4
	L-SPOC	-14.9	-79.9	37.2	0.5	0.4	0.6
	R-M1h	33.0	-21.8	64.4	0.6	1.1	0.5
	R-S1h	29.6	-30.4	51.3	0.7	0.8	0.6
	R-S1f	4.3	-45.4	56.2	0.8	0.6	0.7
	R-PMd	26.6	-7.9	62.0	0.6	0.9	0.7
	R-SMA	6.0	-6.6	55.6	0.5	0.8	0.7
	R-SPL	13.1	-55.3	56.5	0.4	0.4	0.5
	R-V5	39.0	-65.7	17.2	0.7	0.7	0.8
Movement instruction	L-SPL	-14.5	-58.2	58.3	0.2	0.5	0.4
	L-SPOC	-15.2	-77.5	46.6	0.8	0.5	0.7
	R-SPL	5.5	-59.4	55.1	0.7	0.5	0.5

Table 3.2: Mean and standard errors of ROI locations across participants (MNI coordinates) and grouped according to the classification which determined ROI selection and identification (anatomical touch locations; external touch locations; movement goal, movement instruction). In short, ROIs were initially selected based on significant above chance decoding on the group level, but then adjusted based on single-subject decoding accuracies (see methods for details). L, left hemisphere; R, right hemisphere. S1f, foot area of primary somatosensory cortex; ins, insula; SPL, superior parietal lobule; S1f, foot area of primary somatosensory cortex; M1/S1, primary motor cortex/ primary somatosensory cortex; IPL/S2, inferior parietal lobule/ secondary somatosensory cortex; PMd, dorsal premotor cortex; mIPS, medial intraparietal sulcus; M1h, hand area of primary motor cortex; S1h, hand area of primary somatosensory cortex; SMA, supplementary motor area; preSMA, pre-supplementary motor area; aIPS, anterior intraparietal sulcus; SPOC, superior parieto-occipital cortex; V5, middle temporal visual area.

3.4.2.2 Multivariate activation patterns do not code current foot posture

As the computation of external coordinates depends on the interaction with posture, we next tested whether posture is represented in addition to, and independent of, tactile and movement coordinates during the touch localization and planning delay.

In order to identify postural representations which are independent of tactile and movement coordinates, we implemented within-condition classifications that dissociate between uncrossed and crossed foot postures, separately for touch localization and planning delays (*Figure 3.3*, classifiers 14/15). Neither of these classifiers discovered significant multivariate patterns that coded information about foot posture anywhere in the brain. Put differently, classifiers trained to dissociate uncrossed and crossed foot postures were not able to significantly predict the correct foot posture in independent data, neither when training and testing occurred during the touch localization delay, nor when it occurred during the planning delay.

Alternatively, postural information might be coded dependent on tactile or movement coordinates. In order to identify postural representations which depend on tactile coordinates, we implemented within-condition sub-classifications dissociating between uncrossed and crossed foot postures separately for each anatomical and external touch location during the touch localization delay (*Figure 3.2*; classifiers 7/8: anatomical, classifiers 9/10: external). In correspondence, to identify postural representations that depend on movement coordinates, we implemented within-condition sub-classifications dissociating between uncrossed and crossed foot postures separately for each movement goal location during the planning delay (*Figure 3.2*; classifiers 11/12). Neither of these classifiers revealed significant multivariate patterns coding information about foot posture anywhere in the brain. In other words, a classifier trained to dissociate uncrossed and crossed foot postures when the touch was located at the left foot, for example, was not able to predict the foot posture in independent data from the same condition (anatomical touch location at the left foot).

Together, these results suggest that postural information is neither coded in multivariate patterns that are independent of tactile or movement coordinates, nor in multivariate patterns that depend on tactile or movement coordinates.

3.4.2.3 Tactile sensorimotor planning recruits a fronto-parietal network

We hypothesized that movement goal information is represented in activity patterns measured during the planning delay. Results pertaining to the representation of movement coordinates are illustrated in *Figure 3.8*.

Within-condition classification of movement goal locations during the planning delay revealed a network covering bilateral fronto-parietal areas including S1, M1, SMA, SPL, and PMd (*Figure 3.2*; classifier 13; *Figure 3.7A*). Although the cluster spanned areas within both hemispheres, the overall extent was larger, and the decoding accuracies were higher, in areas within the left hemisphere. Here, the network additionally covered regions along the IPS, as well as the parietal occipital sulcus (POS) and the pre-SMA. Within the right hemisphere, the network additionally covered parts of the occipital lobe. *Figure 3.7B* shows the identified ROIs within this cluster. Average ROI coordinates across participants are displayed in *Table 3.2*. The grand mean above chance decoding accuracy of movement coordinates per ROI ranged from 54.1% to 58.4% in the left, and from 53.8% to 58.0% in the right hemisphere, with participant-level confidence intervals covering ranges from 0.3% to 2.4% and from 0.3% to 2.6%, respectively (*Figure 3.7C*).

In sum, a fronto-parietal network spanning both hemispheres appears to be involved in the representation of movement goal information.

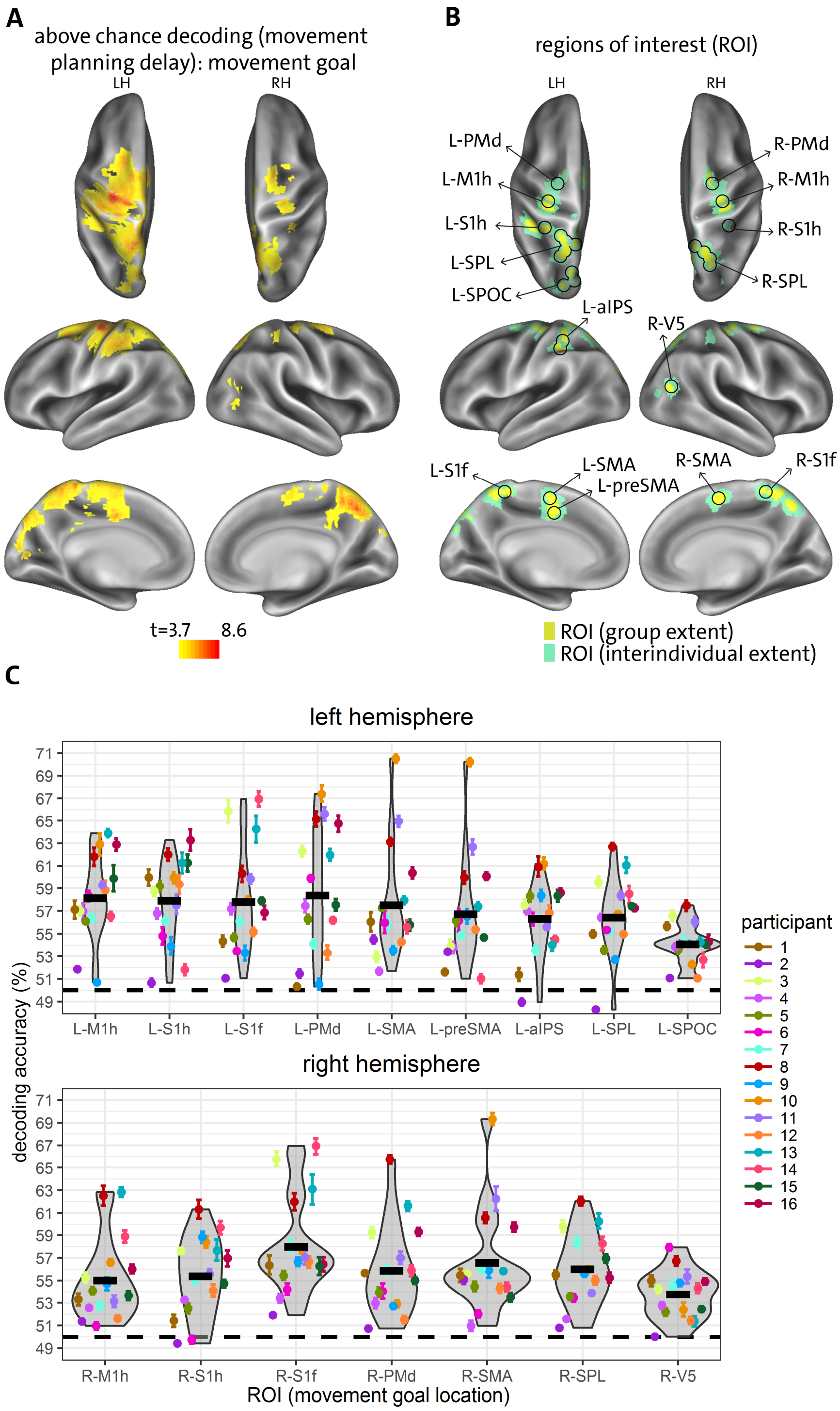


Figure 3.7: Results of the multivariate imaging analysis pertaining to the representation of the movement goal during the movement planning delay. L-M1h, hand area of left primary motor cortex; L-S1h, hand area of left primary somatosensory cortex; L-PMd, left dorsal premotor cortex; L-SMA, left supplementary motor area; L-preSMA, left pre-supplementary motor area; L-aIPS, left anterior intraparietal sulcus; L-SPL, left superior parietal lobule; L-SPOC, left superior parieto-occipital cortex; R-M1h, hand area of right primary motor cortex; R-S1h, hand area of right primary somatosensory cortex; R-PMd, right dorsal premotor cortex; R-SMA, right supplementary motor area; R-SPL, right superior parietal lobule; R-V5, right middle temporal visual area. All other details are equivalent to those in *Figure 3.5. A.* Statistical maps representing significant group-level above chance decoding accuracies of the movement goal corrected for multiple comparisons using a cluster-based permutation test (FWE, p<.05; see *Figure 3.2*

bottom right panel for subsumed experimental conditions). *B.* Regions of interest identified based on the group-level statistical map shown in A and verified on an individual basis. *C.* Violin plots illustrating the distribution of decoding accuracies across subjects per ROI.

3.4.2.4 Bilateral multivariate activation patterns in the SPL code the current movement instruction

The computation of movement coordinates depends on the movement instruction, that is, the rule that has to be applied to the tactile stimulus to derive the movement goal (pro vs. anti). Consequently, we next tested whether the movement instruction is represented in addition to, and independent of, movement coordinates during the planning delay. To identify clusters which contained information about the movement instruction, we implemented a within-condition classifier dissociating between pro- and anti- movement instructions during the planning delay (*Figure 3.3*, classifier 16). Results pertaining to the representation of the movement instruction are illustrated in *Figure 3.7*.

Within-condition classification of movement instruction revealed a network covering areas within the bilateral SPL. The cluster in the left hemisphere extended posteriorly and laterally, as well as anterior and medially (*Figure 3.8A*). *Figure 3.8B* shows the identified ROIs within this cluster. Average ROI coordinates across participants are displayed in *Table 3.2*. The grand mean above chance decoding accuracy of the movement instruction per ROI ranged from 53.8% to 54.1% with participant-level confidence intervals covering ranges from 0.3% to 1.3% (*Figure 3.8C*).

In sum, the movement instruction appears to be coded in bilateral SPL and left SPOC.

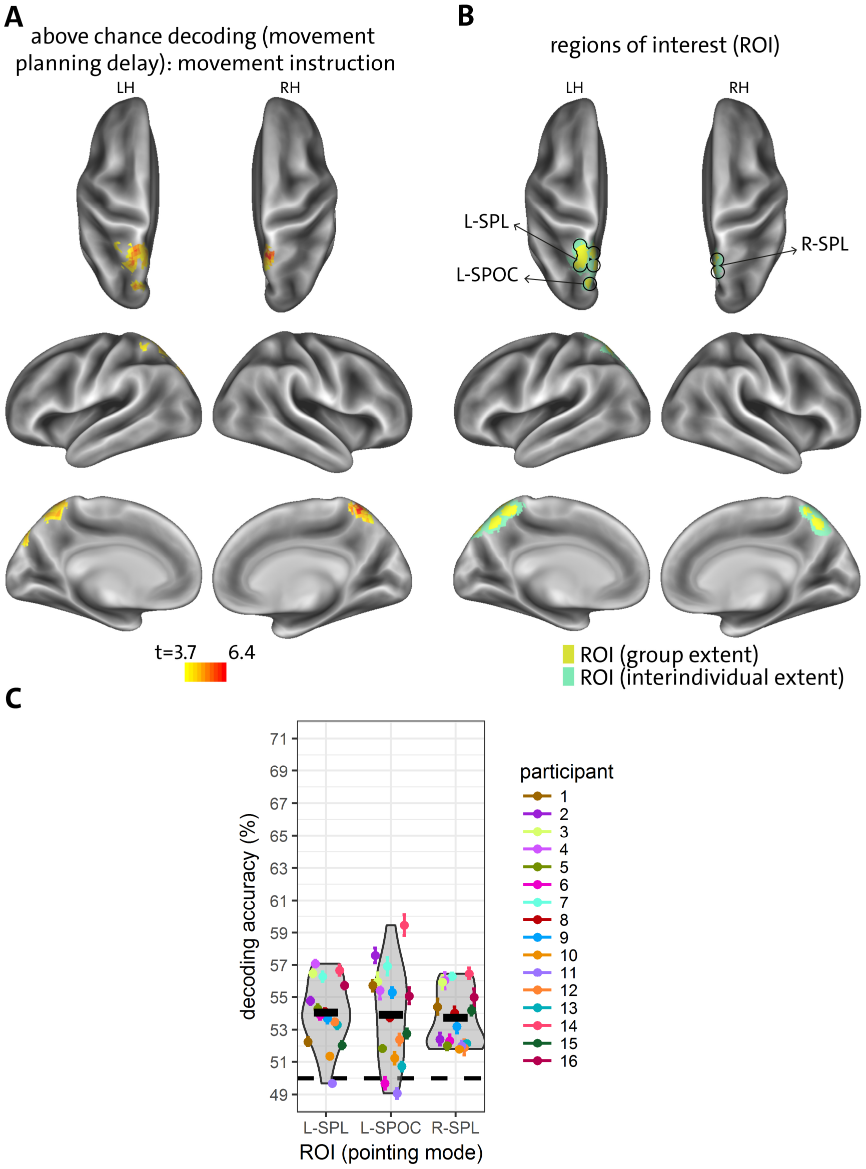


Figure 3.8: Results of the multivariate imaging analysis pertaining to the representation of the movement instruction during the movement planning delay. L-SPL, left superior parietal lobule; L-SPOC, left superior parieto-occipital cortex; R-SPL, right superior parietal lobule. All other details are equivalent to those in *Figure 3.5*. *A.* Statistical maps representing significant group-level above chance decoding accuracies of the movement instruction corrected for multiple comparisons using a cluster-based permutation test (FWE, p<.05). *B.* Regions of interest identified based on the group-level statistical map shown in A and verified on an individual basis. *C.* Violin plots illustrating the distribution of decoding accuracies across subjects per ROI.

3.4.2.5 From touch localization to sensorimotor planning: functional overlap

We hypothesized that areas involved in reference frame transformations and/or their integration would contain information about all processed coordinates. *Figure 3.9* displays clusters in which we decoded both tactile and movement information. Voxels representing tactile coordinates overlapped with voxels representing movement goal locations. Specifically, 34.4% of the cluster representing anatomical coordinates overlapped with the cluster representing movement goal locations in bilateral S1, left SPL, as well as right PMd (overlap of 221 voxels, volume: 5967 mm^3; *Figure 3.9A*). 61.2% of the cluster representing external touch coordinates overlapped with the cluster representing movement goal locations in right mIPS (overlap of 74 voxels, volume: 1998 mm^3; *Figure 3.9B*). Furthermore, voxels representing the movement instruction overlapped with voxels representing movement goal locations. Specifically, 90.4% of the cluster representing the movement instruction overlapped with the cluster representing movement goal locations in bilateral SPL, located posterior and spreading medially, as well as laterally in the left hemisphere, and in left POS (overlap of 422 voxels, volume: 11,394 mm^3; *Figure 3.9A*).

In the left SPL, located between voxels representing both, anatomical and movement goal locations, and voxels representing both, movement instruction and goal locations, the representations of all three classifications overlapped (overlap of 34 voxels, volume: 1161 mm^3; *Figure 3.9A*). Thus, the prevalent information represented in these regions, as decodable with MVPA, varies over the course of the trial. This finding is suggestive of a change of neural function over time: whereas PPC regions that represent tactile coordinates during the touch localization delay, represent movement goals during the planning delay. Moreover, areas containing information about the movement instruction are almost fully enclosed within the cluster representing movement goal locations, suggesting that this bilateral PPC region derives a sensorimotor transformation from stimulus location and instruction into a movement goal.

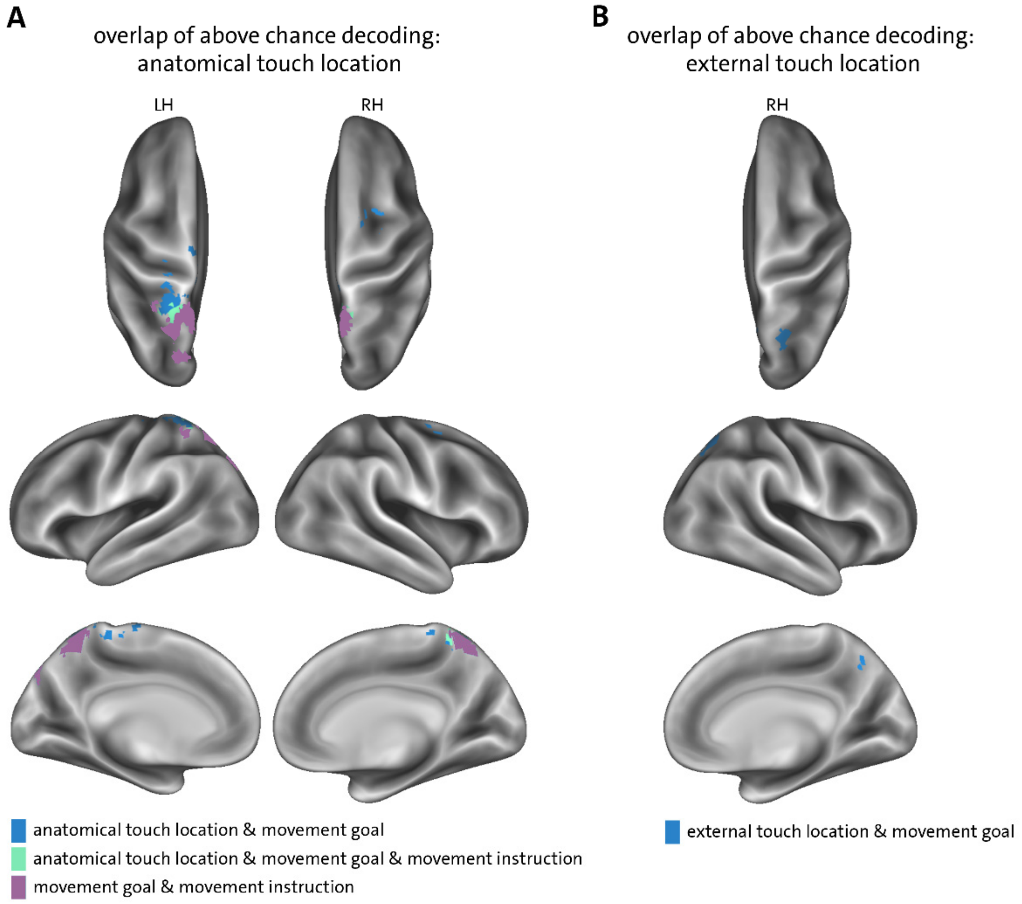


Figure 3.9: Overlap of clusters showing above chance decoding identified in the multivariate imaging analysis, assembled according to which type of tactile representation is implicated (anatomical vs. external touch locations). LH, left hemisphere; RH, right hemisphere. *A.* Overlapping regions involving the representation of anatomical touch coordinates. Regions involved in coding anatomical touch locations and movement goals are shown in dark blue. Regions involved in coding anatomical touch locations, movement goals, and movement instructions are shown in green. Regions involved in coding movement goals and movement instructions are shown in purple. *B.* Overlapping regions involving the representation of external touch coordinates. Regions involved in coding external touch locations and movement goals are shown in dark blue.

3.4.3 Behavioral performance in the perceptual TOJ task

Behavioral performance in the TOJ task is illustrated in *Figure 3.10*, which shows individual and group-level psychophysical curves of the probability of right first temporal order judgment (TOJ) responses plotted against stimulus onset asynchronies (SOA). Average touch localization performance across participants was more accurate with uncrossed as compared to crossed hands, as revealed by steeper slopes (mean uncrossed=0.012, SE=0.003; mean crossed=0.026, SE=0.004; t(15)=3.91, p=.001) and higher accuracy values (mean uncrossed=0.893, SE=0.020, mean crossed=0.775, SE=0.035; t(15)=12.10, p<.001).

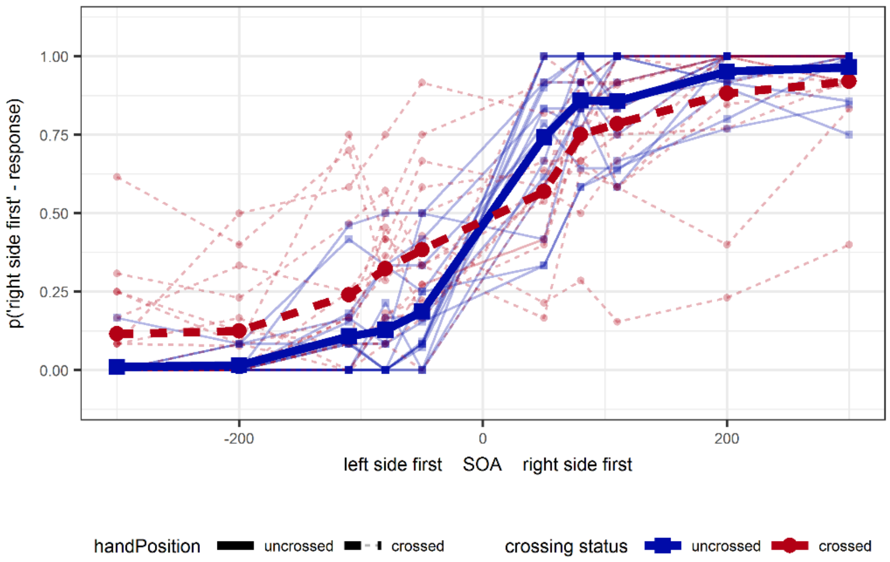


Figure 3.10: Psychophysical curves of the probability of right first temporal order judgment (TOJ) responses plotted against stimulus onset asynchronies (SOA). Negative values indicate that the stimulation occurred on the left hand first. Solid thin blue lines and square symbols represent participant-level performance with uncrossed hands. Dashed thin red lines and circle symbols represent participant-level performance with crossed hands. Correspondingly, thick lines and large symbols represent mean performance across participants.

3.4.3.1 Multivariate coding of tactile coordinates for action is unrelated to a perceptual efficiency measure of touch remapping

We hypothesized that the coding of tactile coordinates during the touch localization delay would be related to the behavioral efficiency of perceptual touch localization in the TOJ task. Presumably, a strong anatomical representation would help to veritably solve the TOJ task, reflected in a relatively small crossing effect. In contrast, a strong external representation would cause more errors in the crossed condition leading to a comparably large crossing effect. In line with this reasoning, we expected participants who exhibit a strong representation of anatomical touch coordinates during the touch localization delay of the sensorimotor task to exhibit a rather small crossing effect in the TOJ task. Likewise, we expected participants who exhibit a strong representation of external touch coordinates during the touch localization delay of the sensorimotor task to exhibit a rather large crossing effect in the TOJ task. We derived several exploratory measures which aimed to capture the strength of anatomical and external representations (see methods for details). In total, we computed 54 correlations (*Table 3.3*, *Table 3.4*) of which one reached significance after correction for multiple comparisons. The difference of the peak decoding accuracy in S1 representing the anatomical touch location and the peak decoding accuracy in R-mIPS representing the external touch location ($\text{decoding}_{\text{diff}}$)

correlated positively with the size of the crossing effect, as measured with the difference in behavioral accuracy in the uncrossed minus crossed condition in the TOJ task (accuracy_{CE}; r=0.82, t(14)=5.45, p<.001; *Table 3.3*, *Figure 3.11*). This correlation indicates that, in contrast to our hypothesis, the larger crossing effect in the TOJ task (accuracy_{CE}), the stronger the anatomical representation in primary somatosensory cortex in the touch localization delay of the sensorimotor task (decoding_{diff}). However, as visual inspection of the scatter plot suggested that the correlation was driven by an outlier. This was confirmed by re-assessing the correlation after removal of the outlier, which rendered the correlation non-significant (r=0.73, t(13)=3.86, p=.002). None of the other correlations reached significance (*Table 3.3*, *Table 3.4*).

	ROI	$\text{decoding}_{percent}$	decoding_{mean}	decoding_{peak}	decoding_{diff}
Anatomical touch locations	S1	0.49	0.67	0.68	0.82
	L-ins	0.18	-0.02	-0.01	0.29
	L-SPL	0.21	0.23	0.26	0.50
	R-M1/S1	-0.10	0.00	-0.08	0.24
	R-IPL/S2	-0.31	-0.27	-0.34	0.15
	R-PMd	0.20	0.11	0.00	0.33
External touch locations	R-mIPS	-0.33	-0.33	-0.32	

Table 3.3: Pearson product moment correlations of different measures ($\text{decoding}_{percent}$, decoding_{mean}, decoding_{peak}), extracted from ROIs signaling either anatomical or external touch coordinates, and the behavioral measure accuracy_{CE}, indexing the crossing effect in the TOJ task. The measure decoding_{diff} relates the representation of anatomical and external coordinates and is calculated for ROIs representing anatomical coordinates only (see methods for details). Cells containing significant correlations after correction for multiple comparisons are shaded in grey (Bonferroni corrected alpha level, p<.001). S1, bilateral primary somatosensory cortex; L-ins, left insula; L-SPL, left superior parietal lobule; R-M1/S1, right primary motor cortex/ primary somatosensory cortex; R-IPL/S2, right inferior parietal lobule/ secondary somatosensory cortex; R-Pmd, right dorsal premotor cortex; R-mIPS, right medial intraparietal sulcus.

	ROI	$\text{decoding}_{percent}$	decoding_{mean}	decoding_{peak}	decoding_{diff}
Anatomical touch locations	S1	0.27	0.25	0.40	0.60
	L-ins	0.14	-0.06	-0.19	0.12
	L-SPL	0.07	-0.03	-0.05	0.24
	R-M1/S1	-0.02	-0.02	-0.18	0.16
	R-IPL/S2	0.12	0.18	0.18	0.45
	R-PMd	-0.03	-0.01	-0.10	0.25
External touch locations	R-mIPS	-0.39	-0.35	-0.34	

Table 3.4: Pearson product moment correlations of different measures ($\text{decoding}_{percent}$, decoding_{mean}, decoding_{peak}), extracted from ROIs signaling either anatomical or external touch coordinates, and the behavioral measure slope_{CE}, indexing the crossing effect in the TOJ task. The measure decoding_{diff} relates the representation of anatomical and external coordinates and is calculated for ROIs representing anatomical coordinates only (see methods for details). None of the correlations reached significance after correction for multiple comparisons (Bonferroni corrected alpha level, p<.001). Abbreviations are equivalent to those in *Table 3.3*.

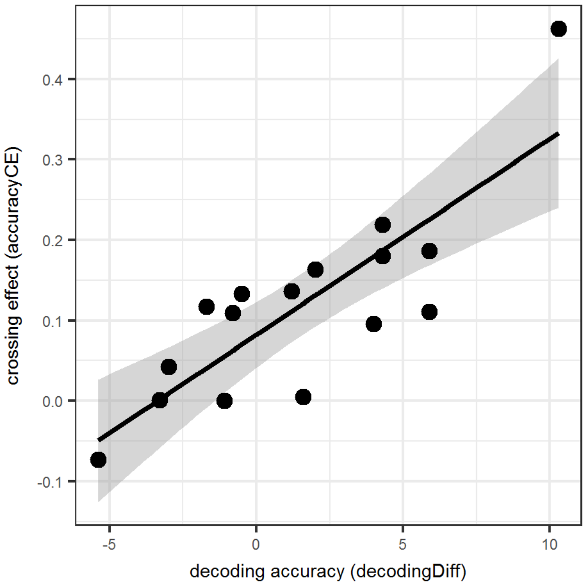


Figure 3.11. Scatterplot showing the positive correlation of $\text{decoding}_{\text{diff}}$ and $\text{accuracy}_{\text{CE}}$. The measure $\text{decoding}_{\text{diff}}$ as shown here relates the strength of the anatomical representation in primary somatosensory cortex (S1) to the strength of the external representation in right medial intraparietal sulcus (R-mIPS). The measure $\text{accuracy}_{\text{CE}}$ indexes the size of the crossing effect in the TOJ task (see methods for details). Black dots represent single subject data. A fitted regression line and its standard error are displayed as black line with grey shading.

3.5 Discussion

Planning a movement based on tactile information, such as using the hand to brush hair out of the face, entails complex spatial computations for the brain. To characterize how the coding of tactile space and movement planning are integrated in the brain, we recorded BOLD signal changes using fMRI while participants executed right hand pointing movements toward tactile stimuli at their feet. Legs were either positioned in a regular, uncrossed posture, or crossed over the shin. In addition, we instructed pointing movements either directly toward the tactile stimulus (pro-movement), or alternatively, toward its mirror location (anti-movement). To characterize how tactile and movement coordinates are coded while a movement plan develops from touch localization to execution, we analyzed multivariate activity patterns using a whole-brain searchlight cross-validation approach. Our study revealed four key results. First, before the movement goal had been specified, anatomical tactile information was coded in S1, IPL/S2, the insula, as well as PMd and SPL, while external tactile information was coded in mIPS. Second, when the movement instruction, that is, the rule that had to be applied to the tactile target, was known, sensory spatial information was no longer detectable; instead, a network covering M1, PMC and PPC now selectively represented information about the movement goal. This cluster partially overlapped with the clusters that had previously represented tactile coordinates. Third, the movement instruction was represented in a cluster within SPL. This cluster was almost fully enclosed within the cluster that represented information about the movement goal. Lastly, multivariate coding of tactile coordinates during the sensorimotor task was unrelated to behavioral performance in a frequently used perceptual touch localization task.

Our study capitalized on several known features of brain responses to characterize tactile sensorimotor planning. Information is thought to be represented in distributed codes across neural populations, which are natively multivariate (Deneve et al., 1999; Ernst & Banks, 2002; Pouget et al., 2000, 2003). Consequently, multivariate analysis of activity patters obtained with fMRI has been suggested to be a sensitive and appropriate analysis approach to quantify how information is represented in the human brain (Haxby et al., 2014; Haynes, 2015; Haynes & Rees, 2006; Kaplan et al., 2015; Kriegeskorte, 2009; Kriegeskorte et al., 2006; Norman et al., 2006), and has been successfully used to characterize sensorimotor transformations for action related to sensory target and effector processing (e.g., Ariani et al., 2015; Barany et al., 2014; Fabbri, Stubbs, Cusack, & Culham, 2016; Gallivan et al., 2011; Gertz et al., 2017; Haynes, 2015; Krasovsky, Gilron, Yeshurun, & Mukamel, 2014; Leoné et al., 2014).

3.5.1 Dissociation of somatosensory function in potential human homologs of non-human primate VIP

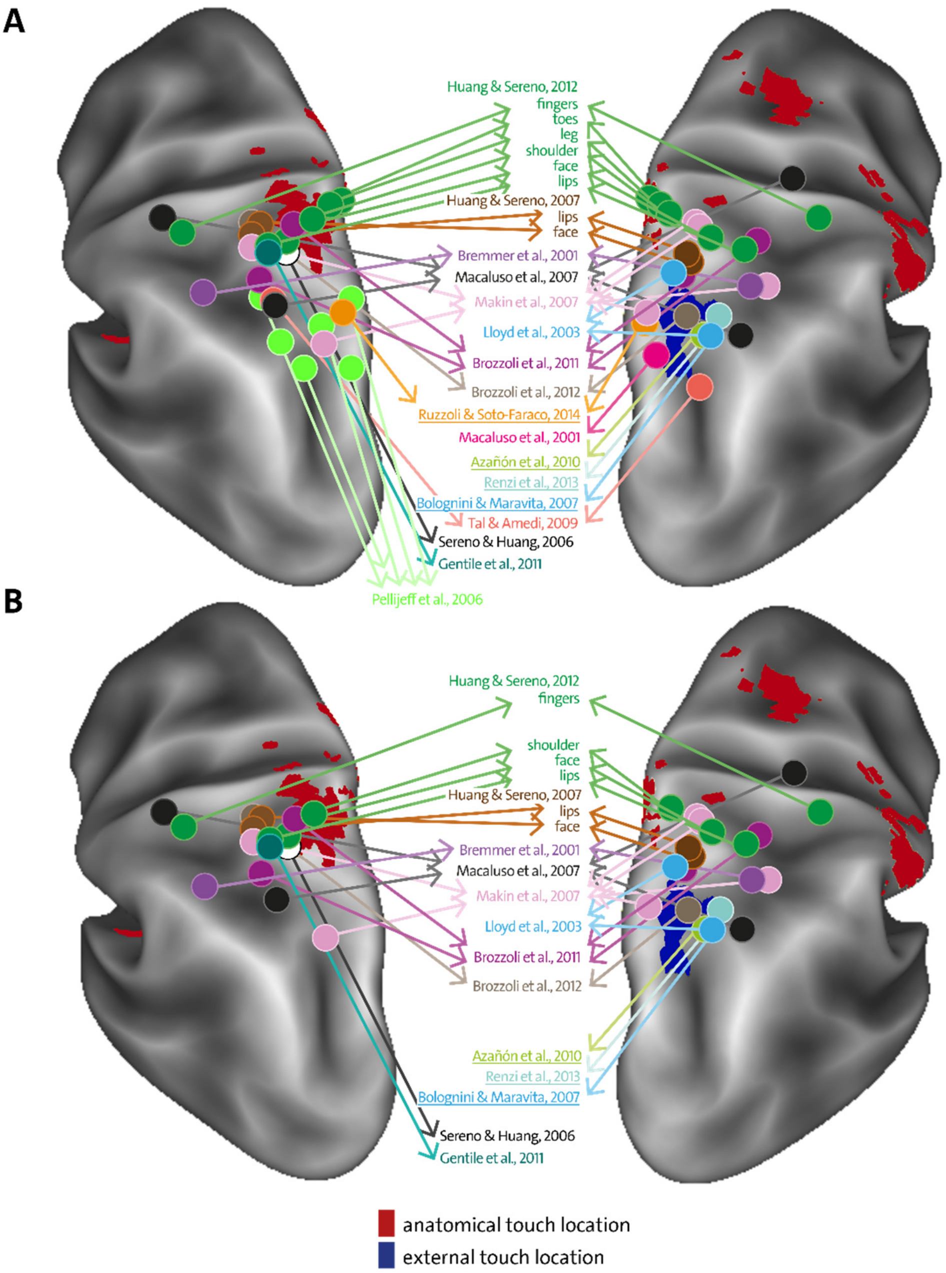
In the present study, information about left and right anatomical target locations was coded in a network including in the anterior part of the left SPL while information about left and right external target locations was coded in a single cluster in right mIPS. Within PPC, we find an anterior to posterior dissociation of the representation of anatomical and external tactile coordinates. Both of these areas have previously been associated with non-human primate VIP (Azañón et al., 2010; Huang et al., 2012). VIP presumably acts as interface between sensory and motor systems, in which somatosensory, visual, auditory, and vestibular information converge.

In line with this idea, non-human primate VIP contains neurons with overlapping, somatosensory and visual, as well as vestibular and auditory receptive fields (Bremmer, Duhamel, et al., 2002; Bremmer, Klam, et al., 2002; Colby et al., 1993; Duhamel et al., 1998; Schlack, Hoffmann, & Bremmer, 2002; Schlack et al., 2005). For instance, neurons with overlapping visuo-tactile receptive fields anchored to the arm respond to both tactile stimulation of the arm as well as visual stimulation presented in the space directly surrounding the arm (Duhamel et al., 1998). Firing of these neurons is independent of current eye position (Duhamel et al., 1998), suggesting that bimodal visuo-tactile neurons code the space surrounding specific body-parts in body-centered coordinates (for neurons anchorched to the face see: Avillac et al., 2007; Avillac, Denève, Olivier, Pouget, & Duhamel, 2005; Cooke et al., 2003). Such neuronal properties allow the construction of peripersonal space (PPS) representations, that is, of the space directly surrounding the body (Graziano & Cooke, 2006). With regard to the function of such coding, PPS representations might act as a "safety zone" around the body to guide defensive behavior and avoid obstacles, as electrical stimulation of VIP subdivisions can elicit stereotyped movements of the face, head, shoulder, and forelimb (Cooke et al., 2003; Graziano & Cooke, 2006). More generally, such coding has been suggested to serve spatial sensorimotor transformations for goal-directed action (Rizzolatti et al., 1981a, 1981b), possibly related to the recoding and integration of information coded in body-centered and sensory reference frames to achieve common space representations across modalities (Pouget, Ducom, et al., 2002). Constructing common spatial representations might then enable interaction with the external world (Graziano & Botvinick, 2002). Consistently, VIP has been shown to contain multisensory information coded in a variety of spatial reference frames (Avillac et al., 2005; Chen et al., 2013). Both views emphasize the close link between sensory and motor processing, which might be the characteristic feature of VIP. Similarly, a close link between sensory and motor processing has been associated to putative hVIPs located in close proximity to SPL and mIPS. In the present study, these areas were associated with anatomical and external spatial coding of touch. *Figure 3.12* illustrates PPC locations obtained in previous fMRI and TMS studies that investigated spatial somatosensory processing and the locations of anatomical and external coordinate representations in the present study.

For instance, fMRI mapping experiments showed overlapping visual and tactile maps in human SPL and anterior IPS, which have been interpreted as "multisensory parietal body areas" (Huang et al., 2012). These are organized according to a rough body homunculus (Huang et al., 2012; Huang & Sereno, 2007; Sereno & Huang, 2006, 2014). Leg and toes are represented medially, in close agreement with the cluster location in SPL that represented anatomical (foot) coordinates in the present study (see *Figure 3.12A*). Also in line with anatomical coding in SPL, another study identified a region in IPS/SPL that codes the spatial location of visual objects in body-centered coordinates based on proprioceptive somatosensory information (Brozzoli et al., 2012). Specifically, visual objects were coded in this region *across* different hand positions, possibly in correspondence to body-centered coding of visuo-tactile neurons in non-human primate VIP (Brozzoli et al., 2012). In correspondence, overlapping activations related to visual, auditory, and tactile motion processing have been identified in aIPS and were interpreted to correspond to overlapping visual, tactile, and auditory receptive fields in non-human primate VIP (Bremmer et al., 2001). Various other human imaging studies identified processing of visual and somatosensory signals in a similar set of regions (Brozzoli et al., 2011; Driver & Noesselt, 2008; Gentile et al., 2011; Macaluso et al., 2007; T. R. Makin et al., 2007; Pasalar et al., 2010; Pellijeff et al., 2006; Tal & Amedi, 2009).

Information about left and right external target locations was represented in a single, right-lateralized mIPS cluster in the current investigation. The location of this cluster closely corresponds to an area that has been causally linked to the remapping of anatomical touch locations into external space (Azañón et al., 2010). In this study, participants had to judge the elevation of touches on the forearm in relation to touches presented to the face. The left forearm was passively moved along the vertical axis, such that the localization task could not be solved based on skin-based touch locations only. TMS over right PPC impaired localization performance, that is, participants made more errors in comparison to when a control site was stimulated using TMS. Neither skin-based localization, nor proprioception were implicated, suggesting that using proprioceptive and skin-based information for the recoding of touch was specifically impaired (Azañón et al., 2010). The brain coordinate used for TMS stimulation in this study was derived from a related fMRI investigation, in which mIPS was shown to respond to passively presented touch to the right hand positioned in left hemispace when the eyes are closed (Lloyd, Shore, Spence, & Calvert, 2003). When visual feedback of the hand was available, activation shifted to the corresponding location in the left hemisphere. Correspondingly, the right hemisphere responded to touches presented to the left hand positioned in right hemispace when visual feedback of the hand was available (Lloyd et al., 2003). Thus, these results suggest that tactile information, as well as proprioceptive and visual information about the hand position, interact. External tactile coordinates appear to be coded relative to the eyes (Buchholz et al., 2011, 2013, Müller & Fiehler, 2014a, 2014b, 2016), possibly derived from overlapping somatosensory and visual neuronal receptive fields in PPC. Correspondingly, a causal role in the alignment of somatosensory and visual maps across hand postures has been assigned to right mIPS (Bolognini & Maravita, 2007). Specifically, the excitability of visual cortex, as measured by eliciting phosphenes with TMS over occipital cortex, was shown to be modulated by a touch presented to a finger placed at the same location as the expected phosphene. Crucially, crossing the hand over the body midline revealed that the external touch location determined the phosphene modulation. Repetitive TMS applied to right mIPS prior to presenting the touch and eliciting phosphenes, caused the modulation of visual excitability by touch to revert to anatomical space. Possibly, the transformation of the tactile location estimate into an eye-centered reference frame was suppressed, suggesting that the identified region in the right mIPS might be causally related to the alignment of tactile and visual maps (Bolognini & Maravita, 2007). In sum, these results suggest that mIPS is involved in recoding touch into external space, regardless of the body site that was initially stimulated, that is, hands, as in most of the reviewed studies so far, or feet, as in the present study. Thus, mIPS presumably projects anatomical touch coordinates into an coordinate system that is independent of the skin and most likely anchored to the eyes.

More generally, right mIPS has been suggested to be a multisensory relay for mapping sensory stimuli in general into coordinates suitable for cross-modal integration, as TMS to mIPS interferes with the influence of touch on auditory processing (Renzi et al., 2013). Conversely, mIPS has also been linked to coding the spatial movement direction of both eye and hand movements (Gallivan et al., 2011) and object-related action intentions (Gallivan, McLean, Flanagan, & Culham, 2013) during visuomotor planning. Collectively, these studies outline a critical role of mIPS for coding spatial target-related information in a format suitable for action and cross-modal integration that, in the case of tactile stimuli, abstracts of the initial skin-based format.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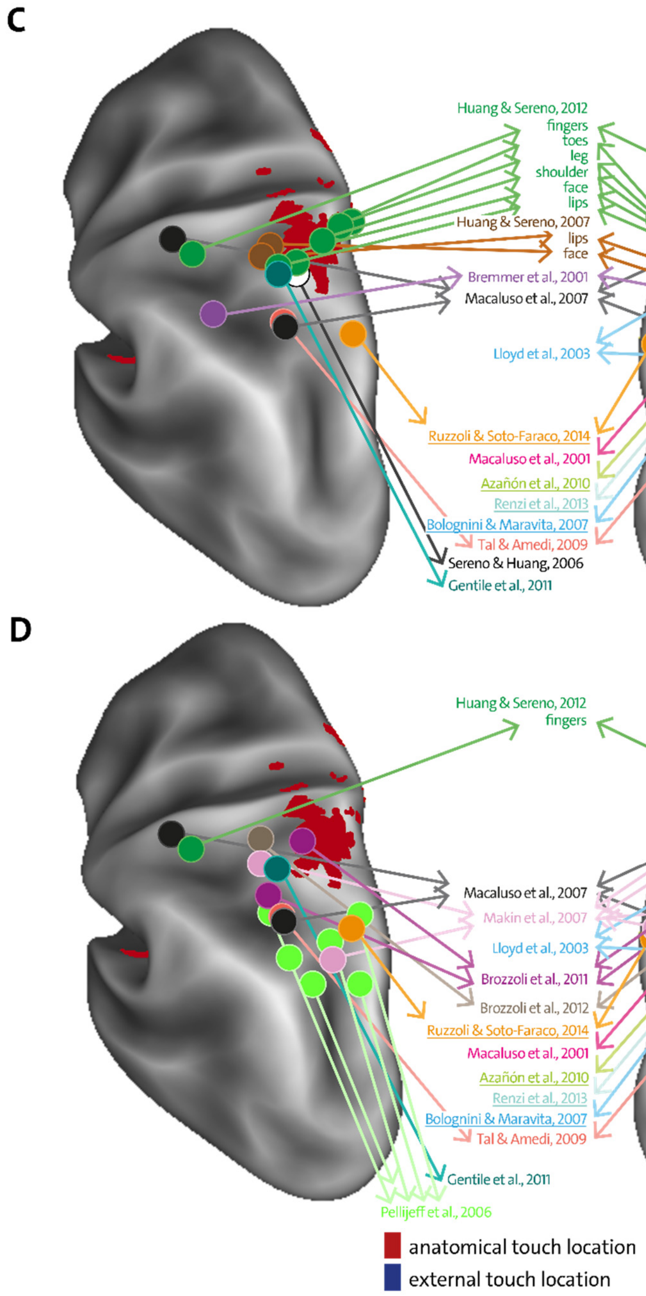


Figure 3.12. Overview of PPC locations reported in previous related studies displayed along with the results of the present study and grouped into panels according to different features of interest. For precise surface mapping of coordinate locations from previous studies, spheres with a radius of 4 mm were constructed around coordinate locations (results not shown). For reference to the results of the present study, clusters with significant above chance decoding of anatomical coordinates are shown in red (see also *Figure 3.2*; classifier 1; *Figure 3.5*). Clusters with significant above chance decoding of external coordinates are shown in blue (see also *Figure 3.2*; classifier 2; *Figure 3.6*). References indexing studies that employed TMS (instead of fMRI) methodology are underlined. *A.* Overview of locations identified in previous related studies. *B.* Selection of studies shown in *A* that explicitly related their findings to neurophysiological results from non-human primate VIP. *C.* Selection of studies shown in *A* that investigated tactile (and proprioceptive) spatial processing. *D.* Selection of studies shown in *A* that investigated somatosensory processing of the hands.

The cluster coding external tactile coordinates in mIPS was right lateralized. Likewise, it has been suggested that right PPC may be specialized for spatial somatosensory function, as somatosensory deficits are more frequent after right, as compared to left, hemispheric lesions (Sterzi et al., 1993; Vallar, 1997). Furthermore, a proportion of neurons in proximity to related non-human primate VIP have been shown to contain receptive fields anchored to both limbs (Iwamura, Iriki, & Tanaka, 1994). Consistently, a human fMRI adaptation study has revealed a right-lateralized cluster in close vicinity that is directionally tuned for movements with either the right or the left hand (Fabbri, Caramazza, & Lingnau, 2010). In the visual domain, a right hemisphere dominance for processing precise metric information has been suggested and related to PPC (Jager & Postma, 2003). In correspondence, participants had to use precise tactile location information for goal-directed planning in the present study. Nonetheless, we are hesitant to interpret the lateralization we found for two reasons. First, the present result is based on a relatively small sample size. Second, the resulting picture from related studies is not conclusive to date. To resolve whether mIPS codes external tactile space of the contralateral body, or alternatively, whether the right mIPS indeed codes external tactile space for both body sides, further investigation is warranted. Possibly, previously reported lateralization effects are related to the largely selective investigation of tactile stimulation sites at the hands. Hands are mostly used independently in everyday life and as such, hand stimulation might result in more lateralized responses than stimulation at other body locations. Feet in turn, have been shown to share many functionalities with hands, especially in the context of motor planning (Heed et al., 2011; Heed, Leoné, et al., 2016; Leoné et al., 2014). Thus, the lateralization of the coding of tactile locations might be specifically related to tactile stimulation at the hands and feet, because the limbs are functionally distinct from the rest of the body. Apart from the potential, yet unresolved lateralization, the representation of external touch coordinates in mIPS in the present study is in close agreement with previous results, which have linked this area to the recoding of touch into external space, and more generally, to the alignment of tactile with other sensory maps.

Previous studies have not investigated the different reference frames involved in the localization of a tactile stimulus in conjunction, that is, they have not specified how the brain codes anatomical *vs.* external tactile information. Tactile stimuli are automatically recoded into external space (Badde, Heed, et al., 2014; Kitazawa, 2002; Röder, Rösler, & Spence, 2004;

Yamamoto & Kitazawa, 2001); nonetheless, there is converging evidence that anatomical information is maintained for calculation of the final location estimate (Badde, Heed, et al., 2015; Brandes & Heed, 2015; Buchholz et al., 2011, 2013). So far, TMS studies on touch localization have selectively disrupted the external coding of touch (e.g., Azañón et al., 2010), and related imaging studies have not manipulated body posture (e.g., Huang et al., 2012), or have exclusively investigated proprioceptive, but not tactile, spatial processing (e.g., Brozzoli et al., 2012). Thus, how the brain codes anatomical tactile coordinates, especially in relation to how it codes external tactile coordinates, remained unclear. The present results fill this gap by showing that the brain dissociates between anatomical and external tactile reference frames and represents information about either in distinct locations in anterior and medial PPC. Furthermore, previous paradigms have often relied on passive stimulation protocols, which did not require participants to react upon or toward the stimuli in any way (e.g., Huang et al., 2012). Here, we show that the involvement of PPC in the processing of tactile information generalizes to a task context that requires exact localization of the stimulus for action, and that even in this task, which theoretically could be solved based on external tactile information alone, anatomical tactile information is maintained, too.

There is ample variance in the PPC locations reported in connection to spatial somatosensory processing in previous studies, although many of these locations were related to the same parietal area in non-human primates (see *Figure 3.12B* for an overview of locations that have been linked to non-human primate VIP). Variance in putative hVIPs might be related to the investigation of proprioceptive vs. tactile spatial processing. Yet, comparing the results of studies investigating tactile (and proprioceptive) spatial processing reveals no systematic pattern of PPC locations either (*Figure 3.12C*). Alternatively, discrepancies with regard to the lateral location along the aIPS/SPL axis might be related to the different location of parietal body maps for foot (present study) vs. face (e.g., Bremmer et al., 2001), vs. hand (e.g., Macaluso et al., 2007), which have been suggested to exist here (Huang et al., 2012). However, across previous studies, somatosensory processing of the hands is not associated with systematic PPC locations either (*Figure 3.12C*). Thus, neither the type of somatosensory information processed (tactile/ proprioceptive vs. proprioceptive only), nor the body part investigated (hands vs. other body parts), appear to be relevant dimensions along which coding in PPC is spatially organized at a larger level. However, previously reported putative hVIPs might be systematized according to whether they are located along the aIPS/SPL axis (Banati, Goerres, Tjoa, Aggleton, & Grasby, 2000; Bremmer et al., 2001; Brozzoli et al., 2012, 2011; Driver & Noesselt, 2008; Gentile et al., 2011; Huang et al., 2012; Macaluso et al., 2007; Pasalar et al., 2010; Tal & Amedi, 2009), or alternatively, whether they are located more posteriorly in mIPS (Azañón et al., 2010; Bolognini & Maravita, 2007; Brozzoli et al., 2012; Lloyd et al., 2003; Pellijeff et al., 2006; Renzi et al., 2013; Ruzzoli & Soto-Faraco, 2014). Our results suggest a dissociation between these two locations, with selective coding of anatomical somatosensory information in anterior SPL and selective coding of external somatosensory information in mIPS. Possibly, the task context then determines whether anatomical or external somatosensory coding is emphasized (Badde, Röder, et al., 2015). According to this reasoning, passive paradigms lead to more anterior anatomical coding in PPC (e.g., Huang et al., 2012), while active paradigms lead to more posterior external coding in PPC (e.g., Pellijeff et al., 2006). In the present study, this anterior to posterior gradient might reflect the progressive recoding of tactile coordinates from a body-centered to an eye-centered reference frame through referral to body posture. Alternatively, the gradient might reflect a two-staged process (Badde & Heed, 2016; Badde, Heed, et al., 2015): quick, automatic recoding of the tactile stimulus into external space by referral to body posture, followed by subsequent top-down modulated integration of anatomical and external coordinates. The former would rely on serial processing of anatomical and external location codes, whereas the latter would be characterized by parallel maintenance of both (Brandes & Heed, 2015). As fMRI lacks the temporal resolution to dissociate these alternatives, future studies using TMS or magnetoencephalography (MEG) could qualify the mechanisms underlying PPC involvement during touch localization.

3.5.2 Anatomical target localization for action in PMd, S1, IPL/S2, and the insula

In addition to SPL, anatomical tactile information was represented in PMd in the present study. Monkey neurophysiology has shown that PMC shares many neural properties with VIP, such as overlapping visual and somatosensory receptive fields (Graziano, Yap, & Gross, 1994; Rizzolatti et al., 1981a, 1981b) that code PPS in body-centered coordinates (Graziano et al., 1994). In correspondence to VIP, electrical stimulation of PMC subdivisions, too, can elicit stereotyped movements of the face, forelimb, or hindlimb (Graziano, Taylor, Moore, & Cooke, 2002; Graziano & Aflalo, 2007; Graziano & Cooke, 2006). Therefore, PMC and VIP have been suggested to form a functional network, acting together to interface between sensory and motor systems (Graziano & Cooke, 2006). Within this network, VIP is thought to be relatively more associated with sensory processing, while PMC is relatively more associated with motor processing (Graziano & Cooke, 2006). In humans, similar to putative hVIP, PMC has been linked to spatial somatosensory functions, such as coding current limb position (Brozzoli et al., 2012; Limanowski & Blankenburg, 2016; Lloyd et al., 2003), limb ownership (Brozzoli et al., 2012; Ehrsson, Spence, & Passingham, 2004; Limanowski & Blankenburg, 2016), and even corporeal awareness more generally (Arzy, Overney, Landis, & Blanke, 2006). These functions have been suggested to be a consequence of overlapping somatosensory and visual receptive fields based on neural properties identified in non-human primate PMC (Brozzoli et al., 2012). Thus, the representation of anatomical touch coordinates in PMd in addition to the representation in SPL in the present study is in close agreement with previous results, as both areas are thought to be functionally related (Graziano & Cooke, 2006). PMd and related ventral premotor cortex (PMv) have been connected to spatial somatosensory functions in previous studies, which have largely focused on the investigation of proprioceptive somatosensory coding (e.g., Brozzoli et al., 2012, 2011). Thus, our results add to existing knowledge by showing that PMd also codes tactile somatosensory information for action and, specifically, is selective for coding anatomical tactile information in concert with a network spanning SPL, S1, IPL/S2 and the insula.

Previous studies investigating touch localization have linked the coding of anatomical coordinates to S1 (e.g., Azañón et al., 2016; Tame et al., 2014). Consistent with this proposal, information about left and right anatomical touch locations was represented in the medial bank of bilateral S1 in the present study, which is considered the part of the somatosensory homunculus that responds to contralateral foot stimulation (Dietrich et al., 2017; Penfield & Boldrey, 1937). The network for anatomical coordinates expanded beyond S1 and further included the left insula and right IPL bordering S2. S2 has been shown to respond to bilateral somatosensory stimulation (Del Gratta et al., 2002; Ruben et al., 2001). It has been suggest that it receives input concurrently with S1 (Karhu & Tesche, 1999), although it has been classically viewed further downstream in the somatosensory hierarchy (Duffy & Burchfiel, 1971; Inui, Wang, Tamura, Kaneoke, & Kakigi, 2004). Moreover, S2 has been shown to be densely connected to parietal cortex in humans (Eickhoff et al., 2010), in line with the fact that non-human primate S2 receives projections from VIP (Lewis & Van Essen, 2000) and that anatomical coordinates were represented both in S2 and SPL in the present study.

Anatomical coordinates were also represented in the insula in the present study. Consistently, the insula has previously been linked to a variety of somatosensory functions, such as processing vibrotactile stimulation (McGlone et al., 2002), tactile memory (Burton & Sinclair, 2000), visuo-tactile processing (Gentile et al., 2011), and processing of the body associated with ownership (Farrer et al., 2003), self-awareness and emotional experience (Craig, 2002, 2004; Karnath, Baier, & Nägele, 2005). Thus, beyond S1, which has been frequently related to anatomical touch coding in the context of tactile remapping, our results show that a network covering classical regions of the somatosensory hierarchy, such as IPL/ S2 and the insula, code anatomical touch information for action, along with specialized premotor and parietal areas.

3.5.3 Posture might not be represented beyond the transformation from anatomical to external space

Information about foot posture was neither represented in multivariate activity patterns, nor reflected in global, univariate activation changes in the present study. With regard to postural effects depending on tactile or movement coordinates, this might be related to the reduced number of runs available for classification. However, limited power of the present design to map posture effects cannot explain why these were also absent when comparing postures independent of tactile and movement coordinates. In contrast to our results, a previous fMRI study has reported higher activation in crossed as compared to uncrossed hand postures in multiple areas, including the left IPL and SPL, during a tactile TOJ task. However, this result was based on a small sample size and stems from statistical testing not corrected for multiple comparisons, reported at a lenient z-value threshold ($p<.05$, uncorrected; Takahashi, Kansaku, Wada, Shibuya, & Kitazawa, 2013). Moreover, another fMRI study reported increased activation in the left IPL and other areas when the hands were crossed as compared to uncrossed (Wada et al., 2012). However, in that study, participants received no tactile stimuli and had no task during scanning beyond infrequent changing between hand postures (Wada et al., 2012). Similarly, another study has implicated areas in the PPC in coding hand posture as assessed by manipulating the congruence of visual and proprioceptive position information, but again, without requiring the localization of tactile stimuli (Limanowski & Blankenburg, 2016). Thus, neither of these studies allows to draw conclusions about how touch localization interacts with the function of these proposed proprioceptive/posture-related regions. It is possible that as soon as touch occurs, their function becomes to relate posture to the tactile event.

The coding of tactile coordinates without explicit representation of posture in the present study could be interpreted as evidence for a two-staged process of tactile remapping, as has previously been suggested (Badde & Heed, 2016). First, external coordinates are computed by integrating postural information quickly and automatically. Crucially, touch localization for perception and action relies on the later integration of anatomical and external coordinates, not on posture per se (for compatible EEG results see: Heed & Röder, 2010). According to this framework, information about posture itself might not be maintained beyond initial coordinate computation and, as a consequence, might not have been decodable in the present study. Specifically, the computation of external coordinates has been shown to take approximately 200 ms, including the integration of conflicting anatomical and external coordinates (i.e., crossed feet; Brandes & Heed, 2015), while the touch localization delay of the present study lasted up to 7.5 seconds. In correspondence, proprioception drifts over time, which can be prevented by visual feedback of the limb, or, by moving the limb (Wann & Ibrahim, 1992), suggesting that posture has to be readout and is not permanently represented (see also: Badde, Röder, et al., 2014). In further support of postural information not being maintained beyond computation of external touch coordinates, probabilistic modeling of behavioral responses in the TOJ task has suggested that crossing effects are not caused by posture as such, but instead, by the incongruence of anatomical and external coordinates in crossed, but not in uncrossed postures (Badde, Heed, et al., 2015). Consistently, we have recently reported behavioral evidence for coordinate integration in touch localization for action using a sensorimotor decision task (Brandes & Heed, 2015). In further support of coordinate integration as the prime mechanism of touch localization, the temporal progression and mode of communication between the networks coding anatomical vs. external coordinates we identified in the present study remain to be established.

3.5.4 Dynamic tactile sensorimotor processing

In the present study, after touch had been localized and the rule that had to be applied to the tactile target was known, sensory spatial information was no longer detectable, suggesting that it is only maintained as long as it is relevant. Indeed, behavioral evidence has suggested that delayed movement tasks such as the one used here, prompt movement planning, not the retention of sensory information (Toni, Thoenissen, Zilles, & Niedeggen, 2002). Compatibly, a previous fMRI study investigating visuomotor control has indicated that sensory codes are only maintained as long as they are relevant (Gertz et al., 2017). In contrast, another fMRI study has demonstrated visual selectivity for contralateral targets in the left occipital cuneus, but did not detect any equivalent activation in the right hemisphere (Cappadocia et al., 2016). Whether the maintenance of sensory information when inferring a movement goal for hand pointing from a target is modality-specific, could be investigated by probing the neural implementation of auditory sensorimotor planning.

A network covering M1, PMC, and PPC selectively represented information about the movement goal location after the movement instruction had been given in the present study. The identified cluster was bilateral, but it was larger in extent and the decoding accuracies were higher in the left hemisphere. This left hemisphere prevalence likely relates to the use of the right hand as the pointing effector in our study. Accordingly, effector information appears to have been integrated at this processing stage. The cluster closely corresponded to the fronto-parietal network that has been previously characterized during visuomotor planning (Blangero, Menz, McNamara, & Binkofski, 2009; Culham & Valyear, 2006; Filimon, 2010; Gallivan & Culham, 2015; Vesia & Crawford, 2012). The cluster contained for example the putative human homolog of non-human primate parietal reach region, SPOC, as wells as PMd, which have both been related to calculating the movement path from effector to target location (Astafiev et al., 2003; Bernier, Cieslak, & Grafton, 2012; Beurze et al., 2007; Connolly et al., 2003; Fernandez-Ruiz et al., 2007; Gallivan et al., 2011; Hagler, Riecke, & Sereno, 2007; Medendorp, 2004). In addition, the cluster spanned the hand area in M1, as well as the SMA and pre-SMA, which have been shown to contain preparatory movement signals related to the effector, target and object-related movement intentions in recent MVPA studies on visuomotor planning (Ariani et al., 2015; Di Bono, Begliomini, Castiello, & Zorzi, 2015; Fabbri, Strnad, Caramazza, & Lingnau, 2014; Gallivan, Johnsrude, & Flanagan, 2015; Gallivan et al., 2013, 2011). The present cluster also contained aIPS, which has been linked to the preparation of grasping and pointing movements (Astafiev et al., 2003; Bernier & Grafton, 2010; Beurze, Toni, Pisella, & Medendorp, 2010; de Jong, van der Graaf, & Paans, 2001; Heed et al., 2011; Konen, Mruczek, Montora, & Kastner, 2013). The identified cluster also contained regions that, according to a review by Gallivan and Culham

(2015), have been “less-well defined” in classical fMRI studies of visuomotor planning, as for example vIPS, mIPS, and pIPS/cIPS, located along the SPL and bordering the IPS anterior to posterior. Nonetheless, converging MVPA evidence suggests that these areas contain rich information patterns related to sensorimotor processing and may be more important for action than could be expected from classical fMRI analysis (Gallivan & Culham, 2015). vIPS and mIPS have been implicated in a variety of spatial somatosensory functions interfacing sensory and motor processing. The region denoted vIPS in the context of visuomotor control (Gallivan & Culham, 2015) corresponds to hVIP distributed across medial to anterior SPL and IPS, which have been suggested in research that primarily focused on sensory processing (see section “Dissociation of somatosensory function in potential human homologs of non-human primate VIP”). The region denoted as mIPS in the context of visuomotor control contains the mIPS cluster of the present study, but spreads further anteriorly and posteriorly, as well as medially and laterally (Gallivan & Culham, 2015). In the context of visuomotor planning, mIPS has been linked to processing spatial target information and object-related action intentions (Bernier et al., 2012; Fabbri et al., 2010; Gallivan et al., 2013, 2011; Grefkes, Ritzl, Zilles, & Fink, 2004). pIPS/cIPS has been associated with a broad range of sensorimotor processes including visual-spatial attention and target and effector integration (Beurze et al., 2010; Gallivan et al., 2013, 2011; Heed et al., 2011; Szczepanski, Konen, & Kastner, 2010). In the present study, these areas represented tactile coordinates during touch localization with an anterior to posterior gradient of anatomical to external coding. Once the rule that had to be applied to the tactile target was known, they changed their selectivity to exclusively represent movement coordinates. Such dynamic tactile sensorimotor processing is consistent with a role connecting sensory and motor systems that has been related to hVIP. However, it remains to be determined whether the spatial, multisensory calculations across multiple reference frames identified in non-human primate and human PPC are a byproduct of another, overarching function, such as anticipation or prediction (e.g., Avillac et al., 2005; Rizzolatti et al., 1981b). According to this reasoning, tactile sensorimotor transformations would for example merely be a means to derive an accurate target prediction for action. Thus, we show here that distinct locations within PPC dynamically code spatial sensory and movement information in different reference frames, progressively abstracting from the initial sensory format.

The movement instruction was also represented in IPS and SPL. In both hemispheres, this cluster was almost fully enclosed within the cluster representing information about the movement goal. Moreover, in the left hemisphere, it additionally overlapped with the cluster that had previously represented anatomical target locations in the SPL. Thus, here, we find an anterior to posterior gradient of areas in the SPL and along the IPS, which dynamically change their selectivity during tactile sensorimotor planning. The most anterior of these PPC locations (SPL) contains information about anatomical coordinates and movement goals. The location posterior to that represents information about all three, anatomical coordinates, movement goals, and movement instructions. The location posterior to that (SPL and precuneus/SPOC) represents information about movement goals and movement instructions. Such overlap of represented information has previously been interpreted as evidence that the corresponding region acts as an interface for the integration of all pieces of information (e.g., Beurze et al., 2007), in line with the central role that has been related to SPOC in sensorimotor planning (Vesia & Crawford, 2012). According to this reasoning, the identified precuneus/SPOC region might derive the movement goal from tactile coordinates by applying the movement instruction and referring to effector position.

Lastly, we found that multivariate coding of tactile coordinates during the sensorimotor task was unrelated to behavioral performance in a frequently used perceptual touch localization task. We hypothesized that the relative strength of anatomical and external representations in the sensorimotor task is related to the crossing effect as measured in the TOJ task, signaling a common coding mechanism of touch localization across tasks. This reasoning implies that participants code anatomical and external information in a stable way, possibly by assigning parameter weights (Badde, Heed, et al., 2015). These might be constant across tasks, that is, determine both, TOJ behavior and touch localization for action. To identify such common coding across tasks, we derived several measures that aimed to capture the (relative) strength of anatomical and external touch coordinate representations. The only tendency toward a relation between behavior and tactile coordinate coding was evident in the association of the measure relating anatomical and external coding ($\text{decoding}_{\text{diff}}$) and the size of the crossing effect in the TOJ task ($\text{accuracy}_{\text{CE}}$). However, this result has to be interpreted with caution, because the relative measure was derived by subtracting the decoding accuracies related to anatomical and external coding from anatomically and functionally different ROIs. Specifically, this result was based on subtracting the decoding accuracies from mIPS from those extracted from S1, and as such, might be contaminated by ROI-dependent noise levels. In line with this cautionary point, subtracting the decoding accuracies from mIPS from those extracted from an anatomically and functionally more similar area in SPL did not result in a similar relation to the crossing effect. In general, the measures derived for this analysis were rather exploratory, because it is not obvious how, or if at all, the relative strength of anatomical and external coordinate representations is related to the decoding accuracy resulting from classification. On a further note, mathematical modeling of behavioral crossing effects across different tasks has shown that these are foremost related to the integration of conflicting anatomical and external coordinates, and in addition, are determined by non-individual weight adjustments across tasks (Badde, Heed, et al., 2015). In terms of neural implementation, common coding of touch localization across tasks might thus alternatively be related to the communication between areas storing anatomical and external information as an index of integration, rather than being related to the relative strength of coordinate representations per se.

3.5.5 Limitations

Classically, fMRI analysis has evaluated each voxel in isolation based on the assumption that the representation of information entails general level differences within functional regions; an approach that has been criticized as oversimplification of representational spaces in the past years (e.g., Haxby et al., 2014). As a supposedly more appropriate and sensitive alternative, multivariate analysis of activation patterns has gained momentum (Haxby et al., 2014; Haynes, 2015; Haynes & Rees, 2006; Kaplan et al., 2015; Kriegeskorte, 2009; Kriegeskorte et al., 2006; Norman et al., 2006). Consequently, univariate vs. multivariate fMRI analysis potentially produce different results, as similar patterns within a region may lead to global activity level changes, but they do not inevitably do so (Davis et al., 2014; Gilron, Rosenblatt, Koyejo, Poldrack, & Mukamel, 2017). Conversely, multivariate classifiers are sensitive to global activation differences (Davis & Poldrack, 2013). In the present study, we found a dissociation between activation and decoding with global activation changes relative to baseline associated with touch localization and movement planning in general but no systematic activation differences dissociating between spatial codes for tactile sensorimotor action. These spatial codes for sensorimotor action in contrast, were represented in distinct multivariate patterns. This result configuration renders it unlikely that classifier results are confounded with global activation differences and suggests that spatial codes are, indeed, represented in multivariate patterns, as would be expected from distributed population coding. However, the relationship between the hemodynamic response and neural activity is complex and yet unresolved (Logothetis, 2007), that is, in principle, the existence of distinct patterns does not necessarily reflect the existence of distinct neural populations (Bartels, Logothetis, & Moutoussis, 2008; Logothetis, 2008). Moreover, as MVPA methods are still being developed and refined, the statistical approach taken in the present study of analyzing single-subject decoding accuracies on a group level using a one sample t-test, has recently been criticized (Allefeld, Görgen, & Haynes, 2016). This strategy is equivalent to analyzing activation differences in a random effects second level analysis and, as such, has been standard procedure both in classical and MVPA analysis to date (Haxby et al., 2001; Haynes et al., 2007; A. P. Holmes & Friston, 1998). But, unlike true activation differences, true decoding accuracies cannot fall below chance, as there cannot be “negative” information contained within a voxel. Consequently, it has been suggested that when testing decoding accuracies, the test reverts to a fixed effects analysis and allows no conclusions about the presence of effects in the population (Allefeld et al., 2016). As an alternative, permutation testing has been recommended. However, as a very computationally expensive approach, we estimated that implementation in the present design would take 64 days on a 24 core PC. Thus, a computationally inexpensive, feasible alternative to one sample t-tests on a group level, as for example explicit Bayesian modeling of the null and alternative hypothesis distributions, remains to be established in the context of fMRI analysis. To allow assessment of the consistency of decodability across subjects, we have furthermore presented plots displaying single subject data for all presented analyses.

On a further note, establishing that patterns are relevant to behavior is necessary to confirm that successful decoding of information from multivariate patterns is reflective of a code that is actually used by the brain and is not simply a byproduct of an alternative format of representation (de Witt, Alexander, Ekroll, & Wagemans, 2016; Raizada et al., 2010; Raizada & Kriegeskorte, 2010). In a first attempt to do so in the context of tactile sensorimotor planning, we tested whether coding of tactile coordinates in the sensorimotor task could be linked to behavioral performance in a perceptual localization task. However, as this analysis was rather exploratory, further in depth investigation of how tactile information is coded within each task would be necessary to resolve whether or not a general coding mechanism exists across tasks.

In the context of the sensorimotor task this would entail the identification of measures that index the integration of anatomical and external coordinates for sensorimotor planning in fMRI analysis. These may be linked to communication between areas coding anatomical and external and anatomical coordinates and might be realized in a variety of different formats, such as common temporal or spatial multivariate patterns, univariate activation levels, or oscillatory phase coupling. In the context of the TOJ task, in depth investigation of how tactile information is coded would entail investigating whether in this task, too, touch localization is implemented in the form of multivariate patterns, whether these are confined to similar areas, and, whether coordinate integration is implemented in a similar manner as in the sensorimotor task. In addition, by manipulating exact touch location coding vs. binary sensorimotor decision making across task contexts, effects of tactile location coding and effects of response-related recoding of tactile coordinates could be scrutinized. For example, in an fMRI implementation of the TOJ task, participants could be required to point toward the exact location estimate, or alternatively, they could be required to make binary sensorimotor decisions. This manipulation would transport exact location coding to the context of the TOJ task.

3.5.6 Conclusions

In brief, our results reveal the dynamic representation of spatial information related to sensory and motor aspects in tactile sensorimotor planning, depending on the stage of the process. Consistent with distributed population coding, dynamic spatial codes were characterized by distinct multivariate activation patterns, which progressively changed their selectivity in PPC from representing sensory information during target localization to representing movement information during planning. Specifically, anatomical and external tactile information was represented in PPC locations along an anterior to medial gradient in regions that have previously been suggested as putative hVIP based on their involvement in spatial somatosensory processing. Here, we show that distinct regions within PPC are specialized for the coding of different tactile reference frames. These are no longer detectable once the motor plan is constructed, suggesting that they are transformed into a higher order representation that abstracts from the initial sensory signal. Information about the movement goal and the movement instruction converged in SPOC, which may play a key role within the network that transforms tactile into movement codes.

4 | Abstract spatial, but not body-related, visual information guides bimanual coordination

4.1 Abstract

Visual spatial information is paramount in guiding bimanual coordination, but anatomical factors, too, modulate performance in bimanual tasks. Vision conveys not only abstract spatial information, but also informs about body-related aspects such as posture. Here, we asked whether, accordingly, visual information induces body-related, or merely abstract, perceptual-spatial constraints in bimanual movement guidance. Human participants made rhythmic, symmetrical and parallel, bimanual index finger movements with the hands held in the same or different orientations. Performance was more accurate for symmetrical than parallel movements in all postures, but additionally when homologous muscles were concurrently active, such as when parallel movements were performed with differently rather than identically oriented hands. Thus, both perceptual and anatomical constraints were evident. We manipulated visual feedback with a mirror between the hands, replacing the image of the right with that of the left hand and creating the visual impression of bimanual symmetry independent of the right hand's true movement. Symmetrical mirror feedback impaired parallel, but improved symmetrical bimanual performance compared with regular hand view. Critically, these modulations were independent of hand posture and muscle homology. Thus, vision appears to contribute exclusively to spatial, but not to body-related, anatomical movement coding in the guidance of bimanual coordination.

4.2 Introduction

Whether we type on a keyboard, unscrew a lid, or ride a bike – bimanual coordination is crucial in many of our everyday activities. Therefore, the principles that guide bimanual coordination have received much interest, not least to inform treatment to restore regular bimanual function in clinical settings. Beyond therapeutic considerations, coordinative action can be viewed as an ecologically valid model to understand the principles of movement planning (Oliveira & Ivry, 2008). Accordingly, experiments have studied the factors that constrain bimanual movement execution. A prominent and consistent finding has been that humans can perform symmetrical movements – with symmetry usually defined relative to the sagittal body midline – with higher precision and at higher speeds than parallel movements (L. Cohen, 1971; Kelso, 1984; Kelso et al., 1986). During symmetrical movements, the two effectors move towards opposite sides of space; for instance, one hand moves to the right while the other concurrently moves to the left. Conversely, parallel movements implicate movements towards the same direction of space; for instance, both hands synchronously move to the left or to the right.

The symmetry bias has been demonstrated across a variety of effectors and movement types, such as finger flexion and extension (Carson & Riek, 1998; Riek, Carson, & Byblow, 1992), finger tapping (Mechsner et al., 2001), wrist movements (L. Cohen, 1971), line drawing (Bogaerts, Buekers, Zaal, & Swinnen, 2003), elbow flexion and extension (Spencer & Ivry, 2007), and circling arm movements (Semjen, Summers, & Cattaert, 1995a). Given its stability across many qualitatively different movements, symmetry is thought to constitute a general organizing principle of bimanual coordination (Swinnen, 2002). One popular experimental paradigm has been finger abduction and adduction, that is, sideways movements of the two index fingers with the hands held palm down. Participants perform these movements rhythmically, and we therefore refer to this task as "finger oscillations". With the palms down, movement accuracy is high when both fingers are abducted at the same time, resulting in symmetrical finger movements. Accuracy is lower when one finger is abducted while the other one is concurrently adducted, resulting in parallel finger movements (Kelso, 1984).

The mechanisms underlying the symmetry bias have been under debate. Early reports suggested that it originates from anatomical constraints within the motor system, that is, from interactions rooted in muscle synergies caused by hemispheric crosstalk (L. Cohen, 1971; Kelso, 1984; Riek & Woolley, 2005). Muscle synergies may arise through reciprocal connections between the cortical regions that control homologous muscles of the two body sides and result in preferred activation of homologous limb movements. In this view, symmetrical movements are stable because they involve the same muscles in both limbs, allowing efficient integration of contra- and ipsilateral motor signals. In contrast, parallel finger movements involve different muscles in the two limbs, resulting in reduced stability due to ongoing interference from conflicting ipsi- and contralateral muscle commands (Shea et al., 2016).

However, others have suggested that, instead, the symmetry bias originates from interactions rooted in perception (Bingham, 2004; Mechsner et al., 2001). The key finding supporting this proposal was that the symmetry bias prevailed when participants performed oscillatory finger movements with the two hands held in opposite orientations, that is, one palm facing up and the other down. In this situation, symmetrical movements involve non-homologous muscles, whereas parallel movements are achieved through homologous muscles. The persistent advantage of symmetrical over parallel movements despite a reversal of the muscles involved in the bimanual movement is at odds with the idea that muscle synergies alone are responsible for the symmetry bias (Bingham, 2004; Mechsner et al., 2001; Shea et al., 2016).

Several studies have suggested that the previous findings of external vs. anatomical symmetry constraints are not a contradiction, but that both factors jointly influence coordination behavior (Oliveira & Ivry, 2008; Spencer & Ivry, 2007; Swinnen et al., 1998; Temprado, Swinnen, Carson, Tourment, & Laurent, 2003). According to this view, anatomical and external contributions flexibly determine bimanual coordination with their relative weighting depending on context and task demands (Shea et al., 2016). In line with this proposal, we recently observed that the perceptual symmetry bias in the finger oscillation task coexisted with an advantage for using homologous muscles (Heed & Röder, 2014), rather than relying on perceptual coding alone, as had been previously suggested (Mechsner et al., 2001).

Whereas the role of perceptual and anatomical codes has, thus, been firmly established, it is less clear what kind of perceptual information these biases are based on. The prevalent experimental approach has been to contrast vision with posture, and to interpret performance biases induced by vision as evidence for perceptually induced, spatial guidance, and biases induced by posture as evidence for anatomical constraints of movement coordination (Mechsner et al., 2001; Riek & Woolley, 2005). Yet, visual information transports not just abstract spatial information, but also information about the body, presumably to contribute to the construction of a body representation. Indeed, we have found that muscle homology affected bimanual finger oscillations less in congenitally blind than in sighted individuals; this finding suggests that vision may induce not just a spatial bias, but may, in addition, contribute body-related, such as postural and muscle-related, information for motor coordination (Heed & Röder, 2014).

One experimental method to investigate the role of body-related visual information is the use of mirror visual feedback. A mirror is placed along the body midline in the sagittal plane; participants look into the mirror from one side, so that the view of the hand behind the mirror is occluded and replaced by the mirror image of the still visible hand. Thus, although one arm is hidden from view, participants have the impression of seeing both of their hands moving in synchrony (Medina, Khurana, & Coslett, 2015). The strong influence of this visual manipulation on body-related, anatomical aspects is maybe most impressively demonstrated in mirror visual feedback therapy (MVT). MVT is used to treat pathological conditions involving unilateral upper extremity pain and motor dysfunction. The mirror replaces visual feedback of the affected arm with that of the intact arm. Viewing mirrored hand movements of the intact arm has been reported to aid recovery of upper extremity function and/or to alleviate pain in different pathological conditions, including stroke, complex regional pain syndrome, and orthopedic injuries, and can even reduce phantom pain after limb amputation when the mirror image of the remaining hand fills the place of the now missing limb (for reviews see: Deconinck et al., 2014; Ezendam, Bongers, & Jannink, 2009; Moseley, Gallace, & Spence, 2008; Ramachandran & Altschuler, 2009). Thus, in such setups, the visual manipulation of anatomical aspects strongly modulates perception.

Mirror setup can also increase movement coupling between the hands, that is, bimanual symmetrical movements are spatially more similar when mirror visual feedback is available, relative to when only one hand is visible (Franz & Packman, 2004). In the finger oscillation paradigm, mirror feedback can create incongruence between the visually perceived and the truly performed bimanual movement; for instance, during parallel finger movements, mirror feedback feigns symmetrical movement through vision while proprioceptive information signals the true, parallel movement. In this incongruent situation, performance declines compared to regular viewing of the hands and relative to when vision is prevented entirely by closing the eyes (Buckingham & Carey, 2008). In other experimental paradigms, such incongruent visual feedback can even induce phantom sensations, such as tickling or numbness, in healthy participants (Daenen, Roussel, Cras, & Nijs, 2010; Foell, Bekrater-Bodmann, McCabe, & Flor, 2013; McCabe, Haigh, Halligan, & Blake, 2005; Medina et al., 2015).

Thus, a large body of evidence suggests an important role of vision for bimanual coordination, but the specific role of vision for the different aspects to which it can contribute, such as abstract spatial or body-related information, is less clear. One account, the perception-action model put forward by Bingham and colleagues, posits that bimanual coordination performance critically depends on the performer’s ability to perceptually detect the phase relationship between the two limbs, expressed in their relative movement directions (Bingham, 2004; Bingham et al., 1999, 2001; Zaal, Bingham, & Schmidt, 2000). Thus, the model specifies visual direction as the aspect of visual information that is relevant for coordination. Difficulty in reliably detecting relative direction presumably leads to maladaptive error detection and correction, which, in turn, impedes performance (Bingham, 2004; Bingham et al., 1999, 2001; Zaal et al., 2000). According to Bingham's model, bimanual coordination, then, is but a special case of any form of visually driven coordination. In fact, they point out that similar constraints appear to govern coordination of a single limb with either a visual stimulus or the limb of another person (Schmidt, Carello, & Turvey, 1990; Temprado et al., 2003; Wilson, Collins, & Bingham, 2005b; Wimmers, Beek, & van Wieringen, 1992). Accordingly, most experiments that have explored Bingham's theory have employed paradigms that required unimanual coordination of a limb with moving visual stimuli presented on a display (Snapp-Childs, Wilson, & Bingham, 2011; Wilson et al., 2005a, 2005b; Wilson, Snapp-Childs, & Bingham, 2010). However, this experimental approach implicitly presumes that the brain abstracts from all movement parameters and, in particular, that it dismisses other body-specific, body-related visual information. Yet, the findings that have demonstrated an influence of anatomical in addition to perceptual factors (Heed & Röder, 2014; Spencer & Ivry, 2007; Swinnen et al., 1998; Temprado et al., 2003) suggest that also visual information pertaining to posture and muscles may be of relevance for bimanual coordination.

Here, we used the finger oscillation task as a strictly bimanual paradigm to scrutinize the proposal that bimanual coordination relies predominately on visual direction information, and to integrate the findings from visuomotor and bimanual coordination that have used different experimental paradigms. The finger oscillation task allowed us to disentangle the three body-related visual aspects that could each potentially be relevant for successful bimanual coordination: first, visual feedback about the spatial direction implied by visual feedback of the performed movement (parallel vs. symmetrical); second, visual feedback about the posture of the hands (same vs. different orientation); and third, visual feedback about the muscles involved in executing the movements (homologous vs. non-homologous).

We conducted the present study to delineate the role of these three aspects of visual information for bimanual coordination. Participants executed oscillatory finger movements that were either parallel or symmetrical relative to the sagittal body midline, with the two hands held either in the same or in different orientations. Participants either viewed their two hands directly, or alternatively viewed their left hand directly and its mirror image at the location in space occupied by the hidden right hand.

4.3 Methods

We report how we determined sample size, all experimental manipulations, all exclusions of data, and all evaluated measures of the study. Data and analysis scripts are available online (see https://osf.io/g8jrt/).

Participants. Previous studies have typically reported significant results pertaining to posture in the finger oscillation task with N<10 (Heed & Röder, 2014; Mechsner et al., 2001). Here, we defined, in advance, a target sample size of 20 participants because we expected that mirror-induced effects would be smaller than posture effects, requiring a larger number of participants for statistical power. Data were acquired from 23 participants, because the data of 3 participants had to be excluded from analysis (see below). None of the participants had participated in our earlier study (Heed & Röder, 2014). All participants were students of the University of Hamburg. They were right-handed according to self-report with an average laterality quotient of 80.4 (50-100 Oldfield, 1971), and had normal or corrected-to-normal vision and did not report any neurological disorders, movement restrictions, or tactile sensitivity problems. They provided written informed consent and received course credit for their participation. The experiment was approved by the ethics committee of the DGPs and all methods were performed in accordance with the relevant guidelines and regulations. Two participants aborted the first experimental session after a few trials, because they were unable to perform the bimanual coordination task. Data of a third participant was excluded because movements were accidentally instructed incorrectly. The final sample thus consisted of 20 students, 15 of them female, mean age 23.6 years (range: 20-32 years).

Experimental design. The experiment was designed based on the studies by Mechsner and colleagues (2001) and Heed and Röder (2014). *Figure 4.1* illustrates the setup and the experimental conditions. Participants performed a finger oscillation task; they executed adduction and abduction movements, that is, right-left movements, with the two index fingers. Instructed movements were either symmetrical, that is, the index fingers moved in- or outwards at the same time, or parallel, that is, fingers moved to the right or left side in space at the same time (*Figure 4.1B*). There were two viewing conditions: non-mirrored and mirrored (*Figure 4.1A*). In the non-mirrored conditions, participants viewed both hands directly and, thus, received regular visual feedback. In the mirrored conditions, a mirror blocked the view of the right hand, so that participants saw the mirror image of the left hand in place of their real right hand; however, this manipulation gives rise to the subjective impression of seeing both hands just like in the non-mirrored condition. The hands were either held in the same (both palms up or down) or in different hand orientations (right palm up, left palm down, or vice versa; *Figure 4.1C*). The experiment comprised four experimental factors. The factors movement instruction (symmetrical vs. parallel), mirror view (non-mirrored vs. mirrored), and hand posture (both palms down vs. both palms up vs. left palm up and right palm down vs. right palm up and left palm down) were varied block-wise in randomized order. The factor speed (10 discrete speeds from 1.4 to 3.4 Hz) was varied within trials. Whereas participants are usually able to perform symmetrical and parallel movements (almost) equally well at low speeds, their performance regularly declines markedly for parallel, but not symmetrical, movements at high speeds (Kelso, 1984). During a trial, each speed level was maintained for 5 beats, resulting in 50 beats per trial, resulting in a trial duration of about 22 seconds. Each of the 16 combinations of the factors instruction, mirror view, and hand posture was presented 4 times across two sessions held on separate days.

Materials and apparatus. Participants sat at a table with both hands resting comfortably in front of the body. Finger movements were tracked with a camera-based motion tracker (Visualeyez II VZ4000v PTI; Phoenix Technologies) using infrared markers sampled at 100 Hz. Four markers were attached to each index finger, one on the finger nail, one opposite the nail on the fingertip, and one on each side between nail and tip. As a result, at least one marker per hand was visible during movement execution in all postures. Movements were instructed by metronome-like sounds presented through two loudspeakers positioned in front of the participant. Experimental protocols were controlled via MATLAB (version 7.14, The Mathworks).

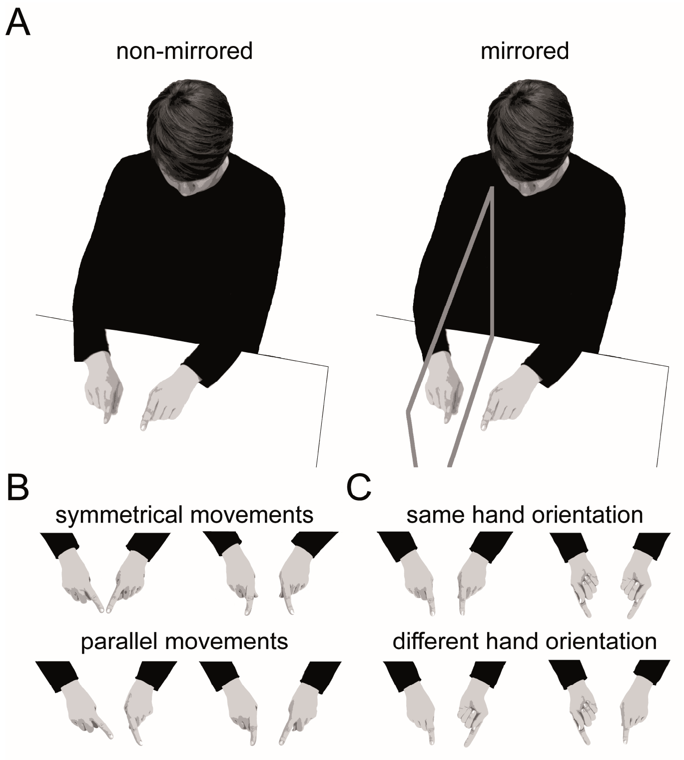


Figure 4.1. Illustration of the finger oscillation task. Participants performed adduction and abduction movements with the index fingers of both hands. *A*. Participants either viewed their hands directly, or looked into a mirror, so that they saw their left hand, and the left hand's mirror image at the location of the right hand. *B*. For symmetrical movements (upper row), participants concurrently moved both fingers in- and outwards. For parallel movements (lower row), participants concurrently moved the two fingers to the left and right in space. *C*. Hands were held either in same (upper row) or in different orientations (lower row).

Procedure. In each trial, participants rhythmically moved both outstretched index fingers to the metronome sounds. Participants were instructed to complete a full movement cycle per beat, that is, move both fingers at the same time in- and outwards when moving symmetrically, or, move both fingers at the same time to the left and right in space when moving in parallel. Instructions stressed that participants should execute movements as correctly as possible, but could change to a more comfortable movement pattern if they were unable to maintain the instructed movement pattern (Lee, Blandin, & Proteau, 1996). Participants had to look at both hands (both real or left real/right mirrored) throughout the experiment. They rested and stretched after every 2 trials.

Data selection and trajectory analysis. Two trials from one participant were excluded because the hand position on the table had accidentally been instructed incorrectly. Two trials were excluded because a participant had partially closed his/her eyes to ease performance. We analyzed the left-right component of finger movement trajectories. Within trials, occasional missing data were interpolated (e.g., if a marker was temporally non-visible), trajectories smoothed with a low-pass filter (first-order Butterworth filter at 7.5 Hz), and normalized by demeaning. Individual movement cycles were then identified as the interval between a consecutive maximum and minimum of the right finger's trajectory. A sine wave was fitted to the trajectory of this interval for each finger (see Y.Q. Chen, 2003, http://www.mathworks.com/matlabcentral/fileexchange/3730-sinefit). See *Figure S1* in the supplemental results (Appendix) for an illustration of the sine wave fit to the raw data. The relative phase of the two fingers was determined as the phase difference of the two fitted sine curves. For symmetrical movements the phase difference should be 180°, because one finger is at its rightmost position when the other is at its leftmost position. For parallel movements the phase difference should be 0°, because both fingers move in synchrony to the left and right in space. The final data set consisted of 62,536 movement cycles from 20 participants with an average of 39 movement cycles per condition and participant (range: 25-46). The reasons for the variability of the number of movements are that participants sometimes paused or made unidentifiably small movements, especially at high speeds; furthermore, participants were sometimes off-beat and then executed fewer movement cycles than instructed.

4.3.1 Statistical inference

General approach. We analyzed the data using a Bayesian statistical analysis approach. In such analyses, credibility is reallocated across candidate parameter values, such as slopes indicating the effect of a certain experimental factor for example, as data, also called 'evidence', is cumulatively taken into account (Kruschke, 2015). These candidate parameters values are given a certain a priori credibility, called the 'prior', which is typically noncommittal. The result of Bayesian model estimation then is a posterior distribution of jointly credible parameter values, given the evidence and the prior belief that certain values are more, less, or equally, likely (Kruschke, Aguinis, & Joo, 2012). Conveniently, the resulting posterior distribution is directly indicative of where in parameter space the true value is most likely to be. For statistical inference, we dichotomized the phase difference of the two fingers into correct (1) and incorrect (0). To this end, the relative location of the two fingers during a movement cycle was compared to the expected relative difference in each condition(+/- 50° around °0 and 180° for parallel and symmetrical movements, respectively, see: Heed & Röder, 2014; Mechsner et al., 2001). The results we report were qualitatively similar when accuracy was dichotomized with a more strict criterion of 20°, see *Figure S2* in the supplemental results; Appendix). We furthermore dichotomized movement speed into slow and fast by collapsing over the five slowest and five fastest movement speeds. This analysis step greatly reduces the computational demands of model fitting, but preserves the well-known modulation of higher performance during slow as compared to fast speeds under parallel instructions. Note, that we illustrate all 10 speed levels in our figures of the raw data, both for comparison with previous studies, and to demonstrate consistency across lower and higher speed levels. Finally, we subsumed hand postures into a two-leveled factor by pooling both hands down and both hands up as 'same hand orientation' and left up/right down and left down/right up as 'different hand orientation' (Heed & Röder, 2014). In response to the concern of a reviewer that based on several earlier reports (Buchanan, Kelso, DeGuzman, & Ding, 1997; Kelso, Buchanan, DeGuzman, & Ding, 1993), we furthermore ascertained that changes in the right-left movements that we report here were not due to a transfer of movement into another movement dimension (such as up-down). We ascertained that (1) the number of movement cycles identified at each speed were comparable across speeds; (2) that the highest velocities were observed in the relevant, and not in an irrelevant, dimension; and (3) that the standard deviation of movement velocity was, accordingly, highest in the relevant dimension (see *Figures S3-S6* in the supplemental results for illustration; Appendix).

Bayesian hierarchical logistic regression. We fitted a hierarchical Bayesian logistic regression model to the dichotomized performance measure to estimate the probability of moving correctly in a given movement cycle through the linear combination of group-level regression beta weights and participant-level intercepts. Regression beta weights are denoted $\beta_{instruction}$ for the main effect of the factor movement instruction, β_{mirror} for the main effect of the factor mirror view, $\beta_{posture}$ for the main effect of the factor hand posture, and β_{speed} for the main effect of the factor speed. Furthermore, regression beta weights were included for all possible factor combinations and are denoted β_{i_n} with *i, n* denoting *i* factors interacting with *n* other factors (Liddell & Kruschke, 2014). For instance, the model parameter denoted $\beta_{instruction\_mirror\_posture}$ represents the regression beta weight for the three-way interaction of movement instruction, mirror view, and hand posture. Beta weights were constrained to sum to zero, with the first factor level dummy-coded as 1 and the second one as -1 ($\beta_{instruction}$: symmetrical=1, parallel=-1; β_{mirror}: non-mirrored=1, mirrored=-1; $\beta_{posture}$: same=1, different=-1; β_{speed}: fast=1, slow=-1).

Uninformative priors were chosen for all model parameters. Specifically, priors were modeled as normal distributions centered on zero, corresponding to a .5 probability of moving correctly. Precision, that is, the width of the normal distribution, of each prior was drawn from an inverse gamma distribution with shape parameter 1 and scale parameter .01 to allow for a large range of possible values (Gill, 2010). We re-sampled our model with several alternative specifications for uninformative priors to ensure that posterior distributions were robust. For instance, we drew the normal distributions' precision from the inverse gamma function with shape parameter .01 and scale parameter .01, rendering qualitatively identical results (not reported).

Model estimation and inference. We used JAGS version 4.0.0 (Plummer, 2015), R version 3.2.2 (R Core Team, 2016), and the R package runjags version 2.0.2-8 (Denwood, M. J., 2016) to perform Markov Chain Monte Carlo (MCMC) sampling. Specifically, we sampled 60,000 representative credible values from the joint posterior distribution of the model parameters in four independent chains. The chains were burned in (1500 samples) and every 20th sample was saved, rendering a total of 12,000 recorded samples. Stable and accurate representation of the parameter posterior distributions was ensured visually using trace, autocorrelation, and density plots, as well as numerically by examining the effective sample size (ESS), and the shrink factor (S. P. Brooks & Gelman, 1998). All model parameters of interest had a minimum EES of 11,550, ensuring stable and accurate estimates of the limits comprising 95% of the posterior samples (i.e., their highest density interval (HDI); Kruschke, 2015). For statistical inference, the model parameters of interest are the normalized group-level regression beta weights, which indicate the influence of each factor or factor combination (i.e., interaction) in determining the probability of moving correctly in the finger oscillation task. If the HDI of a beta weight representing a specific factor or interaction does not span zero, this implies that the factor contributes to the prediction of movement accuracy. In contrast, a HDI that spans zero indicates that a beta weight representing a specific factor does not contribute to the prediction of movement accuracy. In analogy to post-hoc testing in frequentist approaches, we assessed condition differences only if the HDI of the corresponding beta weight representing the overall effect or interaction did not span zero. For such comparisons, we contrasted the posterior predictive distributions of the factor level combinations that represented our hypotheses in the model. When multiple beta weights containing the hypothesis-relevant factors did not span zero, we took the beta weight representing the highest order interaction as the basis for whether a contrast should be evaluated or not. Contrasts are reported in the form of difference_{a_b} with *a, b* indicating *a* factor levels interacting with *b* other factor levels (Liddell & Kruschke, 2014). The distribution resulting from contrasting factor-level posterior predictive distributions are denoted as credible difference distributions. Similar to the inferential strategy applied to the beta weight posterior distributions, an HDI of a credible difference distribution that does not span zero indicates that the model predictions for the two conditions of interest are different from each other, whereas an HDI of a credible difference distribution that spans zero indicates that the model predictions for the two conditions do not differ statistically. In the text, tables, and figures, beta weight and credible difference distributions are characterized by their mean and their upper and lower 95% HDI limit. Figures were prepared using the R package ggplot2 version 2.0.0 (Wickham, 2009).

4.4 Results

Twenty participants performed the finger oscillation task, that is, they made symmetrical and parallel finger abduction and adduction movements with the index fingers of the two hands with gradually increasing speed (Heed & Röder, 2014; Mechsner et al., 2001). In different blocks, the two hands had either the same orientation with both palms up or down, or different orientations, with one hand facing palm up and the other palm down. This latter manipulation reverses the muscles involved in symmetrical vs. parallel movements: whereas symmetrical movements usually require the use of homologous muscles in the two hands, this muscle configuration is now required for parallel movements. To manipulate visual afferent information, a mirror was placed between the hands in half of the experiment; it hid the right hand, and participants saw the mirror image of the left hand in its place, creating the impression that the currently performed movement was symmetrical, and that both hands had the same posture, independent of the true movement type and hand posture. We tested how the congruence and incongruence of these aspects of visual feedback with the truly performed movement affected the accuracy of bimanual movement coordination.

4.4.1 Anatomical and external contributions to bimanual coordination

We first tested whether both external and anatomical influences were at all present in our study; the following analyses then focused on which type of visual information modulated these biases. We compared conditions in which correct performance required the use of homologous and non-homologous muscles in the two hands to make symmetrical or parallel movements. We dichotomized movement accuracy by classifying movements as correct when the phase difference of the two fingers deviated by less than 50° from the instructed movement phase in a single movement cycle of abducting and adducting the fingers. 180° in external space for symmetrical movements, often referred to as 0° when referring to muscles instead; 0° in external space for parallel movements (Heed & Röder, 2014; Mechsner et al., 2001). If bimanual coordination were solely constrained by anatomical factors, performance should be superior whenever homologous muscles as opposed to non-homologous muscles must be used, regardless of hand posture and movement instruction. Alternatively, if movement coordination were solely constrained by external factors, the symmetry advantage should prevail regardless of whether homologous muscles are involved in the instructed movement. If both anatomical and external factors constrained bimanual coordination, performance in either movement condition should benefit from the use of homologous muscles, in addition to a general advantage of symmetrical over parallel movements.

Whether the instructed movement required the use of homologous muscles depended on the experimental factors movement instruction and hand posture. When both palms had the same orientation, symmetrical movements involved homologous muscles, and parallel movements involved non-homologous muscles. In contrast, when the hands were held in different postures, symmetrical movements involved non-homologous muscles, and parallel movements involved homologous muscles.

Performance declined with increasing movement speed, but more so for parallel than for symmetrical movements, evident in a stronger decline of movement cycles in which the phase difference was classified as correct (i.e., deviating maximally +/-50° from the expected phase difference of 180° for symmetrical, and 0° for parallel movements). In addition, performance was better with the hands in the same than in different postures for symmetrical movements, whereas the opposite performance pattern emerged for parallel movements (*Figure 4.2*: left panels; *Figure 4.3*). We assessed the statistical significance of these performance differences with a Bayesian model that included parameters that reflected main effects of the experimental manipulations of movement instruction (symmetrical, parallel), hand posture (same, different), and movement speed (dichotomized into slow, fast) and all interactions between them. The posterior distributions of the beta weights that together reflected modulations by anatomical and external spatial coding ($\beta_{instruction}$, $\beta_{posture}$, β_{speed}, $\beta_{instruction\_posture}$, $\beta_{instruction\_speed}$, $\beta_{instruction\_posture\_speed}$) did not span zero, confirming that each factor, as well as their interactions, contributed to bimanual coordination performance (*Table 4.1*; *Figure 4.4*).

		95% HDI		
	mean	**LL**	**UL**	**EES**
$\boldsymbol{\beta}_{\mathbf{intercept}}$	2.06	1.79	2.35	563
$\boldsymbol{\beta}_{\mathbf{instruction}}$	0.82	0.79	0.85	12000
$\boldsymbol{\beta}_{\mathbf{mirror}}$	0.02	-0.01	0.05	12000
$\boldsymbol{\beta}_{\mathbf{posture}}$	0.12	0.09	0.15	12000
$\boldsymbol{\beta}_{\mathbf{speed}}$	-0.62	-0.65	-0.59	12000
$\boldsymbol{\beta}_{\mathbf{instruction\_mirror}}$	-0.09	-0.12	-0.06	12000
$\boldsymbol{\beta}_{\mathbf{instruction\_posture}}$	0.48	0.45	0.51	12000
$\boldsymbol{\beta}_{\mathbf{instruction\_speed}}$	0.25	0.22	0.28	12000
$\boldsymbol{\beta}_{\mathbf{mirror\_posture}}$	0.00	-0.03	0.03	12000
$\boldsymbol{\beta}_{\mathbf{mirror\_speed}}$	0.00	-0.03	0.03	12000
$\boldsymbol{\beta}_{\mathbf{posture\_speed}}$	0.02	-0.01	0.05	12000
$\boldsymbol{\beta}_{\mathbf{instruction\_mirror\_posture}}$	-0.03	-0.06	0.00	11775
$\boldsymbol{\beta}_{\mathbf{instruction\_mirror\_speed}}$	-0.04	-0.07	-0.01	11550
$\boldsymbol{\beta}_{\mathbf{instruction\_posture\_speed}}$	0.05	0.02	0.07	12000
$\boldsymbol{\beta}_{\mathbf{mirror\_posture\_speed}}$	0.02	-0.01	0.05	12000
$\boldsymbol{\beta}_{\mathbf{instruction\_mirror\_posture\_speed}}$	-0.01	-0.04	0.02	12000

Table 4.1. Results of the statistical analysis. Logit mean posterior beta weights, their lower (LL) and upper (UL) 95% highest density interval (HDI) limits, and their effective sample size (ESS) of the Bayesian hierarchical logistic regression model, estimated with Markov Chain Monte Carlo (MCMC) sampling. Beta distributions of parameters that were relevant to the tested hypotheses of the study had a minimum ESS of 11,550, ensuring stable and accurate MCMC sampling and chain convergence. Grey shading marks posterior beta weights with an HDI that does not span zero. See *Figure 4.4* for graphical illustration of model results and the text for details on the inferential strategy.

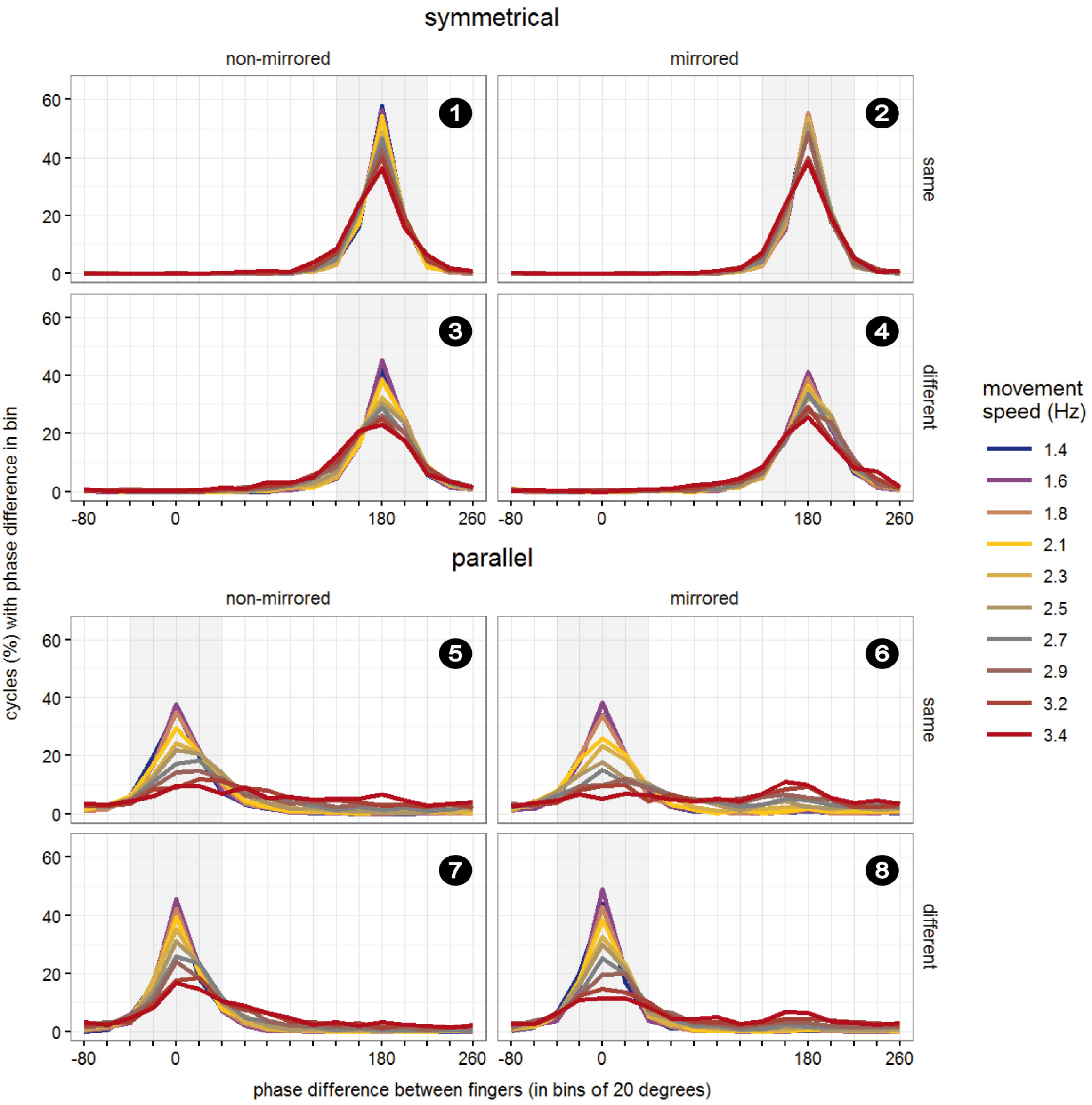


Figure 4.2. Performance in the finger oscillation task. Relative phase difference was binned in intervals of 20° from -90° to +270° and then divided by the total number of cycles within participants to derive percentage values. Results were averaged across participants, separately for symmetrical (upper panels) and parallel movements (lower panels) at 10 movement speeds. Performance is depicted for non-mirrored (left column) and mirrored (right column) visual feedback conditions, as well as for same (upper panel), and different hand orientations (lower panel). Symmetrical and parallel movements are defined in terms of the horizontal spatial dimension: 180° phase difference indicates moving in perfect symmetry, because one hand is at its leftmost, while the other one is at its rightmost location. In contrast, a 0° phase difference indicates moving perfectly in parallel, because both hands are at their left- and rightmost positions at the same time. Grey shading indicates the range of the phase difference considered as "correct" for statistical analysis (180° +/- 50°: correct symmetrical movement vs. 0° +/-50°: correct parallel movement). Panels are numbered chronologically for integration of results with *Figure 4.3* and *Figure 4.5* (white numbers on black circles).

Hypothesis-driven, direct comparison of the model posterior predictions for conditions that involved homologous vs. non-homologous muscles, separately for symmetrical and parallel movements at slow and fast speeds (parameter: $\beta_{\text{instruction\_posture\_speed}}$), revealed two key findings. First, the resulting credible difference distributions did not span zero, and the estimated mean performance was larger for symmetrical than parallel movements, both at slow and fast speeds. This result confirmed superior performance of symmetrical over parallel movements independent of hand posture, implying external-spatial contributions to performance. Second, all resulting credible difference distributions were positive, suggesting that performance benefitted from the use of homologous muscles and, thus, indicating that performance was modulated by anatomical factors. These differences were more pronounced at fast than at slow speeds (homologous minus non-homologous conditions: same-different$_{\text{symmetrical\_fast}}$: M=2.66 [2.43 2.92]; different-same$_{\text{parallel\_fast}}$: M=1.56 [1.43 1.70]; same-different$_{\text{symmetrical\_slow}}$: M=2.17 [1.85 2.49]; different-same$_{\text{parallel\_slow}}$: M=1.33 [1.13 1.53]).

In sum, these results indicate that bimanual coordination is constrained by external factors, but additionally modulated by anatomical factors, replicating the result of our previous report (Heed & Röder, 2014) in an independent sample and supporting previous accounts of a mixed influence of both in bimanual coordination (Oliveira & Ivry, 2008; Spencer & Ivry, 2007; Swinnen et al., 1998; Temprado et al., 2003).

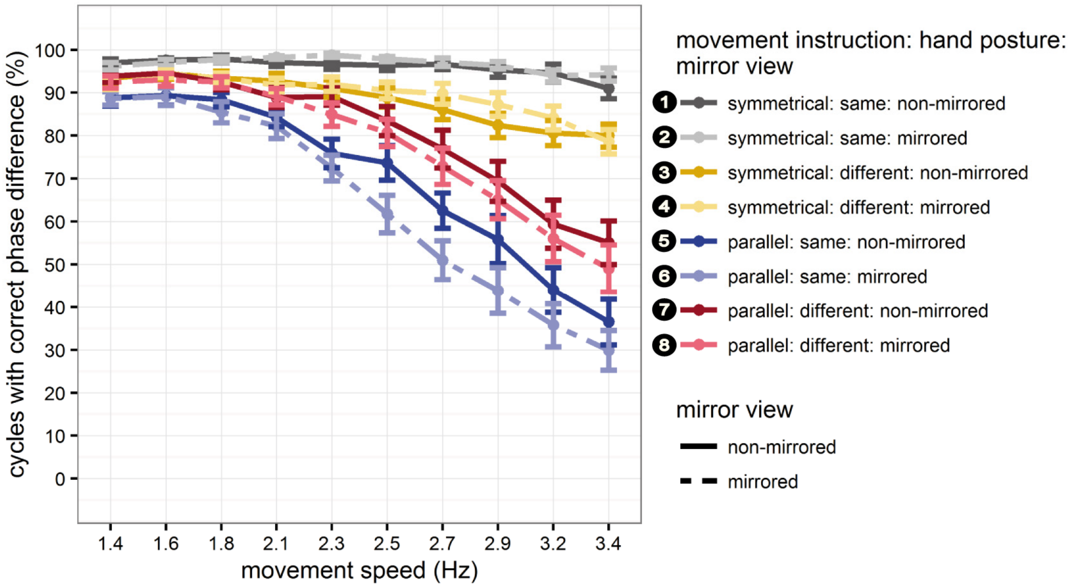


Figure 4.3. Accuracy in the finger oscillation task. Data points correspond to the grey regions in *Figure 4.2*. Percentage of movement cycles with the correct phase difference (+/-50°, as explained in *Figure 4.2*) between the two index fingers. Line colors represent the interaction of movement instruction (symmetrical vs. parallel) and hand posture (same vs. different). Dark colors and solid lines represent non-mirrored conditions, and bright colors and dashed lines indicate mirrored feedback conditions. Error bars represent standard errors of the mean. Conditions are numbered in correspondence to *Figure 4.2* and *Figure 4.5*. (white numbers on black circles).

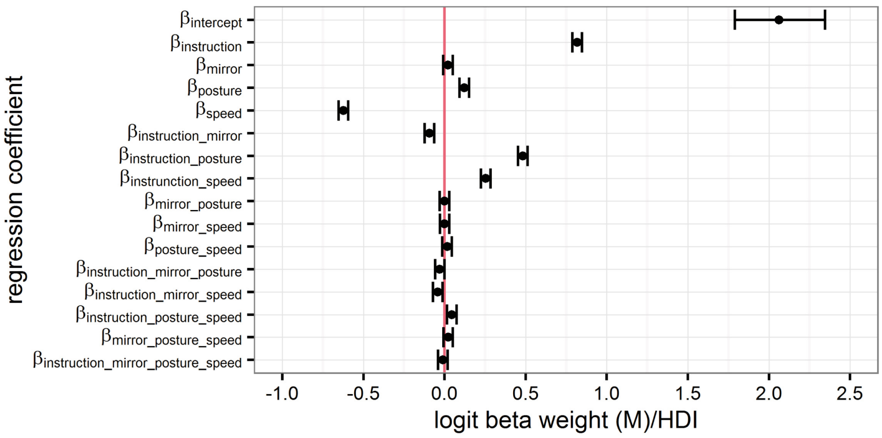


Figure 4.4. Illustration of the results of the statistical analysis listed in *Table 4.1*. Logit mean posterior beta weights of the Bayesian hierarchical logistic regression model. The area between whiskers represents the highest density interval (HDI) of a beta weight's posterior distribution, as estimated with Markov Chain Monte Carlo (MCMC) sampling. If a beta weight contributes to the prediction of movement accuracy in the finger oscillation task, its HDI does not span zero (depicted as vertical red line).

4.4.2 Body-related visual information integrated for action

The present study's main aim was to determine whether, and if so, which specific kind of abstract spatial or body-related visual information constrains movement coordination. Therefore, our experiment was designed to disentangle different kinds of visual feedback: about movement direction, about hand posture, and about the muscles involved in the current action.

Each of these potential influences makes distinct predictions about the pattern of bimanual coordination performance across our experimental factors, and we will briefly introduce each predicted pattern (see *Figure 4.5* for a visual illustration of the three different visual feedback conditions induced by the mirror).

Visual feedback about movement direction. One potential source of information could be the direction of movement, independent of the further specification of how this movement is achieved, that is, irrespective of posture and involved muscles. In our paradigm, this influence of visual information about movement direction (symmetrical vs. parallel) would be evident in a difference between conditions in which visual and proprioceptive modalities provided congruent vs. incongruent information about the type of performed movement (*Figure 4.5A*). Without the mirror, visual and proprioceptive information about the executed movement were always congruent (uneven numbered conditions in *Figure 4.2*, *Figure 4.3*). With the mirror, visual-proprioceptive feedback was incongruent whenever the fingers moved parallel; in these conditions, visual feedback indicated that the fingers were moving symmetrically. If visual feedback about movement direction were relevant for bimanual coordination, performance in congruent feedback conditions (numbered 2 and 4 in *Figure 4.2*, *Figure 4.3*, *Figure 4.5A*) should be superior to that in conditions with incongruent visual-proprioceptive information (numbered 6 and 8 in *Figure 4.2*, *Figure 4.3*, *Figure 4.5A*). Critically, this difference should be independent of hand posture. Accordingly, congruence of visual-proprioceptive information about movement direction depended on the experimental factors movement instruction and mirror view.

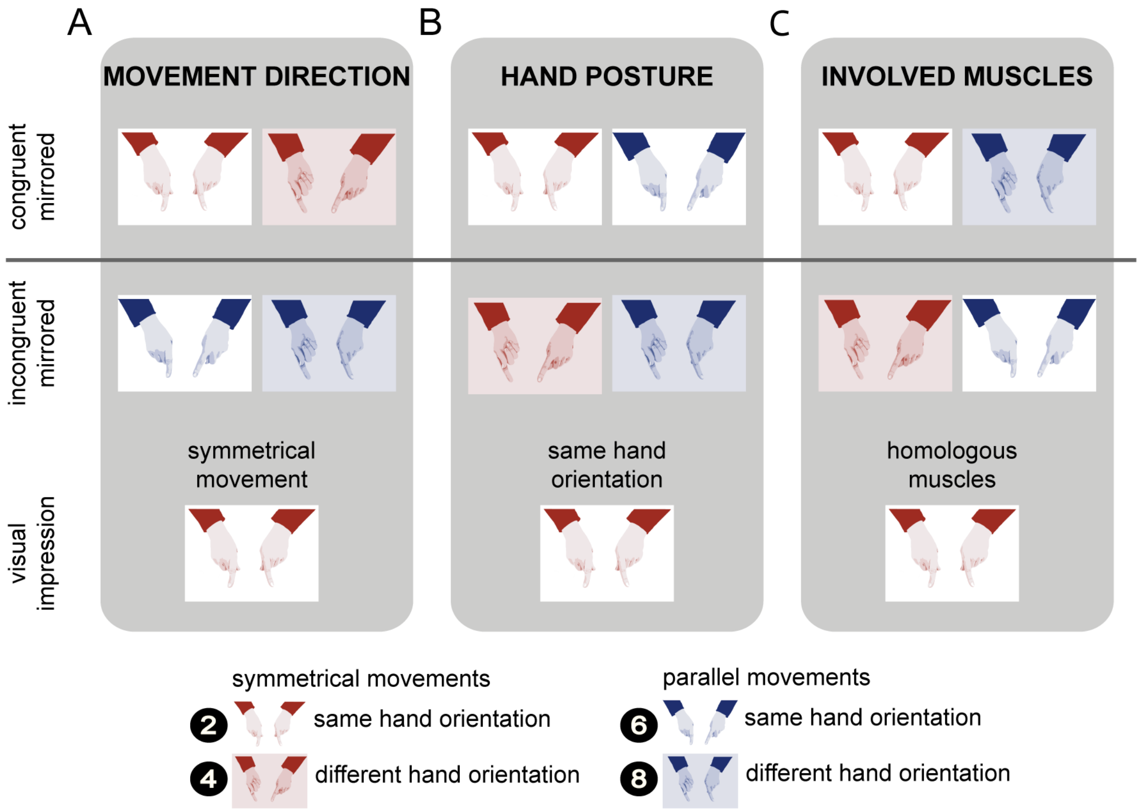


Figure 4.5. Illustration of the different visual feedback conditions induced by the mirror. Columns structure the mirrored experimental conditions according to visual feedback about movement direction (*A*), hand posture (*B*), and involved muscles (*C*). Rows represent experimental conditions structured according to congruent mirrored, and incongruent mirrored conditions, as well as according to the participants' visual impression concerning each feedback aspect. Color indicates the movement instruction, with red designating symmetrical movements, and blue parallel movements. Background configuration indicates the hand posture, with no filling designating hands held in the same orientation, and a colored background designating hands held in different orientations. Conditions are numbered in correspondence to *Figure 4.2* and *Figure 4.3* (white numbers on black circles).

Visual feedback about posture. A potential influence of visual information about hand posture would be evident in a difference between conditions with congruent vs. incongruent information about posture from vision and proprioception (*Figure 4.5B*). Without the mirror, visual-proprioceptive information about posture was always congruent (uneven numbered conditions in *Figure 4.2*, *Figure 4.3*). With the mirror, visual-proprioceptive information was incongruent when the two hands had different postures; in these conditions, mirror feedback indicated that the hands had the same orientation. If visual feedback about hand posture were relevant for bimanual coordination, performance should be superior in congruent (numbered 2 and 6 in *Figure 4.2*, *Figure 4.3*, *Figure 4.5*B) over incongruent (numbered 4 and 8 in *Figure 4.2*, *Figure 4.3*, *Figure 4.5*B) visual-proprioceptive posture conditions. Critically, this performance advantage should be independent of movement instruction, that is, of whether executed movements are symmetrical or parallel. Accordingly, congruence of visual and proprioceptive feedback about hand posture depended on the experimental factors mirror view and hand posture.

Visual feedback about the involved muscles. A potential influence of visual information about the muscles involved in the current action would be evident in a difference between congruent vs. incongruent visual-proprioceptive information about the currently active muscles (*Figure 4.5C*). Without the mirror, visual-proprioceptive information about involved muscles was always congruent (uneven numbered conditions in *Figure 4.2*, *Figure 4.3*). With the mirror, the combination of movement instruction and hand posture determined whether visual-proprioceptive feedback was congruent or not. Visual-proprioceptive information was, for instance, incongruent when participants made symmetrical movements with differently oriented hands. In this situation, the hands appeared to be oriented in the same posture due to the mirror, and, thus, vision suggested that homologous muscles were used, although truly participants had to use non-homogenous muscles. Further conflict conditions are illustrated in *Figure 4.5C*. If visual feedback about muscles were relevant for bimanual coordination, performance in congruent apparent muscle conditions (numbered 2 and 8 in *Figure 4.2*, *Figure 4.3*, *Figure 4.5*C) should be superior over incongruent conditions (numbered 4 and 6 in *Figure 4.2*, *Figure 4.3*, *Figure 4.5C*). Accordingly, congruence of visual-proprioceptive feedback about involved muscles depended on the experimental factors movement instruction, mirror view, and hand posture.

4.4.3 Visual feedback about movement direction is relevant for bimanual coordination

With the mirror present, performance improved for symmetrical movements, but deteriorated for parallel movements, both relative to regular viewing without the mirror. These effects were evident in a gradual decline of the percentage of correctly executed movement cycles with increasing movement speed (*Figure 4.2*, *Figure 4.3*). For symmetrical movements, this effect was small due to performance near ceiling even at high speeds with the hands held in the same posture. Crucially, the effect of visual feedback varied systematically with movement instruction, but not with hand posture. The posterior distributions of the relevant model beta weights, $\beta_{instruction\_mirror}$ and $\beta_{instruction\_mirror\_speed}$, did not span zero, confirming that they contributed to explaining the probability of moving both fingers (*Table 4.1*, *Figure 4.4*). This result indicates an effect of visual information about movement direction, but not about hand posture and involved muscles.

To further scrutinize this result, we subtracted posterior model predictions in the non-mirrored conditions from those in the mirrored conditions, separately for symmetrical and parallel movements at slow and fast speeds (parameter: $\beta_{instruction\_mirror\_speed}$). The credible difference distributions are displayed in *Figure 4.6*. Performance deteriorated during parallel movements in mirror as compared to non-mirrored conditions, as evident in the negative distribution of credible differences at both slow and fast speeds, all of which did not span zero. In contrast, performance improved during symmetrical movements in mirrored relative to non-mirrored conditions, as evident in the positive distribution of credible differences at fast speeds, which again did not span zero. This performance improvement was not evident at low speeds, presumably because performance was more similar overall during slow movements, in line with previous reports (see *Figure 4.3*).

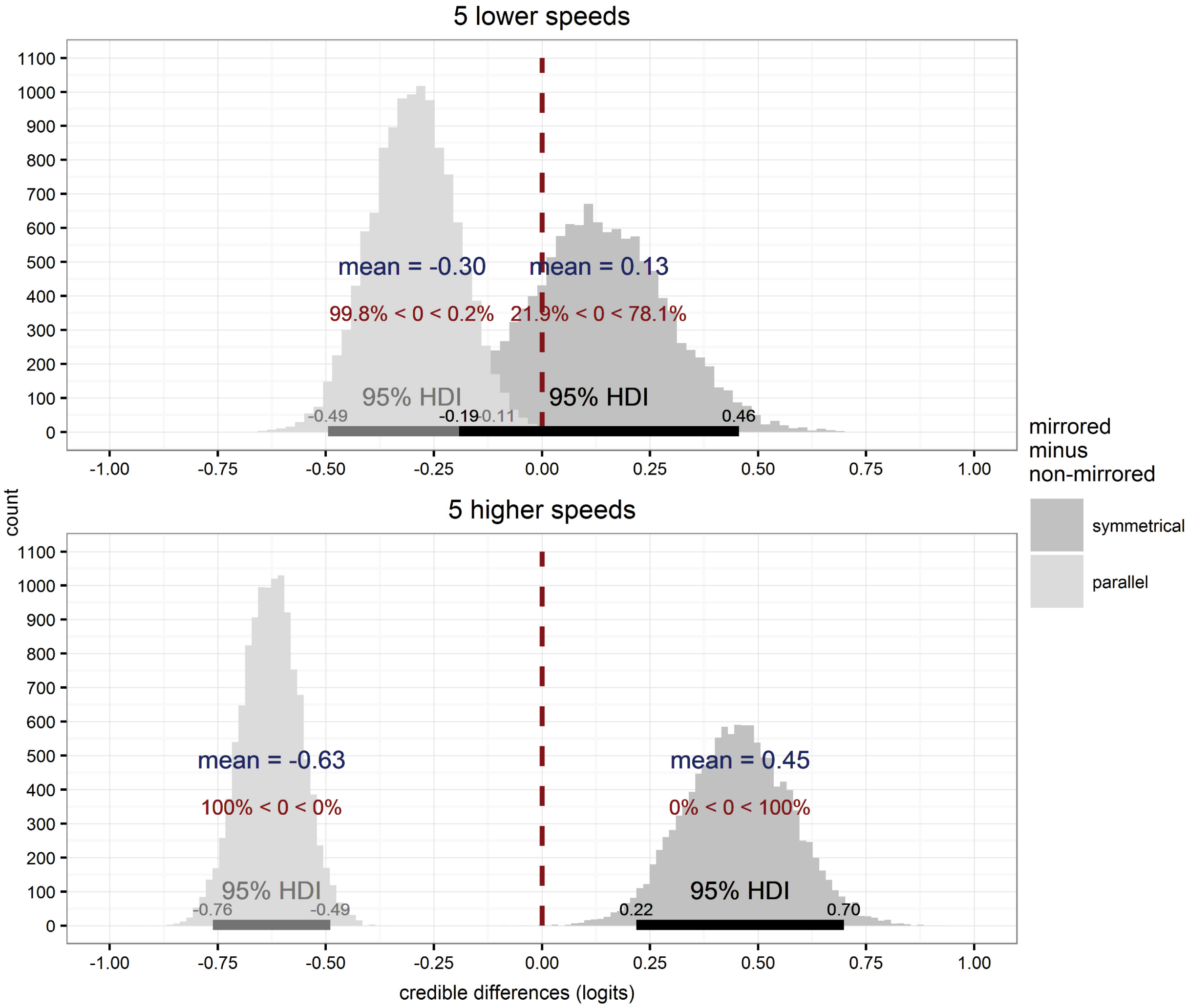


Figure 4.6. Illustration of credible difference distributions of the parameter $\beta_{\text{instruction\_mirror\_speed}}$ estimated within the Bayesian hierarchical logistic regression model. Mirrored and non-mirrored visual feedback conditions are contrasted separately for symmetrical and parallel movements (dark and light grey) across slow and fast movement speeds (top and bottom row). Red inscriptions per distribution indicate the percentage of distributions' samples falling below and above zero. Horizontal bars indicate 95% highest density interval (HDI) limits. Credible difference distributions indicated that visual feedback about movement direction influenced bimanual coordination. At low speeds, performance deteriorated for parallel movements when the mirror was present (light distribution in upper panel). In contrast, no reliable change was evident for symmetrical movements, evident in that the darker distribution in the upper panel includes zero. At high speeds, too, performance deteriorated for parallel movements when the mirror was present (light distribution in the lower panel), but improved for symmetrical movements with the mirror present as compared to regular viewing (dark distribution in the lower panel).

4.4.4 Visual information about hand posture and involved muscles are irrelevant for bimanual coordination

To further test whether, indeed, coordination relied solely on visual direction information, we directly examined the parameter estimates relevant for the potential alternatives, namely, hand posture and involved muscles.

For hand posture, the posterior distributions of the model beta weights $\beta_{mirror\_posture,}$ and $\beta_{mirror\_posture\_speed}$ spanned zero, suggesting that this experimental factor did not contribute to explaining the probability of moving correctly (*Table 4.1*, *Figure 4.4*). Thus, statistical analysis did not provide any evidence that visual information about hand posture constrained movement coordination in the present experiment.

An effect of visual information about involved muscles would be evident in the interaction of the experimental factors movement instruction, mirror view, and hand posture (*Figure 4.5C*). Note that a modulation of visual information about involved muscles would thus encompass the same factors that also indicate a modulation of visual information about movement direction, namely movement instruction and mirror view, but would warrant an additional modulation by hand posture. The posterior distributions of the corresponding model beta weight $\beta_{instruction\_mirror\_posture}$ just barely excluded zero (*Table 4.1*, *Figure 4.4*). Nonetheless, we followed up on this finding by subtracting posterior model predictions for incongruent from congruent mirror conditions, separately for symmetrical and parallel movements. The distributions of credible differences were positive and did not span zero, indicating that performance in congruent feedback conditions was superior to performance in incongruent conditions, as would be predicted if visual information about involved muscles were relevant for coordination (congruent minus incongruent conditions: same-different$_{symmetrical\_mirrored}$: M=2.53 [2.23 2.83]; different-same$_{parallel\_mirrored}$: M=1.56 [1.39 1.72]).

We further reasoned that, if visual feedback about the involved muscles indeed determined coordination, performance in congruent mirror conditions should be indistinguishable from performance in corresponding conditions without mirror, because in both cases, visual and proprioceptive feedback unanimously indicate that corresponding muscles are used. Additionally, along with altering visual feedback concerning muscle identity, the mirror manipulation presumably affected visual feedback concerning the relative timing of bimanual muscle activation. With regular visual feedback of the hands, the dominant hand has been observed to lead the non-dominant hand by about 25 ms in bimanual coordination tasks (Semjen et al., 1995a). Correspondingly, mirrored feedback about the timing of muscle activation would not correspond exactly to its actual timing, given the slight lag of the non-dominant hand. Therefore, we predicted that performance in congruent mirrored conditions should be worse than in congruent non-mirrored conditions if visual information concerning involved muscles determined coordination. To test this prediction, we subtracted posterior model predictions for congruent non-mirrored from congruent mirror conditions, separately for symmetrical and parallel movements. Note that a differential effect of mirror view depending on movement instruction cannot be accounted for by a visual effect of involved muscles, as both conditions are identical concerning muscle information. If nonetheless the effect of mirror view depends on the movement instruction, this would further corroborate the effect of visual movement direction, as parallel and symmetrical movements differ concerning this aspect.

The effect of mirror view indeed differed according to the movement instruction. Performance improved with mirrored feedback, relative to non-mirrored conditions, when moving symmetrically (mirrored-non-mirrored$_{\text{symmetrical\_same}}$: M=0.41 [0.06 0.76]). The opposite pattern was evident when moving in parallel, that is, mirrored visual feedback was detrimental to performance (mirrored-non-mirrored$_{\text{parallel\_different}}$: M=-0.35 [-0.52 -0.16]).

Contrary to the comparison of congruent vs. incongruent mirrored conditions concerning involved muscles, the comparison of congruent mirrored with congruent non-mirrored conditions, thus, did not support the notion that visual feedback about the involved muscles constrains bimanual coordination. Instead, the credible, but differential effect of mirrored visual feedback on performance depended on the movement instruction and corroborates that visual movement direction affected coordination performance.

4.4.5 Temporal aspects of visual feedback concerning movement direction

The performance improvement during the viewing of mirrored symmetrical feedback struck us as surprising, as one might expect that the perception of non-veridical visual movement timing feedback would be detrimental to, rather than supportive of, the production of coordinated movement. The present finding led us to speculate that the temporal synchrony of visual feedback in the mirrored condition may actually lead to a decrease of the true lag between the dominant and non-dominant hands in our experiment, potentially marking a mechanism by which the mirror-induced performance improvements observed here may be explained.

When movement direction was visually and proprioceptively congruent, performance was better in mirrored than non-mirrored conditions; this difference was small, but associated with a credible difference parameter estimate in our model. Performance of symmetrical movements was generally near ceiling, so that even substantial differences on the logit scale translate to very small differences in performance measured as percentage correct. Accordingly, the 0.45 improvement on the logit scale translates to only a 0.3% percentage correct improvement at high movement speeds (beta weight in the model: $\beta_{instruction\_mirror\_speed}$). Conversely, smaller differences on the logit scale in other conditions were much more clearly evident on the percentage correct scale. The performance improvement with mirrored relative to non-mirrored feedback (beta weight in the model: $\beta_{instruction\_mirror\_posture}$) and hands held in different orientations was estimated at 2.3% (logit: 0.19; baseline performance level: 85.2%, logit: 1.75), as compared to a 1.0% (logit: 0.26, base performance level: 95.5%, logit: 3.05) improvement with hands held in the same orientation. Nonetheless we are hesitant to capitalize on this result, as the beta weight including posture (beta weight in the model: $\beta_{instruction\_mirror\_posture}$) just barely excluded zero and the performance decline when performing parallel movements with the mirror present relative to non-mirrored visual feedback, was larger (13.7%; 0.63 logits; beta weight in the model: $\beta_{instruction\_mirror\_speed}$).

4.5 Discussion

The present study aimed at specifying anatomical and external-spatial contributions to bimanual coordination performance. Previous findings, mainly from experiments requiring the coordination of limb movements with visual cues, have led to a theoretical account of bimanual coordination, and motor coordination more generally, that stresses the relevance of the perceivability of phase synchrony implied in visual direction information (Bingham, 2004; Bingham et al., 1999, 2001; Zaal et al., 2000). In contrast, findings from some bimanual coordination paradigms have stressed the importance also of anatomical factors such as the muscles involved in a particular bimanual movement, suggesting that visual information about factors other than solely movement direction may play a role in coordinative behavior of the limbs (Heed & Röder, 2014; Swinnen et al., 1998; Temprado et al., 2003). We exploited the well-known bias towards symmetrical over parallel finger movements to delineate different potential sources of visual modulation by introducing a mirror through which participants saw the reflection of one hand projected onto the location of the hidden, other hand. Our study revealed three key results. First, anatomical factors modulated bimanual coordination.

Specifically, participants performed better when bimanual movements required the concurrent activation of homologous rather than non-homologous muscles. Second, external spatial factors, too, modulated bimanual coordination. An advantage of symmetrical movements prevailed regardless of hand posture, and, thus, irrespective of whether homologous muscles had to be activated. Third, of the three kinds of visual information manipulated in the present study – movement direction, hand posture, and the muscles involved in the performed movements –, only movement direction information modulated bimanual performance. In contrast, visual information pertaining to hand posture appeared to be irrelevant for coordination performance, and there was only weak evidence that visual information pertaining to the muscles involved in the current movement may play a role in coordination performance.

In line with the specific modulation by visual direction information we observed in the present experiment, previous studies have demonstrated that visual directional cues are relevant for bimanual coordination. For instance, most coordination tasks result in inherently stable performance only when the bimanual phase patterns are symmetrical or parallel, but not for intermediate phase differences (Kelso, 1984). Yet, participants can execute such out-of-phase movements if their movement is yoked to concurrent symmetrical or parallel visual information while the hands are hidden from view. For instance, human participants can execute four circular hand movements with one hand, and concurrently five with the other only if these movements are translated into equally fast visual circular movements (Mechsner et al., 2001). Furthermore, performance of orthogonal bimanual movements, such as one hand moving up and down, while the other hand moves to the left and right, improves if visual feedback is given in one plane, that is, as if both hands were moving up and/or down (Bogaerts et al., 2003). These studies suggest that performance of less stable coordination patterns improves if directional visual feedback indicates that an inherently stable coordination pattern, that is, symmetrical or parallel movement, is performed.

Bimanual movements can also be stable when visual feedback is not symmetrical or parallel, but if, instead, movement paths of both hands can be visually perceived as forming a common, coherent shape (Franz, Zelaznik, Swinnen, & Walter, 2001). In a similar vein, participants can execute polyrhythmic two-hand movements when guided by visual displays that integrate directional information of the two hands into one common visual signal (Shea et al., 2016).

These so-called Lissajous displays integrate the position of the two hands into a single point on the display by mapping the movement of each limb onto one axis. Performance in this setup is best if the display shows both the visual target pattern and a cursor that indicates the current (transformed) limb position (Kovacs, Buchanan, & Shea, 2008, 2009, 2010; Kovacs & Shea, 2011). Performance declines rapidly if the display is turned off, suggesting that the integration of the immediate visual direction information about the to-be-performed coordination pattern is a prerequisite for its execution (Kovacs et al., 2008; Kovacs & Shea, 2011).

Kovacs and colleagues have interpreted these findings as empirical support of the perception-action model proposed by Bingham and colleagues, which capitalizes on visual direction information as the cardinal factor for successful bimanual coordination (Bingham, 2004; Bingham et al., 1999, 2001; Kovacs et al., 2010; Zaal et al., 2000). Visual conditions such as those created by the above-mentioned experimental setups then presumably aid error detection, because they facilitate the perceivability of relative movement direction (Kovacs et al., 2009, 2010). In line with the idea of visual movement direction driving coordinative behavior, typical coordination phenomena, such as the advantage of symmetrical over parallel movements, persist even if movements are coordinated only visually. This is the case, for instance, when two people must coordinate their movements (Schmidt et al., 1990; Temprado et al., 2003) and when participants must coordinate their movement with moving visual stimuli on a display (Wilson et al., 2005b; Wimmers et al., 1992). Using such a visual coordination paradigm, it has been demonstrated for example that training participants abilities' to detect relative movement direction, improves coordination performance with a moving visual stimulus on a display (Wilson et al., 2010). In a similar vein, perceptual detection of relative phase has been shown to be largely unaffected by alternative candidate movement parameters, such as frequency and speed, thus further scrutinizing the importance of relative movement direction for the perceivability of relative phase (Wilson & Bingham, 2008). In light of these results, it has been suggested that bimanual coordination is but a special case of any form of visually driven coordination and as such similarly relies on the perceptual ability to detect relative phase from movement direction. Crucially, this conclusion presumes that the brain abstracts movement direction and dismisses all other body-specific visual information. We provide direct experimental evidence for this assumption here, using a strictly bimanual paradigm and thus bridging the gap between findings from visuomotor and bimanual coordination that have used different experimental approaches.

Collectively, then, these results stress the importance of visual movement direction for bimanual coordination and provide a comprehensive account for the dominant role of visual direction information we observed in the present study. In contrast, a general degeneration of vision does not impair performance (Buckingham & Carey, 2008; Mechsner et al., 2001; Swinnen, Lee, Verschueren, Serrien, & Bogaerds, 1997), or, leads to only a minor destabilization (Salesse, Oullier, & Temprado, 2005). Similarly, visual augmentation by marking fingers that have to move together to produce symmetric or parallel tapping patterns does not affect performance (Mechsner, 2004). Moreover, previous studies have suggested that movement execution is modulated by the level of abstraction of visual effector feedback (Brand et al., 2016; Veilleux & Proteau, 2010). Our study did not abstract visual direction information, but, through the mirror setup, provided participants with visual feedback that appeared to reflect the real hands. This experimental situation, thus, more closely resembles the true visual feedback of everyday situations, in which we usually have full vision of our effectors (N. P. Holmes & Spence, 2005). Our results show that the brain indeed abstracts movement direction from body-related visual feedback during bimanual coordination, while discarding visual information regarding hand orientation, as well as involved muscles, and thus validates a generalization of the findings obtained with more abstract feedback situations, such as cursors on a screen, to realistic feedback situations.

It is under debate whether continuous, rhythmic movements and short, goal-directed movements rely on similar brain mechanisms. The role of visual information has been investigated in the context of bimanual goal-directed movement (Reichenbach, Franklin, Zatka-Haas, & Diedrichsen, 2014; C. Weigelt & Cardoso de Oliveira, 2002; M. Weigelt, Rieger, Mechsner, & Prinz, 2007) and especially in the context of unimanual goal-directed movement (e.g., Wolpert, Ghahramani, & Jordan, 1995). In these studies, visual information about effector position affected performance, in line with the requirement of integrating target location with current limb position (Kalaska, Scott, Cisek, & Sergio, 1997; Saunders & Knill, 2003). For instance, visual information about the limb can dominate proprioceptive position, information a phenomenon termed ‘visual capture’ (Hay, Pick, & Ikeda, 1965; N. P. Holmes, Crozier, & Spence, 2004). Furthermore, specific resources appear to be devoted to monitoring hand position during goal-directed movement (Reichenbach et al., 2014). The relative contribution of – usually redundant – visual and proprioceptive signals to movement planning depends on the reliability of each informational source (Ernst & Banks, 2002; McGuire & Sabes, 2009; Morgan, DeAngelis, & Angelaki, 2008; Sober & Sabes, 2003; van Beers, Sittig, & Denier van der Gon, 1998; van Beers et al., 1999), and the relative weighting of visual and proprioceptive signals differs according to the stage in motor planning (Sarlegna et al., 2003; Sober & Sabes, 2003). Visual information appears to be most important when inferring external spatial movement parameters, whereas primarily proprioceptive feedback is used when inferring muscular-based, position-related information, as is necessary to translate a motor plan into body-or hand-centered coordinates for execution (Sarlegna et al., 2003; Sarlegna & Sainburg, 2009; Sober & Sabes, 2003).

To relate the present study to these findings from studies on goal-related movement, one can conceptualize the present repetitive finger oscillation task in an analogous framework. Here, visual direction information outweighed proprioceptive and motor signals to guide continuous bimanual coordination, in line with the finding goal-directed movements primarily rely on visual information when external spatial movement parameters must be inferred. In contrast, visual information about hand posture and involved muscles did not affect performance, suggesting that proprioceptive information outweighed visual feedback for these properties in the present task. This pattern is in line with the prominent role of proprioceptive signals when muscular-based, position-related information must be derived for goal-directed movement to translate a motor plan into body- or hand-centered coordinates for movement execution. However, the repetitive nature of the present bimanual task prohibits formally distinguishing between planning and execution stages of the movements, and, thus, makes it difficult to draw firm conclusions about the potential overlap regarding the processing principles of goal-directed, unimanual and continuous, bimanual movements.

In the present task, mirrored visual movement information was always integrated for bimanual coordination, but the behavioral consequences of integration depended on whether visual movement information was congruent or incongruent with proprioceptive and motor signals. This result pattern seems to be at odds with previous studies that reported that integration of mirrored visual feedback scaled with the degree of congruency of visual and proprioceptive movement information (Bultitude, Juravle, & Spence, 2016; N. P. Holmes, Snijders, & Spence, 2006; Medina et al., 2015). In these studies, synchronous movements led to reliance primarily on visual information, whereas asynchronous movements led to reliance primarily on proprioceptive information. Notably, the dependent measures marking integration of visual information in these studies – gap detection at, or pointing movements with, the hidden hand – were acquired after bimanual movements with mirrored visual feedback had been performed for some time. Thus, the dependent measures were unimanual and as such not indicative of visual contributions to bimanual coordination performance. Furthermore, both measures might differ considerably with regard to the reliability and relevance assigned to bimanual visual information, as compared to continuous bimanual coordination performance assessed in the present task.

Incongruence of movement-related visual, proprioceptive, and motor information led to a performance decline of bimanual coordination in our study. This result is in line with reports of MVT suggesting that incongruent sensory feedback induces phantom sensations, such as tickling and numbness, in healthy participants (Daenen et al., 2010; Foell et al., 2013; McCabe et al., 2005; Medina et al., 2015). In contrast, congruence of mirrored visual, proprioceptive, and motor information led to a performance improvement, possibly because the mirrored movement information during symmetrical movements provided optimized visual feedback about the temporal aspects of bimanual movements. These findings bear relevance on clinical applications of the mirror manipulation. So far, few standardized MVT treatment protocols exist, and those that do have specified that movements should be bilateral and performed in synchrony, but have not stressed that they should be symmetrical as well (Grünert-Plüss, Hufschmid, Santschi, & Grünert, 2008; McCabe, 2011). It has even been suggested that the "[…] actual manner of movement appears not to matter as long as it is bilateral and synchronized" (McCabe, 2011). Additionally, it has been suggested that therapeutic aids should be used unilaterally using the healthy arm in front of the mirror (Grünert-Plüss et al., 2008). These and similar instructions possibly produce incongruence of proprioceptive and visual movement direction, which might produce undesired effects and explain why scientific evidence in favor of MVT as a tool to aid bimanual function is still scarce to date. Consequently, the selective performance benefit of mirrored symmetrical movements and the detrimental effect of incongruent visual movement information for bimanual coordination we report here suggest that applications of MVT should stringently ensure that congruent, symmetrical movements are performed, and further imply that unimanual mirrored handling of therapeutic aids may be disadvantageous to the facilitation of bimanual coordination.

In conclusion, bimanual coordination is guided both by anatomical, muscle-based constraints, as well as by perceptually based, visual constraints. For the latter, information about direction appears to play a key role, whereas effects of posture and muscle homology appear to be mediated only through non-visual channels, and visual cues pertaining to these aspects did not further modulate performance. These results integrate well with current models of bimanual control and goal-directed movement that posit a guiding role of abstract visual direction information for movement planning and execution.

5 | General discussion

Smooth interaction with the environment requires flexible processing of information derived through different sensory channels. Multisensory information is in part redundant, for instance, vision as well as proprioception may inform about identical body-related aspects, like limb posture or muscles that are used. Next to redundant coding, the different sensory channels also complement each other. Color, for example, is uniquely coded in vision, whereas tickling is uniquely coded in touch. Tickling informs about stimulus location as well as size, and potentially shape, whereas color carries information about stimulus identity, for example, is it a mosquito or leaf that tickled the skin? Moreover, reliability varies across the senses, for example with regard to spatial resolution, which is high in vision and comparably low in touch. Together, coding redundant and complementary information across the senses reveals more about the environment than could be conveyed by each sense in isolation. Each sensory channel codes information relative to a distinct spatial anchor, such as the retina in vision or the skin in touch. Thus, information has to be matched across the senses so that it can be used to act in the external world. For instance, the skin-based location of a tactile stimulus alone is not sufficient for goal-directed action because the body can be moved in space. Against this background, it has been shown that tactile skin-based information is recoded into 3D space. Native tactile coding must therefore be complemented by other senses that code space relative to different, skin-independent anchors. For instance, vision generalizes across body-related and environmental information by coding both relative to the retina. Thus, the spatial system provided by vision may be a prime candidate for a supramodal spatial code of body-related information.

The principles that describe how the brain translates and combines sensory information for action can be investigated using movements that mimic everyday situations. Squatting a mosquito, that is, controlling a goal-directed movement toward a tactile target, and applauding at a concert, that is, continuous bimanual coordination, are seemingly simple, but computationally complex actions. Both involve multisensory coding of body-related and spatial aspects, guided by unique processing principles. Tactile sensorimotor processing relies on recoding body-related information into 3D space, whereas continuous bimanual coordination relies on organizing body-related and spatial coding across vision and proprioception. Consequently, their investigation is suitable to inform conceptual models of how we achieve dynamic interaction with the environment more generally.

The present thesis investigated the organizing principles of processing body-related and spatial information for action. Three studies approached this topic from different perspectives. The first two studies examined how body-related information is spatially processed when a tactile stimulus, which is natively coded relative to the skin, is recoded into an external movement target. The first study focused on the processing principles of touch localization for action (Chapter 2) and the second study investigated their neural implementation (Chapter 3). The third study examined how body-related and spatial aspects are coded across vision and proprioception during continuous bimanual coordination (Chapter 4). Specifically, this study investigated whether vision, in addition to proprioception, contributes to coding body-related aspects, such as posture and the muscles that are used. An alternative possibility is that vision exclusively contributes to coding spatial aspects, such as movement direction. In the following, I first discuss principles that are unique to goal-directed action toward a tactile target, as well as its neural implementation, and continuous bimanual coordination, as identified in the present thesis. Second, I consolidate the results by suggesting that the flexible, task-dependent integration of body-related and spatial information is a processing principle that is shared by both kinds of action. In particular, I propose that the present results could provide a foundation for future investigation of tactile sensorimotor processing and continuous bimanual coordination against the theoretical background of OFC. Finally, I outline a research plan designed to further advance our understanding of how sensorimotor processing guides flexible interaction with the environment.

5.1 Key characteristics of spatial integration for touch localization

Our first study scrutinized the processing principles of localizing a tactile stimulus on the body and in external space for goal-directed action (Chapter 2). Tactile localization has been suggested to encompass two separate processes: coordinate transformation from anatomical into external coordinates and subsequent integration of anatomical and external location codes (Badde, Heed, et al., 2014, 2015; Badde, Röder, et al., 2015; Heed, Buchholz, et al., 2015). To clarify how both of these processes contribute to goal-directed action toward a touch, we asked participants to reach with one hand toward visual and tactile targets located at the feet. To dissociate anatomical and external touch locations, the feet were positioned either in an uncrossed or in a crossed posture relative to the body midline. Participants initiated straight reaches and redirected their hand toward a visual or tactile target presented during the movement. The timing and spatial profile of hand reaches informed about the processing principles of recoding a touch for action. Trajectories were unaffected by foot crossing when reaching to visual targets, consistent with their native coding in external space, which is independent of foot posture. When the target was tactile, participants redirected their hand toward the target later than when the target was visual. Redirection was even later when the feet were crossed as opposed to uncrossed. Crucially, there was no consistent spatial bias toward the anatomical stimulus location in the crossed condition, incompatible with the predictions of the transformation account of tactile remapping. In contrast, the majority of trajectories turned toward the correct target at locations centered horizontally on the start position, just like reaches toward uncrossed feet. A subset of reaches exhibited pronounced initial deviations toward the incorrect target, subsequently followed by a turn toward the correct target. However, analysis of the trial history revealed that target repetition biased trajectories toward the repeated location. When repetition had induced a bias toward the incorrect target compared to the correct target, the proportion of turn-around reaches was twice as high with crossed feet. This result suggests that the time delays induced by foot crossing originate from prolonged integration of conflicting information. Further, information about the relative probability of the external target location as extracted from trial history seems to be progressively integrated in addition to anatomical and external location codes. These probabilities might operate as a short-term prior distribution that influences the outcome of the integration process in addition to weights assigned to tactile coordinates (Azañón, Stenner, Cardini, & Haggard, 2015; Chapman et al., 2010b). In sum, the results of our first study show that spatial processing of body-related information for goal-directed action relies on flexibly weighted integration of anatomical and external coordinates, as well as prior probabilities, as the principal computational mechanism.

Our interpretation of these results in favor of the integration account of tactile remapping capitalizes on the parallel maintenance of anatomically and externally coded information. Parallel maintenance of different location codes constitutes a key characteristic, which distinguishes theoretical models that assume hierarchical transformation between reference frames from those that assume flexible weighted integration of reference frames. The findings from our first study in favor of the integration account of tactile remapping are in line with a number of other studies suggesting that anatomical and external touch coordinates are maintained at the same time (for review see: Badde & Heed, 2016). For instance, two previous studies have shown that attentional processing functions in anatomical and external reference frames concurrently, both in anticipation of a stimulus (Schubert et al., 2015) and after a stimulus has been delivered (Heed & Röder, 2010). Beyond attentional modulation, two previous MEG studies have shown that brain oscillations reflect anatomical and external touch locations at the same time in different frequency bands when preparing an action toward a tactile target (Buchholz et al., 2011, 2013). Together, the results of these investigations and our study converge on the conclusion that tactile action targets are concurrently coded in anatomical and external reference frames.

Besides the parallel maintenance of multiple tactile location codes, task-dependent weighting of reference frames is a key proposition of the integration account of tactile remapping (Badde, Heed, et al., 2015). Consistent with this proposal, it has been shown that a secondary irrelevant task modulates touch localization, presumably by changing the overall task context (Badde, Röder, et al., 2015). In one study, participants performed a TOJ task with uncrossed or crossed hands. In secondary task conditions, participants additionally judged spatial or temporal vibration frequency characteristics of the tactile stimuli after each TOJ. Secondary judgements were always reported verbally. During the secondary spatial task, participants reported either the hand (anatomical response mode; Experiment 1) or the external side (external response mode; Experiment 2) that was stimulated with a specific target frequency (higher or lower than the other hand/side). During the secondary temporal task, participants reported whether the target frequency was presented first or second. Crossing effects emerged in all conditions. The effect of the secondary spatial task depended on the response mode: TOJ performance with crossed hands in the primary task improved when responses were coded anatomically. When responses were coded externally, however, crossing effects corresponded to those observed without the secondary spatial task. Emphasizing external coordinates in the secondary task did not lead to a decrease in performance, suggesting that the modulation in the spatial secondary condition was relative. The temporal secondary task improved crossed hands performance relative to performance without the secondary task, suggesting that attending to frequency characteristics might emphasize anatomical coding more generally. Performance with uncrossed hands was unaffected by the different secondary tasks (Badde, Röder, et al., 2015). This result suggests that the modulatory effects induced by the secondary tasks in the crossed condition cannot be attributed to increased load demands, as these have been shown to lead to a performance decline with uncrossed hands, presumably because integration of redundant anatomical and external coordinates is hindered (Badde, Heed, et al., 2014). Touch localization at crossed limbs, too, is sensitive to processing load manipulations, incompatible with effortless coordinate integration. In contrast, these results suggest that the integration of tactile location codes is under top-down control rather than automatic (Badde, Heed, et al., 2014). Collectively, these context-dependent performance modulations suggest that the integration of anatomical and external coordinates is flexibly controlled depending on the task demands.

In the context of tactile sensorimotor processing, the task context has also been shown to modulate the reference frames used to code tactile targets (Müller & Fiehler, 2014b, 2014a, 2016). For instance, when participants reached toward a remembered tactile location, the distribution of reach end points was either best explained by body-centered reference frames, or alternatively, by a mixture of body-centered and gaze-centered reference frames. The reference frames that coded the reach target depended on whether or not the hand receiving the touch was moved between target presentation and responding (with the other hand; Müller & Fiehler, 2016). Such flexible, task-dependent coding of a tactile stimulus complies with the integration account of tactile remapping, which was originally developed in light of crossing effects emerging in perceptual decision tasks. Thus, these results suggest that planning a movement toward a touch relies on the flexible, task-dependent coding of the tactile target, too.

In line with the idea that the task context modulates touch localization, it has been suggested that tasks involving sensorimotor processing induce a higher weighting of external coordinates

(Badde & Heed, 2016). In correspondence with this proposal, spatial response requirements, such as reporting binary tactile locations by moving the heel or toe, increase crossing effects in comparison to verbal responses (Gallace et al., 2008). Furthermore, as discussed earlier, introducing a movement between tactile stimulation and reporting the location leads to the coding of touch relative to gaze, as opposed to body-centered coding in stationary conditions (Müller & Fiehler, 2014a, 2016; Pritchett, Carnevale, & Harris, 2012). On a related note, lateralized ERPs operate both in anatomical and external coordinates during an attention task, while they operate solely in external coordinates during a motor task (Gherri & Forster, 2012). Likewise, frequent posture changes during a TOJ task increase crossing effects, that is, they bias localization toward external reference frames, as compared to when posture is changed only rarely (Azañón et al., 2015). Taken together, these results support the idea that sensorimotor processing biases touch localization toward external coding.

Furthermore, the integration account of tactile remapping proposes that all available information is integrated to derive a final location estimate (Badde, Heed, et al., 2015). Consistent with this conceptualization, it has been shown that TOJ crossing effects are modulated by forward models of body posture that are estimated for efficient motor control (Heed, Möller, & Röder, 2015; Hermosillo, Ritterband-Rosenbaum, & van Donkelaar, 2011). Specifically, planning to cross the hands worsens TOJ of tactile stimuli applied to the hands relative to planning to move hands in an uncrossed posture. In contrast, planning to uncross the hands improves TOJ performance relative to planning to move hands in a crossed posture. These performance modulations have been observed not only during movement planning (Heed, Möller, et al., 2015; Hermosillo et al., 2011), but also during movement execution (Heed, Möller, et al., 2015). During planning, forward models are constructed based on sensory predictions and efference copy signals, whereas both are supplemented by sensory feedback during execution (Desmurget & Grafton, 2000; Todorov & Jordan, 2002). Thus, relative to planning stages, the brain has access to a richer spatial data set constructed from forward and feedback signals during execution. Consistent with the idea that localization is the result of the integration of all available information, TOJ performance modulations are larger during movement execution as compared to movement planning (Heed, Möller, et al., 2015). Together, these results illustrate that sensorimotor processing determines the integration of tactile coordinates, or, put differently, they show how action modulates the perception of touch. In line with the integration account of tactile remapping (Badde, Heed, et al., 2015), these results and the findings of our second study converge on the idea that the brain uses all available information to arrive at a unified location, including motor signals and prior probabilities.

The results of our first study are, thus, in line with other results in the field of tactile remapping, together corroborating the integration account of tactile remapping. In light of the results of our second study, I highlighted the parallel maintenance of anatomical and external tactile location codes as well as their task-specific integration as two key aspects of the integration account of tactile remapping. In the field of motor control, similar processing characteristics have been proposed. For instance, according to OFC, the nervous system is thought to prepare multiple goal-directed movements in parallel, of which the final movement is flexibly selected by minimizing a task-specific cost function (Gallivan, Barton, Chapman, Wolpert, & Flanagan, 2015; Gallivan, Logan, Wolpert, & Flanagan, 2016). Thus, both sensory and motor perspectives emphasize flexible and task-specific processing rather than automatic unwinding of a default plan. Accordingly, theoretical models have developed from assuming sequential and hierarchical reference frame transformations toward proposing flexible and parallel coding of information in both fields. In the field of tactile remapping, it has been suggested, as discussed earlier, that touch localization is modulated by a sensorimotor task context (Badde, Röder, et al., 2015). It follows that it is not clear, if and how principles that characterize touch localization during perceptual tasks apply to contexts that require touch localization for action. In the field of motor control, visuomotor processing has been investigated most frequently. However, if the body is both the target and the effector of action, basic principles of motor control, for example related to state estimation, might markedly differ from visuomotor control because spatial and body-related coding is supplemented by native skin-based information. Future studies could unify sensory and motor perspectives in evaluating specific aspects of tactile sensorimotor processing within the framework of OFC and further extend our understanding of how sensorimotor processing guides flexible interaction with the environment. In Section 5.5 (Outlook: OFC of tactile sensorimotor processing), I detail open questions and draft exemplary experiments that follow the consideration of the present results within the framework of OFC.

5.2 Presumed neural mechanisms of tactile sensorimotor processing

Our second study delineated the neural networks involved in planning movements toward tactile targets using fMRI (Chapter 3). Tactile sensorimotor processing involves tactile coordinates signaling sensory target location relative to the skin and in external space. Moreover, it involves movement coordinates that translate sensory information into a movement goal for action. Touch localization as well as movement planning have been associated with PPC (Azañón et al., 2010; Gallivan & Culham, 2015; Ruzzoli & Soto-Faraco, 2014; Vesia & Crawford, 2012). Our second study investigated how both functions are realized in this brain region. To this end, participants executed right hand pointing movements toward tactile targets at their feet while BOLD signal changes were recorded. To disentangle anatomical and external information, the feet were either uncrossed or crossed over the body midline. To dissociate tactile from movement coordinates, participants either pointed directly toward the stimulus (pro-movement) or toward its mirror location (anti-movement). MVPA of fMRI activation revealed that S1, S2, PMC, and anterior SPL coded anatomical touch coordinates, whereas mIPS exclusively coded external coordinates, both as long as the movement goal was still unknown. When the movement goal was specified, however, sensory coordinates were no longer detectable in the fMRI activation pattern. Instead, a network covering M1, PMC, and PPC represented information about the movement goal location. This network partially overlapped with areas that had previously coded anatomical and external touch coordinates, indicating that some nodes of the identified network progressively change their function. In sum, the results of our second study show that spatial processing of body-related information for goal-directed action relies on dynamically employed spatial codes, which differ depending on the stage of planning and are flexibly implemented in PPC.

Our second study showed a dissociation between anterior SPL and mIPS, representing anatomical and external touch coordinates, respectively. Previous human fMRI and TMS studies have linked both of these regions to VIP of non-human primates, which in turn has been related to body-centered coding of external visuo-tactile signals (Colby et al., 1993; Duhamel et al., 1998). However, external coding of touch has been repeatedly related to eye-centered coding (Buchholz et al., 2011, 2013; Heed, Backhaus, et al., 2016; Müller & Fiehler, 2014b, 2014a, 2016). Consequently, external coding of touch might alternatively be achieved by a region that is specialized for coding stimuli relative to the eyes, as has been demonstrated in LIP and PRR of non-human primates (Batista et al., 1999; Bisley & Goldberg, 2003; Y. E. Cohen & Andersen, 2002; Fattori, Gamberini, Kutz, & Galletti, 2001; Galletti, Kutz, Gamberini, Breveglieri, & Fattori, 2003; Mirpour & Bisley, 2015; Snyder et al., 1997) as well as their presumed functionally equivalent human PPC regions. Thus, although it has frequently been assumed that hVIP codes touch in space (Azañón et al., 2010; Bremmer et al., 2001; Lloyd et al., 2003), it is unclear whether PPC contains hVIP at all, and if so, where it is located. Moreover, it is unknown whether hVIP exclusively, or if a human homolog of LIP (hLIP) additionally vs. exclusively, contributes to the external coding of touch.

Identifying homologies between non-human primate and human brain anatomy and function has been extremely difficult. As a matter of fact, beyond the two anterior and medial regions we identified in our study, regions covering almost the entire human SPL have been linked to VIP in studies that investigated somatosensory spatial coding (see *Figure 3.12*). The large distribution of suggested hVIPs across PPC indicates that there is no single hVIP. In Chapter 3, I discussed that this may in part be related to different paradigms and criteria that have been used to identify hVIP, although no systematic localization pattern emerges when grouping the results (see *Figure 3.12*). Conversely, the number of neurons in VIP that have been identified to code visuo-tactile stimuli in a body-centered reference frame is relative rather than absolute (e.g., Chen et al., 2013), implying that localization of function in non-human primates might also not be unambiguous as well. In a similar vein, human neuroimaging studies are not clear-cut as to where in PPC hLIP might be situated. This functional region has also been assigned to different locations (Grefkes & Fink, 2005; Medendorp et al., 2011; Sereno et al., 2001; Silver & Kastner, 2009). Across these different studies, hLIP appears to be situated in medial rather than lateral IPS, in line with the notion that anatomical differences between species translate to differences in functional localization (Grefkes & Fink, 2005). The human brain appears to include several additional functional areas in comparison to the non-human primate brain (Caminiti et al., 2015; Kastner et al., 2017). Furthermore, linking non-human primate neurophysiological to human neuroimaging research entails establishing homologies between very different measures of brain function. In non-human primates, single neuron properties are recorded from a very limited number of neurons. In contrast, human neuroimaging measurements by large rely on recording proxies of neuronal properties, such as BOLD signal changes and ERPs, which map the activity of vast neuronal populations rather than single neurons. To address this issue, researchers have started to use fMRI paradigms in non-human primates (for reviews see: Cléry, Guipponi, Wardak, & Ben Hamed, 2015; Orban, 2016). Nonetheless, it has proven difficult to precisely localize hVIP and VIP even when the same methodology was used across species (Orban, 2016). Collectively, establishing homologies between non-human primates and humans has been extremely difficult for various reasons in addition to anatomical differences between the species, as for example related to brain size. Although the involvement of PPC in spatial somatosensory processing as shown in our second study in PPC may theoretically indicate a correspondence to VIP or even LIP, it is unquestionable that suggesting such theoretical correspondence of brain function entails considerable simplification.

Instead of trying to map the present result to corresponding neuronal functions identified in non-human primates, it may be more useful to interpret them in light of more general ideas about the function of PPC. PPC has been proposed to play a key role in sensorimotor predictions (Avillac et al., 2005; Wolpert, Goodbody, & Husain, 1998). In particular, from the perspective of motor control, PPC has been related to state estimation for example (Desmurget & Grafton, 2000; Wolpert et al., 1998), which is a key aspect of OFC (Todorov & Jordan, 2002). In PPC, goal and movement information is thought to converge to predict the upcoming state of the effector - information that is passed along to frontal cortex (Mulliken, Musallam, & Andersen, 2008). The neurons that have been related to state estimation mostly encode straight lines in visual coordinates that are a suitable output for different effectors, presumably allowing flexible online control (Mulliken et al., 2008). Moreover, according to the perspective of active inference (Adams, Shipp, & Friston, 2013), PPC is part of a coding hierarchy that generates predictions of sensory consequences of a movement. Contrasting these predictions with sensory feedback then presumably generates prediction errors that are resolved by action. In contrast to OFC, for example, this view proposes that M1 sends descending proprioceptive predictions rather than motor commands to the spinal cord. Thus, this view unifies perceptual and motor systems by suggesting that they function together as a “single active inference machine”, which predicts its sensory input across different domains, such as visual, auditory, somatosensory, and proprioceptive (Adams et al., 2013). Common to active inference and OFC is the emphasis on predictive coding as a prerequisite of successful interaction with the external world. In correspondence, the anterior and medial PPC regions identified in our study may code the predicted state of the body in anatomical and external space, respectively.

In sum, our second study has identified a network subserving tactile sensorimotor processing. Future studies could investigate the mechanism underlying the coding of information in this network, the code that is used to route information between nodes of the network, and the principles that determine the integration of body-related and spatial information about the target and the effector to further advance our understanding of the overarching function of PPC. In Section 5.7 (Outlook: PPC as a key network node involved in tactile sensorimotor processing), I detail open questions and draft exemplary experiments that follow the consideration of how the role of PPC as a key network node of tactile sensorimotor processing may be further scrutinized.

5.3 Coalition of constraints during continuous bimanual coordination

Our third study investigated how muscular and visual contributions jointly determine continuous bimanual coordination (Chapter 4). Body-related aspects such as posture and the muscles currently in use can be perceived redundantly across vision and proprioception. Accordingly, we investigated whether visual information induces body-related or merely abstract, perceptual-spatial constraints in bimanual coordination. Participants made continuous, symmetrical and parallel, bimanual index finger movements with the hands held in the same or different orientations by changing whether one or both palms faced up or down. Both perceptual and anatomical constraints were evident in the results. Performance was more accurate for symmetrical than parallel movements in all orientations. In addition, performance was more accurate when homologous muscles were concurrently active, such as when parallel movements were performed with differently rather than identically oriented hands. Moreover, we manipulated visual feedback with a mirror placed between the hands. The mirror replaced the image of the right with that of the left hand and created the visual impression of bimanual symmetry independent of the right hand’s true movement. Symmetrical mirror feedback impaired parallel performance, but improved symmetrical bimanual performance compared to regular hand view. Critically, these modulations were independent of hand posture and muscle homology. Thus, vision appears to contribute exclusively to spatial, but not to body-related, anatomical movement coding in the guidance of bimanual coordination.

The coalition of muscular and perceptual aspects, which constrained motor control in our third study, is consistent with previous suggestions of a joined influence of these two factors. Although some authors in the field of bimanual coordination have propagated that exclusively perceptual constraints determine coordination (e.g., Mechsner et al., 2001), many have suggested that both perceptual and muscular factors are complementary and inclusive instead (Carson & Kelso, 2004; Temprado et al., 2003). The coupling of the hands during continuous bimanual coordination has been investigated for more than 35 years. Two key characteristics are evident in these tasks: Only symmetrical and parallel coordination modes, but no intermediate frequency relationships (e.g., 5:3 coordination mode), are inherently stable, and among those two, symmetrical is more stable than parallel coordination (Kelso, 1984; Kelso et al., 1986). Since the first reports of such strong and specific bimanual coupling, research has moved from characterizing a broad range of constraining factors of bimanual coordination toward focusing more on how these constraints can be overcome (Shea et al., 2016). Thus, investigating the factors that determine the flexible coding of body-related and spatial aspects during bimanual coordination has recently moved into the center of attention.

The field of bimanual coordination has been heavily influenced by DST. According to influential models of bimanual coordination inspired by DST, continuous movements are self-sustaining as a result of converging external and non-hierarchical internal dynamics (Haken et al., 1985). In this framework, internal dynamics are related to muscular and perceptual constraints that are not under “higher order” control, but instead dynamically self-organize in response to external demands (Huys, 2010). However, the remarkable flexibility of the nervous system to overcome what seems to be a “default tendency” for both hands to act as a functional unit is difficult to reconcile with this suggestion. For instance, frequency relationships between both hands, such as a 5:3 coordination pattern, which are usually impossible to perform without extensive practice, can be performed after minimal practice if visual feedback in form of a Lissajous display is provided (Kovacs et al., 2009). These displays integrate the movements of the left and right hand into a single moving cursor by mapping them onto different axes (Kovacs et al., 2008, 2009, 2010; Kovacs & Shea, 2011). In this setup, performance is best if the hands are not visible (Kovacs et al., 2010). Moreover, if the display is removed, performance immediately returns to baseline level (Kovacs & Shea, 2011). These results imply that constraints are hierarchically organized with vision overriding muscular constraints under certain circumstances; a suggestion that is in conflict with the DST perspective (Shea et al., 2016). To accommodate these findings, it has been suggested that the strong coupling of the hands can be overcome using the display because attentional demands are reduced by focusing on a single point instead of two hands, which might facilitate perceiving the goal frequency (Shea et al., 2016). Presumably, attention is shifted from an internal to an external focus, thereby allowing flexible online motor control mechanisms to adapt movements to the external feedback (Kovacs & Shea, 2011). Conversely, attentional demands are thought to be split between the display and hands when both are visible, leading to an overall performance drop (Kovacs et al., 2010). Consistent with the idea that stabilizing bimanual coordination depends on cognitive resources determined by the coordination pattern, it has been shown that parallel movements were more affected than symmetrical movements by cognitive load demands induced by a secondary task (Temprado, Zanone, Monno, & Laurent, 1999). Thus, attention is thought to be a modulating factor of continuous bimanual coordination, though other factors might determine coordination stability as well.

The mechanisms underlying modulations of continuous bimanual coordination could be further characterized within the framework of OFC, which may provide a broader alternative to the DST framework. For instance, it has been proposed that no “internal model” of a new, complex coordination pattern is developed when movements are performed with aid of the Lissajous display, because performance almost instantly returns to baseline levels after the display is removed (Kovacs et al., 2010). Instead, bimanual coordination is thought to primarily rely on forward models that can be based on an external Lissajous display (Shea et al., 2016). It is unknown whether state estimation in the context of bimanual coordination is flexibly determined on a trial-by-trial basis based on prior sensorimotor input, as has been demonstrated for goal-directed action (Crevecoeur & Scott, 2013). Similarly, it is unclear whether the body model estimated during bimanual coordination refers to either hand or whether some features are coded in a common hand model, depending on the degree of coupling of the two hands during coordination. For instance, it has been shown that focusing attention on one hand improves coordination stability (Swinnen, Jardin, & Meulenbroek, 1996; Wuyts, Summers, Carson, Byblow, & Semjen, 1996). Possibly, attention de-couples the rather automatic control of the hands, which in turn counteracts muscular constraints and thus improves performance (Shea et al., 2016). In correspondence, it has been suggested that two distinct modes, one automatic and another under top-down control, guide continuous bimanual coordination (Debaere et al., 2001; Debaere, Wenderoth, Sunaert, Van Hecke, & Swinnen, 2003). However, it is unclear how flexible such coupling and decoupling of the hands actually is. That is, it may only be induced by shifts of attention or, in line with OFC, the general task context might possibly function to modulate the coupling and decoupling of the hands as well. Potentially separate modes of control may be reflected in unified vs. separate state estimation.

Moreover, it is unclear whether attention is indeed at the heart of flexible behavioral improvements under visual guidance, as for example using Lissajous displays, or whether task-dependent weighting of body-related and spatial information additionally contributes to this effect. Such flexible weighting of body-related and spatial information has been demonstrated with regard to tactile sensorimotor processing (Badde & Heed, 2016; Badde, Heed, et al., 2015; Badde, Röder, et al., 2015). Possibly, proprioceptive and visual information are similarly bound by an integrative process, which stabilizes and destabilizes continuous bimanual movements. Consistently, the results of our third study indicate that vision and proprioception contribute to body-related and spatial bimanual movement coding, respectively. However, it remains unclear whether this association is fixed or whether it is subject to flexible task-dependent modulation. The latter would suggest that it is, at least partially, under top-down control.

Future studies could probe the mechanisms underlying previously demonstrated performance modulations during continuous bimanual coordination. For example, several results suggest that perceptuo-cognitive factors, such as attention to a visual display, can function to overcome the strong coupling of the hands. However, the top-down modulated integration of multisensory information may also contribute to the coupling of the hands. More generally, future studies could further specify the mechanisms that determine the dynamic interplay of perception and action for continuous bimanual coordination to further extend our knowledge of how sensorimotor processing contributes to flexible interaction with the environment. In Section 5.6 (Outlook: OFC of continuous bimanual coordination), I detail open questions and draft exemplary experiments that follow the consideration of the present results within the framework of OFC.

5.4 Shared processing principles of tactile sensorimotor control and continuous bimanual coordination

As discussed in the previous sections, tactile sensorimotor processing and continuous bimanual coordination are each guided by unique principles related to, for example, touch localization and the symmetry bias. Nonetheless, both involve processing of body-related and spatial information. Effortless everyday interaction with the environment consists of a combination of goal-directed and coordinative movements. Consequently, considering body-related and spatial processing across these distinct movement types offers higher ecological validity than investigating each in isolation. The general introduction (Chapter 1) gave an overview of the theoretical and computational concepts of multisensory processing and motor control that set the background for the studies of the present thesis. Different views have often either emphasized the relevance of perception, as for example in research on multisensory processing, or action, as for example in research on OFC and DST, for processing body-related and spatial information. Especially in the fields of motor control and decision making, the view has emerged that perception and action are intimately linked, reciprocally influencing each other (e.g., Adams et al., 2013). Although very different theoretical perspectives exist on the actions investigated in the present thesis, both kinds of movement potentially implicate similar processing principles of body-related and spatial information.

5.4.1 Dynamic integration of body-related and spatial information across different kinds of actions

A shared principle of processing body-related and spatial aspects across tactile sensorimotor processing and continuous bimanual coordination may be the flexible integration of information depending on the task context. Our first study demonstrated that reaches were biased toward the movement goal location that had been relevant in the previous trials. The influence of trial history was dependent on whether the movement target of the present trial coincided with the previously relevant goal location or not. In other words, trial history reinforced either anatomical or external touch coordinates, both, or none of them, depending on foot posture, the touch location during the current trial and the previously implicated goal location. Thus, the task context, as determined by the locations that had previously been relevant for movement, influenced coordinate integration for touch localization. Our second study showed that the brain dynamically employs different spatial codes for different stages of movement planning. The task context, as determined by whether a touch had to be localized or whether a movement had to be prepared, modulated the spatial code used by the brain. In our third study, we systematically manipulated visual information either about body-related or spatial aspects of the movement so that it conflicted with proprioceptive movement coding. The task context, as determined by whether body-related or spatial aspects of the movement were in conflict, determined the weighting of proprioceptive and visual information for their dynamic integration. When information from the two senses was in conflict regarding movement direction, that is, spatial movement aspects, vision outweighed proprioception. In contrast, if they were in conflict regarding posture or muscles that were used, that is, body-related movement aspects, proprioception outweighed vision. To date, sensorimotor processing and bimanual coordination have been investigated in two largely separate research fields, in part because research on these different kinds of movements was motivated by distinct theoretical concepts. The present results emphasize that both kinds of action share important processing principles. Specifically, body-related and spatial information appears to be dynamically integrated according to the task context across tactile sensorimotor processing and bimanual coordination.

5.4.2 OFC of tactile sensorimotor processing and continuous bimanual coordination

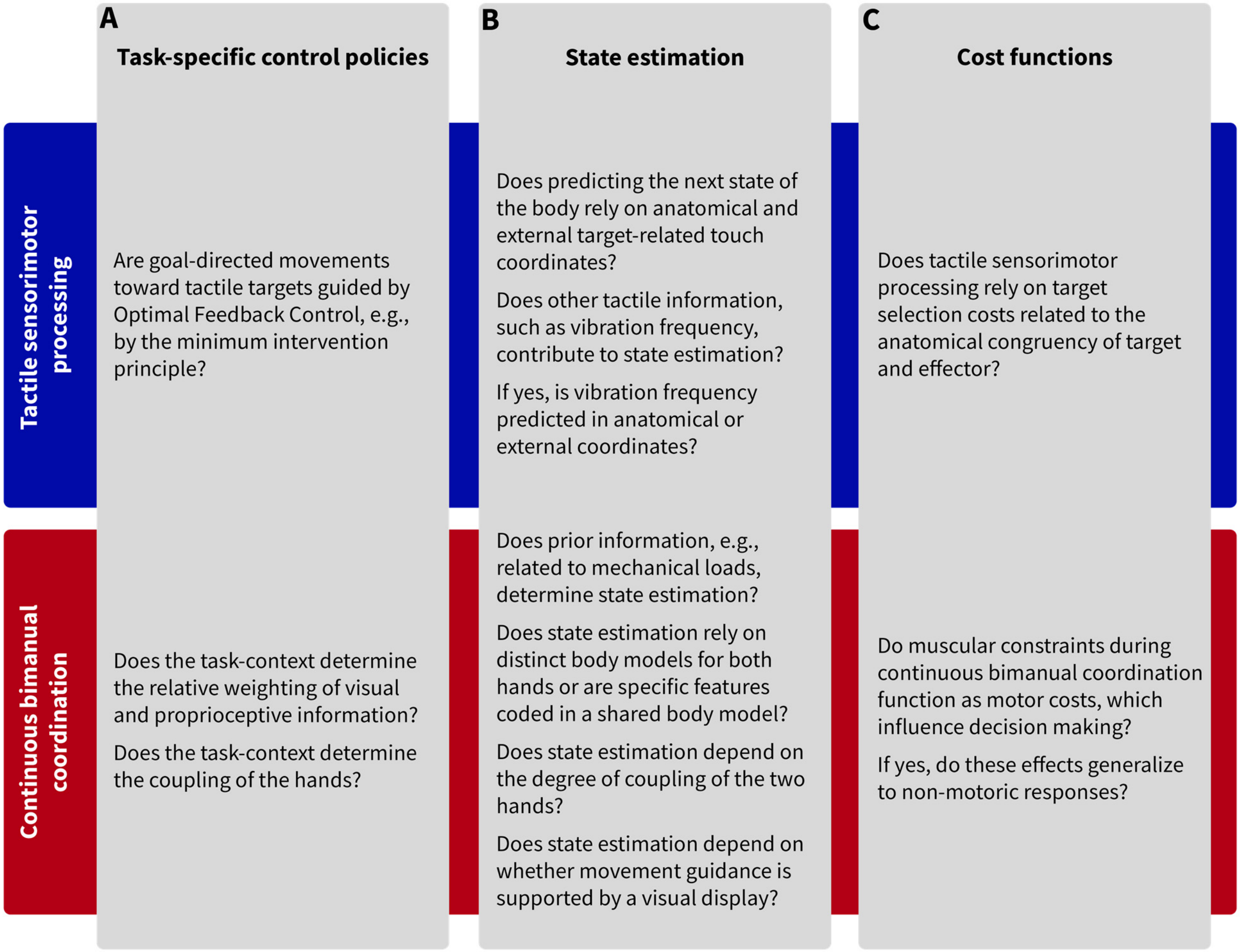
The unique and shared processing principles of body-related and spatial information across different kinds of action characterized in the present thesis may be taken as foundation for future investigations of sensorimotor processing. In particular, further research could address open questions that result from a structured consideration of these different kinds of action against the same theoretical background. Research motivated by a framework that unifies unique and shared principles of tactile sensorimotor processing and continuous bimanual coordination could potentially advance our understanding of how we flexibly process multisensory information about the body and the environment more generally. Future research could investigate the boundary conditions of shared processing principles, such as the flexible integration of body-related and spatial coordinates identified here. Moreover, a cohesive theoretical framework of both kinds of action could motivate research on the boundary conditions of unique principles, such as the symmetry bias during bimanual coordination. Both approaches, that is, identifying and testing unique and shared principles, would further extend our knowledge of sensorimotor control by scrutinizing the basic building blocks of effortless interaction with the external world.

OFC and DST may be useful frameworks for the investigation of sensorimotor processing across different kinds of action. The present thesis identified the flexible, task-dependent integration of body-related and spatial information as a shared principle of tactile sensorimotor processing and bimanual coordination, which may, in correspondence to OFC, reflect the deployment of control policies that optimize task-specific cost functions (Todorov & Jordan, 2002). In contrast, theories of motor control inspired by DST propose non-hierarchical, self-organization of environmental, perceptual, and motor factors (Bingham, 2004; Haken et al., 1985). This view is, as discussed earlier, at conflict with the flexible integration of sensory information depending on the task context, as this finding suggests that sensory coding is at least to some extent top-down controlled (Shea et al., 2016). On a further note, OFC has been successfully used to characterize shared principles of goal-directed visuomotor control and goal-directed bimanual coordination (Diedrichsen, 2007; Diedrichsen & Dowling, 2009; Diedrichsen et al., 2010). Collectively, research inspired by OFC has previously identified shared principles of discrete unimanual and bimanual movements and, in line with the present results, recognizes the task content as the prime determining factor of dynamic sensorimotor processing. Hence, against the background of previous results and the results of the present thesis, the framework of OFC appears to be suitable to unify the investigation of body-related and spatial processing across tactile sensorimotor processing and continuous bimanual coordination in the future.

Unique and shared principles of both kinds of action could be further investigated by considering three different aspects of OFC, namely task-specific control policies, state estimation, and costs functions for action. I develop exemplary research questions concerning each of these aspects (for an overview see *Figure 5.1*), which I address in sections 5.5.1-5.5.3 (tactile sensorimotor processing) and sections 5.6.1-5.6.3 (continuous bimanual coordination) by drafting experiments that could be implemented in the future. Investigating each of these aspects would advance our knowledge of how we successfully interact with the environment in a different way.

According to OFC, task-specific control policies provide a road map for behavior that determines the dynamic interplay of perceptual and motor systems (Scott, 2004, 2012; Todorov

& Jordan, 2002). As a consequence, investigating how perception and action are flexibly adapted to the task during goal-directed and coordinative movements may reveal unique and shared principles (see exemplary research questions outlined in *Figure 5.1A*). Together, these principles structure how we process information about a constantly changing environment, derived through complementary and noisy sensory channels for a redundant motor apparatus. Therefore, further researching these principles may inform about successful interaction with the environment more generally.



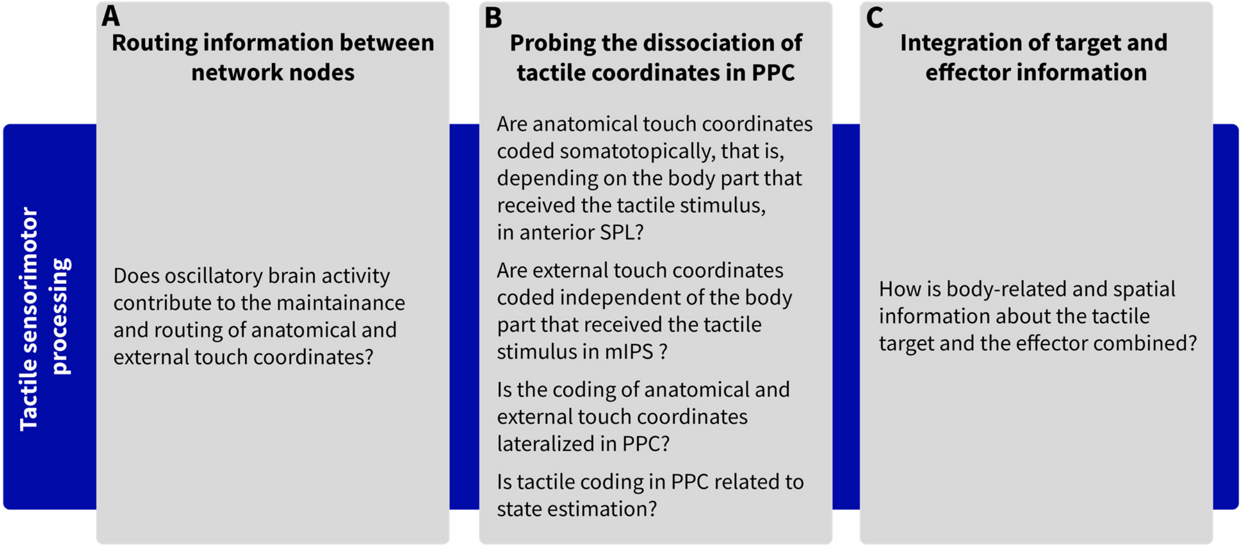
	A **Task-specific control policies**	**B** **State estimation**	**C** **Cost functions**
Tactile sensorimotor processing	Are goal-directed movements toward tactile targets guided by Optimal Feedback Control, e.g., by the minimum intervention principle?	Does predicting the next state of the body rely on anatomical and external target-related touch coordinates? Does other tactile information, such as vibration frequency, contribute to state estimation? If yes, is vibration frequency predicted in anatomical or external coordinates?	Does tactile sensorimotor processing rely on target selection costs related to the anatomical congruency of target and effector?
Continuous bimanual coordination	Does the task-context determine the relative weighting of visual and proprioceptive information? Does the task-context determine the coupling of the hands?	Does prior information, e.g., related to mechanical loads, determine state estimation? Does state estimation rely on distinct body models for both hands or are specific features coded in a shared body model? Does state estimation depend on the degree of coupling of the two hands? Does state estimation depend on whether movement guidance is supported by a visual display?	Do muscular constraints during continuous bimanual coordination function as motor costs, which influence decision making? If yes, do these effects generalize to non-motoric responses?

Figure 5.1. Questions for future research concerning task-specific control policies (*A*), state estimation (*B*), and cost functions (*C*) during tactile sensorimotor processing and continuous bimanual coordination.

According to OFC, state estimation is the process of using all available information, that is, sensory predictions and feedback as well as efference copy signals, in order to guess the consequences of movement on the body (Todorov & Jordan, 2002). Consequently, investigating how different kinds of body-related and spatial information are used to represent the body in the current (task) context may inform about how we develop body models in the long term (see exemplary research questions outlined in *Figure 5.1B*). It may also inform about how we distinguish between our body and the environment by specifying when information is processed in a body-centered code and when it is abstracted from the body, that is, external. Moreover, it may inform about whether strong inter-limb coupling of movements also translates to a coupled model of the limbs and whether the coupling and decoupling of movements and body models depends on the task context. This would advance our understanding of how movement and body models might be connected during motor ontogeny.

According to OFC, cost functions are related to movement features, such as variability, and more general aspects, such as effort or satisfaction of task goals (Flash & Hogan, 1985; Scott, 2002, 2004, 2012, 2016; Todorov & Jordan, 2002; Uno et al., 1989). When planning a movement toward the own body, the spatial distance of target and effector may modulate the general effort that has to be invested for action. The anatomical congruency of target and effector might additionally influence the general effort of motor control, that is, target selection may, for example, be faster if both are confined to homologous limbs or body sides. Hence, cost functions guiding tactile sensorimotor control may include parameters related to anatomical target-effector coupling. Moreover, motor costs related to physical effort have been shown to bias perceptual decisions (Hagura, Haggard, & Diedrichsen, 2017; Marcos, Cos, Girard, & Verschure, 2015). If motor costs are determined by the general effort that has to be invested, this effect should generalize to motor costs that are not experimentally induced, but native, such as muscular constraints. Together, investigating cost functions during both kinds of action, as native target selection and motor costs for example, may reveal control mechanisms that potentially influence the interplay of action and perception throughout motor ontogeny (see exemplary research questions outlined in *Figure 5.1C*). Collectively, the present results may be taken as a foundation that motivates the future investigation of task-specific control policies, state estimation, and cost functions across tactile sensorimotor processing and continuous bimanual coordination.

In the following sections, I first outline questions and experiments for future research concerning tactile sensorimotor processing (sections 5.5.1-5.5.3) and continuous bimanual coordination (sections 5.6.1-5.6.3) to highlight that investigation of both kinds of action would profit from a parallel structure. Second, I detail questions and experiments for a future investigation of the neural networks involved in tactile sensorimotor processing (sections 5.7.1-5.7.3). These are motivated by considering how the role of PPC as a key network node of tactile sensorimotor processing may be further scrutinized (for an overview see *Figure 5.2*).



Routing information between network nodes

Does oscillatory brain activity contribute to the maintainance and routing of anatomical and external touch coordinates?

Probing the dissociation of tactile coordinates in PPC

Are anatomical touch coordinates coded somatotopically, that is, depending on the body part that received the tactile stimulus, in anterior SPL?

Are external touch coordinates coded independent of the body part that received the tactile stimulus in mIPS ?

Is the coding of anatomical and external touch coordinates lateralized in PPC?

Is tactile coding in PPC related to state estimation?

Integration of target and effector information

How is body-related and spatial information about the tactile target and the effector combined?

Figure 5.2. Questions for future research concerning the routing of information between network nodes (*A*), probing the dissociation of tactile coordinates in PPC (*B*) and the integration of target and effector information (*C*) during tactile sensorimotor processing.

5.5 Outlook: OFC of tactile sensorimotor processing

The following section builds on the results of our first study, which identified coordinate integration as the computational mechanism underlying touch localization for goal-directed action. I draft exemplary experiments that address open questions related to task-specific control policies, sensory predictions for state estimation, and cost functions during tactile sensorimotor processing (see *Figure 5.1* for an overview). These are motivated by considering the present and related results within the framework of OFC.

5.5.1 Task-specific control policies

According to OFC, the nervous system accepts variability as long as achieving the task goal is not affected (Todorov & Jordan, 2002). Behavior in line with such task-specific control policies has been characterized during visuomotor control. For instance, it has been shown that corrective responses after a mechanical perturbation depend on the size of the visual target (Nashed et al., 2012). If the target is small, reach perturbations orthogonal to the reach direction are corrected, returning the hand to its initial path. In contrast, if the target is large, such perturbations are not corrected because the goal can be reached even if the hand is displaced laterally and, thus, without returning to the original path (Nashed et al., 2012). Put differently, in this situation, the nervous system does not intervene, but instead accepts variability because it is irrelevant to achieving the task goal (minimum intervention principle; Todorov & Jordan, 2002). Although there is ample evidence that tactile coordinates are flexibly integrated according to the task context, it has not been investigated whether tactile sensorimotor control relies on the same basic computational principles as visuomotor control.

To address this gap, it could be investigated whether tactile sensorimotor processing complies, for example, with the minimum intervention principle. To this end, tasks that have been used in the context of visuomotor control could be adapted for tactile sensorimotor processing. For instance, participants could reach with one hand toward large or small tactile locations positioned along a line from wrist to the crook of the other arm, while reaches are perturbed in midflight. In line with the minimum intervention principle, only movements toward small targets should be corrected after perturbation. A number of factors should be considered when adapting tasks that have been used to probe visuomotor control for tactile sensorimotor processing. For instance, reaching toward locations on the body potentially implicates smaller, minimally separated targets in comparison to visual targets. Furthermore, tactile sensitivity differs across the body and localization biases potentially interact with task-specific control policies (e.g., Vignemont, Majid, Jola, & Haggard, 2009).

In sum, our first study revealed unique processing principles of tactile sensorimotor processing by comparing it to visuomotor control. Unique and shared processing principles of both could be further qualified by adapting visuomotor experiments for tactile targets to test to which extent OFC control principles depend on the target modality.

5.5.2 Sensory predictions for state estimation

According to OFC, state estimation for motor control is flexibly determined based on sensory prediction, feedback, and efference copy signals (Todorov & Jordan, 2002). Reframed in the context of state estimation, our first study showed that the prior movement goal location influences the estimated location of the targeted body part during tactile sensorimotor control. This modulation of state estimation might be mediated by efference copy signals and/or sensory predictions as well and may be independent of the target modality. Indeed, an effect of prior goal locations on reach trajectories was also shown for visuomotor processing (Chapman et al., 2010b). Crucially, when reaching toward tactile locations, targets are defined by their anatomical location and other characteristics, such as target vibration frequency, in addition to their external location. Thus, this target-related information also informs about the state of the body and might be used for tactile sensorimotor processing in addition to prior movement goals. Hence, anatomical and external location codes, as well as vibration frequency information, should determine state estimation for tactile sensorimotor control.

In the context of a TOJ task, anatomical and external touch coordinates have been shown to influence state estimation (Heed, Möller, et al., 2015; Hermosillo et al., 2011). In these studies, tactile stimuli were localized for a TOJ at the same time as a movement was planned, but the tactile stimulations were not the targets for goal-directed action. Moreover, efference copy signals were not dissociated from sensory predictions. The contributions of efference copy signals and sensory prediction to state estimation has been dissociated during visuomotor control. Here, it was shown that the expected load of a perturbation influences trial-wise corrective responses to perturbations applied to the arm within the first 50 ms of movement (Crevecoeur & Scott, 2013). These corrective responses are unlikely to be confounded by efference copy signals due to sensorimotor delays. Thus, they offer a chance to probe the contribution of sensory predictions to state estimation (Crevecoeur & Scott, 2013). In correspondence, when moving toward a touch, weighted sensory predictions should determine motor behavior early on, that is, before efference copy signals have been generated due to sensorimotor delays. Specifically, according to OFC, the weighting of target-related anatomical and external coordinates, as well as vibration frequency for state estimation should be flexibly adjusted during action.

To investigate whether anatomical and external coordinates are flexibly used to predict the state of the body during tactile sensorimotor processing, our first study could be adapted to a setup in which mechanical loads could be applied to the arm while reaching toward tactile stimuli that have dissociable anatomical and external locations (i.e., at the feet). In this setup, either anatomical or external coding could be accentuated by introducing an irrelevant secondary task (Badde, Röder, et al., 2015). In the primary task, reaching movements could be executed with the left or right hand toward visual locations, which correspond to tactile locations at uncrossed or crossed feet. At the beginning of each trial, a tactile stimulus could be applied to one hand that indicates which hand is not the effector. Crucially, this first tactile stimulus would be necessary for the secondary task, but would be irrelevant for the goal-directed movement of the primary task. Then, the tactile target stimulus for the reaching movement could be applied to one foot and the hand that was not stimulated before trial begin could be used to reach toward the visual target, which corresponds to the tactile target location on the foot. Both tactile stimuli, that is, the touch applied to the irrelevant hand at the beginning of the trial and the tactile target on the foot, could vibrate with different frequencies. These would have to be compared during the secondary task. To accentuate anatomical coding, participants could be asked to verbally indicate the limb that received a specific target vibration frequency (hand vs. foot). To accentuate external coding, participants could be asked to indicate the side that received the target vibration frequency (left vs. right). The task context implemented by the secondary task should determine the relative weighting of anatomical or external tactile sensory predictions for state estimation. To probe whether the state of the body is predicted in anatomical and external coordinates, hand reaches could be perturbed early during the reach (<50 ms after movement initiation) so that they unlikely to be confounded with efference copy signals (Crevecoeur & Scott, 2013). Temporal and spatial characteristics of corrective kinematic and electromyography (EMG) responses should scale with task-dependent manipulations. For instance, if the secondary task emphasizes anatomical coding and participants could reach toward a tactile location at a crossed foot in the primary task, corrections in response to perturbations should occur later than without secondary task, because the anatomical prediction implicates the opposite side of space. Conversely, if the secondary task emphasizes external coding and participants could reach toward a tactile location at a crossed foot, corrections in response to perturbations should occur earlier than without secondary task, because the external prediction coincides with the movement goal. Secondary tasks should not affect corrective responses when reaching toward targets at uncrossed feet because anatomical and external predictions coincide. Collectively, this experiment would specify whether anatomical and external target coordinates are used for state estimation when planning a movement toward a touch.

Further adaptations of this experiment could test whether sensory predictions for state estimation only refer to the target location or whether they also contain information about vibration frequency characteristics, which are unique to on-body targets (see also: Badde, Röder, et al., 2015). In particular, different biases could be introduced by manipulating the relative probability of tactile vibration frequencies occurring at different anatomical or external locations. If state estimation relies on vibration frequency information in addition to location codes, vibration frequency predispositions introduced by the irrelevant secondary task should influence corrective responses depending on the spatial coordinate system that they are coded in.

In sum, reframed in the context of OFC, our first study revealed that the prior movement goal location influences the estimated location of the targeted body part during tactile sensorimotor control. How native body-related and spatial target information influence tactile sensorimotor control could be further tested by experiments that probe whether predicting the state of the body during action relies on anatomical and external touch locations, as well as vibration frequency characteristics.

5.5.3 Cost functions during tactile sensorimotor processing

According to OFC, movements are controlled by minimizing task-specific cost functions (Todorov & Jordan, 2002). When controlling a movement toward the own body, these cost functions might include parameters related to the anatomical and spatial relation of target and effector. For instance, target selection costs might be smaller if target and effector are confined to the same body side or if homologous muscles and/or limbs across body sides define both. A study by Kim and Cruse (2001) reported a mixed influence of anatomical and spatial distance when participants could freely choose a hand to reach toward tactile locations on the body, suggesting that target-effector coupling influences tactile sensorimotor processing.

To investigate, for example, whether anatomical costs that are specific to tactile sensorimotor processing determine motor control, a binary online movement correction paradigm could be implemented (see Chapter 2). Tactile targets at two fingers could serve as movement targets that have to be reached with one finger of the other hand. One tactile stimulus would be applied after the movement was started. Across different finger combinations of target and effector, movements should be redirected faster toward the tactile target if both are anatomically congruent (e.g., index finger) as compared to when they are incongruent (e.g., target: ring finger, effector: index finger). Alternatively, tactile stimulation could be used to prompt movement initiation. In this setup, reaction and movement times are expected to similarly depend on anatomical congruency of target and effector. A direct comparison using visual targets attached to the fingers may be implemented to ensure that effects are unrelated to the saliency of the effector.

Further adaptations of this experiment could use more than two potential targets of which two become relevant during each trial and participants freely choose one movement target. If cost functions for tactile sensorimotor control include parameters related to the anatomical coupling of target and effector, choices implicating the anatomically congruent target should be most frequent. The spatial locations of potential targets and the start position of the effector should be balanced to ensure that target selection costs are not confounded with costs related to target-effector distance.

In sum, unique processing principles of OFC of movements toward the own body could be further tested by experiments that probe whether cost functions during tactile sensorimotor control include, for example, parameters related to the anatomical congruency of target and effector.

5.6 Outlook: OFC of continuous bimanual coordination

The following section builds on the results of our third study, which identified a joined influence of muscular and visuo-perceptual constraints on continuous bimanual coordination. I draft exemplary experiments that address open questions related to task-specific control policies, priors that determine state estimation, and cost functions during continuous bimanual coordination (see *Figure 5.1* for an overview). These are motivated by considering the present and related results within the framework of OFC.

5.6.1 Task-specific control policies

According to OFC, the task context is the key factor that organizes sensorimotor processing (Todorov & Jordan, 2002). The results of our third study showed that the relative contributions of proprioceptive and visual information depend on the feature they code: vision outweighed proprioception with regard to spatial aspects, whereas proprioception outweighed vision with regard to body-related aspects. Although several related findings suggest that the weighting of sensory information might be flexibly determined during bimanual coordination, it is unclear whether this also applies to the association of visual with spatial and proprioception with body-related information. In line with OFC, the association of visual with spatial and proprioception with body-related information should be subject to manipulations of the overall task context.

To test whether the relative weighting of proprioceptive and visual information identified in our third study is subject to task-depended modulations, the mirror paradigm of our third study could be adapted. The task context could be changed so that it accentuates proprioceptive movement coding during bimanual coordination by tactile stimulation of homologous or non-homologous muscles of the fingers. In correspondence, visual movement coding could be emphasized by illuminating three LEDs attached to the index fingers. Both manipulations could be reinforced by introducing a secondary, irrelevant task involving the detection of a tactile target vibration frequency, color or visual movement direction (yes/no answers). Visual contributions to spatial movement coding should be modulated depending on the modality accentuated in the secondary task, resulting in an increase in visual, and a decrease in tactile conditions, respectively. Moreover, the modulation should scale according to whether the secondary task reinforces visual color or direction coding, leading to more or less modulation in turn. Crucially, these manipulations should exert specific effects on the relative weighting of visual and proprioceptive information relative to conditions without secondary task, which cannot be explained by a general attention effect. For instance, if proprioceptive and visual information is weighted according to the task context, accentuating visual direction coding should worsen parallel movement performance with incongruent mirror feedback showing symmetrical movements, reflecting a higher weighting of visual information. In contrast, if the overall attentional load determines movement coding, performance in this condition should be improved, as the integration of conflicting visual information may be hindered (for a similar reasoning see: Badde, Röder, et al., 2015). Nonetheless, dividing attention between two tasks may, in addition, lead to a general performance decline, which could even be useful to prevent ceiling effects of symmetrical movement execution (see Chapter 4).

In sum, reframed in the framework of OFC, our third study revealed that the task context, as determined by whether body-related or spatial aspects of the movement were in conflict, determined the weighting of proprioceptive and visual information for their dynamic integration. The flexibility of the identified association of vision with spatial and proprioception with body-related information could be further tested by experiments that accentuate either visual or proprioceptive movement coding.

5.6.2 Priors determining state estimation

According to OFC, the next state of the body is estimated based on sensory prediction, feedback, and efference copy signals (Todorov & Jordan, 2002). Presumably, continuous bimanual coordination requires parallel and ongoing movement planning and execution. Hence, a formal dissociation of how these three different aspects contribute to state estimation is not possible because they cannot be temporally dissociated. Nonetheless, the combined influence of sensory prediction, feedback, and efference copy signals on state estimation could be investigated.

To investigate whether prior information more generally determines state estimation during continuous bimanual coordination, a circling task could be implemented using hand-held handles (e.g., Semjen, Summers, & Cattaert, 1995b). Over the course of a trial, mechanical loads could be applied to the hands while performing symmetrical or parallel movements. At multiple times during a trial, the left or right hand could be perturbed. Corrective kinematic and EMG responses should scale with the loads that have been applied up to this point, reflecting that state estimation is flexibly determined based on prior information. For instance, if large loads have been employed to this point, corrections to a medium perturbation should be larger as compared to when small perturbations have been applied thus far. Next, the loads employed to each hand could be varied to test whether state estimation is computed for each hand in isolation, or whether load features are coded in an average hand model. Corrections could be more flexible, that is, faster and fine grained, when performing symmetrical, as compared to parallel movements, because they are more easily controlled. Alternatively, corrections could be more flexible when performing parallel, as compared to symmetrical movements, because they are coupled to a lesser degree. Thus, switching between bimanual and unimanual motor control to correct the perturbation of one hand may be more readily achieved.

Further adaptations of this experiment could test whether guiding symmetrical and parallel movements via a Lissajous-like visual display integrating the movements of both hands (e.g., Boyles, Panzer, & Shea, 2012) introduces a control mode that is characterized by a stronger coupling as compared to coordination without a display. If coupling is increased through use of the display, state estimation should be more compatible with a single body model even if both hands experienced distinct loads. In contrast, without the display, state estimation should be more compatible with separate hand models. State estimation effects with and without visual display might in addition be distinct for symmetrical and parallel movements, because they differ according to the degree of inherent coupling.

In sum, continuous bimanual coordination is guided by unique principles related to the coupling of the two hands, such as the coalition of muscular and perceptual constraints that contribute to the symmetry bias as identified in our third study. How the native coupling of the hands influences other aspects of motor control as conceptualized in OFC could be tested by experiments that probe, for example, state estimation during continuous bimanual coordination.

5.6.3 Motor costs during continuous bimanual coordination

According to OFC, task-specific cost functions include parameters related to movement features, such as variability and effort, which are minimized to achieve the task goal (Flash & Hogan, 1985; Scott, 2002, 2004, 2012, 2016; Todorov & Jordan, 2002; Uno et al., 1989). Muscular constraints that are specific to continuous bimanual coordination (for reviews see: Carson & Kelso, 2004; Shea et al., 2016) might also function as motor costs as conceptualized within OFC. A recent study demonstrated that motor costs can influence how sensory information is transformed into a decision. In a study by Hagura and colleagues (2017), participants had to decide in which direction the majority of dots on a visual display were moving. Left or right decisions were reported by moving a handle with the left or right hand respectively from a start to a goal location. The motor cost associated with one choice was progressively raised during an adaptation phase by increasing the mechanical load applied to one handle. The choice that exhibited the higher associated motor cost was less likely to be reported during the test phase. Verbal responses after adaptation were similarly affected by manipulating the motor costs. This generalization beyond the manipulated movement suggests that the associated motor cost changed how sensory information is transformed into a decision and not merely how a decision is translated into a motor command (Hagura et al., 2017). If motor costs are in fact determined by the general effort that has to be invested, this effect should generalize to costs that are not experimentally induced, but native to the nervous system, such as muscular constraints.

To investigate whether muscular constraints native to continuous bimanual coordination can function as motor costs, the experimental paradigm by Hagura and colleagues (2017) could be adapted by asking participants to either make parallel or symmetrical movements when reporting a decision. The choice associated with parallel movements should be less likely after adaptation. Additionally, participants could be required to respond verbally after adaptation to test whether transforming sensory information into a decision is modulated beyond dependency on any motor response. Furthermore, hand posture could be manipulated to further scrutinize whether choice probability scales with muscular constraints during continuous bimanual coordination. For instance, movements are more easily controlled if homologous muscles are used (e.g., symmetrical movements with palms facing downwards) than when non-homologous muscles are used (e.g., symmetrical movements with one palm facing upwards).

In sum, unique processing principles of continuous bimanual coordination could be further tested by experiments that probe whether muscular constraints function as motor costs as conceptualized within the framework of OFC.

5.7 Outlook: PPC as a key network node involved in tactile sensorimotor processing

The following section builds on the results of our second study, which characterized the neural networks of tactile sensorimotor processing. I draft exemplary experiments that address open questions related to information routing between network nodes, the dissociation of anatomical and external coordinates in PPC, and the integration of target and effector information (see *Figure 5.2* for an overview). These are motivated by considering how the role of PPC as a key network node of tactile sensorimotor processing may be further scrutinized.

5.7.1 Routing information between network nodes

Our second study identified a fronto-parietal network associated with tactile sensorimotor processing. The mechanisms of how this network utilizes tactile spatial information for action could be specified using different approaches. For instance, the modulation of network dynamics could be manipulated by altering task demands or temporarily entraining or disrupting nodes of the network using TMS. To investigate how information is routed between network nodes, the fMRI data acquired in our study could be analyzed using connectivity measures that index the correlation of multivariate patterns over the course of the different planning phases. A suitable method to delineate the mechanism of touch localization for action more generally may for example be representational similarity analysis (Kriegeskorte, Mur, & Bandettini, 2008; Nili et al., 2014), which could be useful to characterize the features that dissociate sensory from motor representations. Moreover, the setup of our second study could be adapted for MEG such that a connectivity analysis of frequency bands, as has been used to characterize multisensory integration (e.g., Göschl, Friese, Daume, König, & Engel, 2015), could be implemented.

Alpha entrainment of mIPS has been shown to influence tactile perception in a similar way as has been shown for visual targets in this region (Ruzzoli & Soto-Faraco, 2014). Consequently, it has been suggested that oscillatory alpha activity in PPC plays a causal role in coding spatial representations, independent of their initial sensory modality (Ruzzoli & Soto-Faraco, 2014). To test whether band-limited oscillatory activity is a mechanism by which tactile information is routed and/or maintained in PPC, the networks coding anatomical vs. external tactile information identified in our second study could be probed using TMS entrainment when processing touch for action. If indeed the networks communicate via distinct frequencies for anatomical vs. external information, selective performance modulations in a sensorimotor task should follow TMS entrainment of the relevant PPC area at the suitable frequency.

In sum, our second study revealed that PPC plays a central role in planning goal-directed movements toward the tactile locations on the body. The function of PPC during tactile sensorimotor processing could be further tested with experiments and analysis strategies that probe the mechanisms of how regions within PPC communicate when localizing a tactile target for action.

5.7.2 Probing the dissociation of anatomical and external coordinates in PPC

Previous studies have related anatomical coding of touch to S1, while external coding was related to PPC (e.g., Azañón et al., 2010). However, our study revealed a dissociation of anatomical and external coding of touch in anterior and medial PPC. TMS may be a suitable means to further clarify this dissociation, as it has successfully been used to differentiate locations varying by only 12 mm within PPC (Reichenbach, Bresciani, Peer, Bulthoff, & Thielscher, 2010). Previous results have shown that task demands shape the integration of anatomical and external tactile information, with their relative weights being determined by the experimental instruction (Badde, Röder, et al., 2015). This finding could be utilized to further probe the role of anterior SPL and mIPS during tactile sensorimotor processing.

To investigate whether anterior SPL and mIPS are causally involved in coding tactile coordinates for action, future work could probe touch localization under varying task instructions across changing anatomical and external locations at the hands and feet while selectively disrupting hand or foot parietal body maps using TMS. Such somatotopic parietal body maps have been suggested to exist along anterior IPS to medial SPL (Huang et al., 2012). If anatomical information is indeed maintained in anterior SPL in a somatotopic manner, behavior should be selectively disrupted in situations where anatomical coding is stressed and the disrupted parietal body map corresponds to the limb that receives the touch. Conversely, TMS stimulation of mIPS should disrupt localization behavior regardless of the limb that receives the touch, but depending on the task instruction, that is, if external coding is required. Furthermore, the results of our study suggest that coding of tactile information in PPC is lateralized, both for anatomical and external information, which could be verified by stringently applying TMS to each hemisphere in this setup.

To investigate whether PPC contributes to state estimation during tactile sensorimotor processing, future studies could implement a design that allows to dissociate anatomical and external sensory predictions (e.g., section 5.5.2) and combine it with TMS stimulation over anterior and medial PPC. If PPC is causally involved in state estimation, TMS over anterior PPC should selectively disrupt anatomical state estimation. Conversely, TMS over medial PPC should selectively disrupt external state estimation. In contrast, if PPC is involved in anatomical and external coding more generally, TMS over either PPC region should lead to a general performance decline.

In sum, our second study revealed that PPC contributes to the coding of anatomical as well as external location codes for action. Its specific role during tactile sensorimotor processing could be further scrutinized with experiments that dissociate tactile anatomical and external coding in PPC and probe whether it contributes to state estimation in body-related and spatial coordinates. Such investigations in turn would inform theories of the overarching function of PPC, as for example, its suggested role during state estimation.

5.7.3 Integration of target and effector information

When planning a movement toward a touch, both the effector and the target of goal-directed action are part of the body. Whereas the previous sections focused on how body-related and spatial information about the target is used for motor control, it remains to be determined how this information is combined with body-related and spatial information about the effector. For instance, it is unknown whether target- and effector-related information is integrated in anatomical or external space during tactile sensorimotor planning, or, if both reference frames contribute to reconciling target and effector location.

To fill this gap, the setup of our fMRI study could be adapted to manipulate the effector (e.g., left vs. right hand) and its position in space (e.g., uncrossed vs. crossed with the finger tips facing toward the feet) in combination with varying anatomical and external target locations. This would allow to quantify the mechanism of how both body-related and spatial information about the effector and the target are combined.

In sum, our second study has delineated the network involved in processing tactile targets in anatomical and external space for action. The mechanisms of tactile sensorimotor processing could be further tested with experiments that probe how body-related and spatial information about the target is combined with body-related and spatial information about the effector.

5.8 Conclusion

Collectively, the three studies of the present thesis reveal both unique and shared processing principles of tactile sensorimotor processing and continuous bimanual coordination. Tactile sensorimotor processing seems to rely on the flexible integration of anatomical and external information, as well as prior probabilities implicating previous movement goals. On the cortical level, tactile sensorimotor processing appears to be guided by flexibly employed spatial codes implemented in PPC that differ depending on the stage of planning. Continuous bimanual coordination seems to depend on a coalition of muscular and perceptual constraints. Beyond specification of these unique processing principles of tactile sensorimotor processing and continuous bimanual coordination, the present results emphasize that both kinds of action might share important processing principles. Specifically, tactile sensorimotor processing and continuous bimanual coordination appear to rely on the flexible integration of body-related and spatial information according to the task context. The present results may be taken as foundation for future investigation of both kinds of action to deepen our knowledge of how sensorimotor processing guides effortless interaction with the external world. Against the theoretical background of OFC, future investigations could focus on task-specific control policies, state estimation, and cost functions of tactile sensorimotor processing and continuous bimanual coordination. By drafting an exemplar parallel investigation of both kinds of action, I have illustrated that this approach is suitable to identify and consolidate their unique and shared processing principles. Moreover, future studies on the neural implementation of tactile sensorimotor processing could focus on the functional role of PPC to extend our knowledge of its overarching function. Taken together, the present thesis advances our understanding of how perceptual and motor aspects of behavior interact during seemingly ordinary movements, such as squatting a mosquito or applauding at a concert.

References

Adams, R. A., Shipp, S., & Friston, K. J. (2013). Predictions not commands: active inference in the motor system. *Brain Structure and Function*, *218*(3), 611–643. https://doi.org/10.1007/s00429-012-0475-5

Aivar, M. P., Brenner, E., & Smeets, J. B. J. (2008). Avoiding moving obstacles. *Experimental Brain Research*, *190*(3), 251–264. https://doi.org/10.1007/s00221-008-1475-9

Alais, D., & Burr, D. (2004). The Ventriloquist Effect Results from Near-Optimal Bimodal Integration. *Current Biology*, *14*(3), 257–262. https://doi.org/10.1016/j.cub.2004.01.029

Alexander, G. E., & Crutcher, M. D. (1990). Neural representations of the target (goal) of visually guided arm movements in three motor areas of the monkey. *Journal of Neurophysiology*, *64*(1), 164–178.

Allefeld, C., Görgen, K., & Haynes, J.-D. (2016). Valid population inference for information-based imaging: From the second-level t-test to prevalence inference. *NeuroImage*, *141*, 378–392. https://doi.org/10.1016/j.neuroimage.2016.07.040

Amedi, A., Raz, N., Pianka, P., Malach, R., & Zohary, E. (2003). Early “visual” cortex activation correlates with superior verbal memory performance in the blind. *Nature Neuroscience*, *6*(7), 758–766. https://doi.org/10.1038/nn1072

Andersen, R. A., & Cui, H. (2009). Intention, Action Planning, and Decision Making in Parietal-Frontal Circuits. *Neuron*, *63*(5), 568–583. https://doi.org/10.1016/j.neuron.2009.08.028

Andersen, R. A., Snyder, L. H., Li, C.-S., & Stricanne, B. (1993). Coordinate transformations in the representation of spatial information. *Current Opinion in Neurobiology*, *3*(2), 171–176. https://doi.org/10.1016/0959-4388(93)90206-E

Ariani, G., Wurm, M. F., & Lingnau, A. (2015). Decoding Internally and Externally Driven Movement Plans. *The Journal of Neuroscience*, *35*(42), 14160–14171. https://doi.org/10.1523/JNEUROSCI.0596-15.2015

Arzy, S., Overney, L. S., Landis, T., & Blanke, O. (2006). Neural Mechanisms of Embodiment: Asomatognosia Due to Premotor Cortex Damage. *Archives of Neurology*, *63*(7), 1022–1025. https://doi.org/10.1001/archneur.63.7.1022

Astafiev, S. V., Shulman, G. L., Stanley, C. M., Snyder, A. Z., Van Essen, D. C., & Corbetta, M. (2003). Functional organization of human intraparietal and frontal cortex for attending, looking, and pointing. *The Journal of Neuroscience*, *23*(11), 4689–4699.

Avillac, M., Ben Hamed, S., & Duhamel, J.-R. (2007). Multisensory Integration in the Ventral Intraparietal Area of the Macaque Monkey. *The Journal of Neuroscience*, *27*(8), 1922–1932. https://doi.org/10.1523/JNEUROSCI.2646-06.2007

Avillac, M., Denève, S., Olivier, E., Pouget, A., & Duhamel, J.-R. (2005). Reference frames for representing visual and tactile locations in parietal cortex. *Nature Neuroscience*, *8*(7), 941–949. https://doi.org/10.1038/nn1480

Azañón, E., Longo, M. R., Soto-Faraco, S., & Haggard, P. (2010). The Posterior Parietal Cortex Remaps Touch into External Space. *Current Biology*, *20*(14), 1304–1309. https://doi.org/10.1016/j.cub.2010.05.063

Azañón, E., Radulova, S., Haggard, P., & Longo, M. R. (2016). Does the Crossed-Limb Deficit Affect the Uncrossed Portions of Limbs? *Journal of Experimental Psychology. Human Perception and Performance*. https://doi.org/10.1037/xhp0000206

Azañón, E., & Soto-Faraco, S. (2008). Changing Reference Frames during the Encoding of Tactile Events. *Current Biology*, *18*(14), 1044–1049. https://doi.org/10.1016/j.cub.2008.06.045

Azañón, E., Stenner, M.-P., Cardini, F., & Haggard, P. (2015). Dynamic Tuning of Tactile Localization to Body Posture. *Current Biology*, *25*(4), 512–517. https://doi.org/10.1016/j.cub.2014.12.038

Badde, S., & Heed, T. (2016). Towards explaining spatial touch perception: Weighted integration of multiple location codes. *Cognitive Neuropsychology*, *33*(1–2), 26–47. https://doi.org/10.1080/02643294.2016.1168791

Badde, S., Heed, T., & Röder, B. (2014). Processing load impairs coordinate integration for the localization of touch. *Attention, Perception, & Psychophysics*, *76*(4), 1136–1150. https://doi.org/10.3758/s13414-013-0590-2

Badde, S., Heed, T., & Röder, B. (2015). Integration of anatomical and external response mappings explains crossing effects in tactile localization: A probabilistic modeling approach. *Psychonomic Bulletin & Review*, *23*(2), 387–404. https://doi.org/10.3758/s13423-015-0918-0

Badde, S., Röder, B., & Heed, 0. (2015). Flexibly weighted integration of tactile reference frames. *Neuropsychologia*, *70*, 367–374. https://doi.org/10.1016/j.neuropsychologia.2014.10.001

Badde, S., Röder, B., & Heed, T. (2014). Multiple spatial representations determine touch localization on the fingers. *Journal of Experimental Psychology: Human Perception and Performance*, *40*(2), 784–801. https://doi.org/10.1037/a0034690

Banati, R. B., Goerres, G. W., Tjoa, C., Aggleton, J. P., & Grasby, P. (2000). The functional anatomy of visual-tactile integration in man: a study using positron emission tomography. *Neuropsychologia*, *38*(2), 115–124.

Barany, D. A., Della-Maggiore, V., Viswanathan, S., Cieslak, M., & Grafton, S. T. (2014). Feature Interactions Enable Decoding of Sensorimotor Transformations for Goal-Directed Movement. *The Journal of Neuroscience*, *34*(20), 6860–6873. https://doi.org/10.1523/JNEUROSCI.5173-13.2014

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001

Bartels, A., Logothetis, N. K., & Moutoussis, K. (2008). fMRI and its interpretations: an illustration on directional selectivity in area V5/MT. *Trends in Neurosciences*, *31*(9), 444–453. https://doi.org/10.1016/j.tins.2008.06.004

Bates, D. M., Maechler, M., Bolker, B., & Walker, S. (2015). *lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1– 8.* Retrieved from https://github.com/lme4/lme4/

Batista, A. P., Buneo, C. A., Snyder, L. H., & Andersen, R. A. (1999). Reach Plans in Eye-Centered Coordinates. *Science*, *285*(5425), 257–260. https://doi.org/10.1126/science.285.5425.257

Batista, A. P., & Newsome, W. T. (2000). Visuo-motor control: giving the brain a hand. *Current Biology*, *10*(4), R145–R148.

Bernier, P.-M., Cieslak, M., & Grafton, S. T. (2012). Effector selection precedes reach planning in the dorsal parietofrontal cortex. *Journal of Neurophysiology*, *108*(1), 57–68. https://doi.org/10.1152/jn.00011.2012

Bernier, P.-M., Gauthier, G. M., & Blouin, J. (2007). Evidence for Distinct, Differentially Adaptable Sensorimotor Transformations for Reaches to Visual and Proprioceptive Targets. *Journal of Neurophysiology*, *98*(3), 1815–1819. https://doi.org/10.1152/jn.00570.2007

Bernier, P.-M., & Grafton, S. T. (2010). Human Posterior Parietal Cortex Flexibly Determines Reference Frames for Reaching Based on Sensory Context. *Neuron*, *68*(4), 776–788. https://doi.org/10.1016/j.neuron.2010.11.002

Beurze, S. M., Lange, F. P. de, Toni, I., & Medendorp, W. P. (2007). Integration of Target and Effector Information in the Human Brain During Reach Planning. *Journal of Neurophysiology*, *97*(1), 188–199. https://doi.org/10.1152/jn.00456.2006

Beurze, S. M., Toni, I., Pisella, L., & Medendorp, W. P. (2010). Reference Frames for Reach Planning in Human Parietofrontal Cortex. *Journal of Neurophysiology*, *104*(3), 1736–1745. https://doi.org/10.1152/jn.01044.2009

Bingham, G. P. (2004). A Perceptually Driven Dynamical Model of Bimanual Rhythmic Movement (and Phase Perception). *Ecological Psychology*, *16*(1), 45–53. https://doi.org/10.1207/s15326969eco1601_6

Bingham, G. P., Schmidt, R. C., & Zaal, F. T. J. M. (1999). Visual perception of the relative phasing of human limb movements. *Perception & Psychophysics*, *61*(2), 246–258. https://doi.org/10.3758/BF03206886

Bingham, G. P., Zaal, F. T. J. M., Shull, J. A., & Collins, D. R. (2001). The effect of frequency on the visual perception of relative phase and phase variability of two oscillating objects. *Experimental Brain Research*, *136*(4), 543–552. https://doi.org/10.1007/s002210000610

Bisley, J. W., & Goldberg, M. E. (2003). Neuronal Activity in the Lateral Intraparietal Area and Spatial Attention. *Science*, *299*(5603), 81–86. https://doi.org/10.1126/science.1077395

Blangero, A., Menz, M. M., McNamara, A., & Binkofski, F. (2009). Parietal modules for reaching. *Neuropsychologia*, *47*(6), 1500–1507. https://doi.org/10.1016/j.neuropsychologia.2008.11.030

Blangero, A., Rossetti, Y., Honoré, J., & Pisella, L. (2005). Influence of gaze direction on pointing to unseen proprioceptive targets. *Advances in Cognitive Psychology*, *1*(1), 9–16.

Bogaerts, H., Buekers, M. J., Zaal, F. T. J. M., & Swinnen, S. P. (2003). When visuo-motor incongruence aids motor performance: the effect of perceiving motion structures during transformed visual feedback on bimanual coordination. *Behavioural Brain Research*, *138*(1), 45–57. https://doi.org/10.1016/S0166-4328(02)00226-7

Bolognini, N., & Maravita, A. (2007). Proprioceptive Alignment of Visual and Somatosensory Maps in the Posterior Parietal Cortex. *Current Biology*, *17*(21), 1890–1895. https://doi.org/10.1016/j.cub.2007.09.057

Box, G. E. P., & Cox, D. R. (1964). An Analysis of Transformations. *Journal of the Royal Statistical Society. Series B (Methodological)*, *26*(2), 211–252.

Boyles, J., Panzer, S., & Shea, C. H. (2012). Increasingly complex bimanual multi-frequency coordination patterns are equally easy to perform with on-line relative velocity feedback. *Experimental Brain Research*, *216*(4), 515–525. https://doi.org/10.1007/s00221-011-2955-x

Brand, J., Piccirelli, M., Hepp-Reymond, M.-C., Morari, M., Michels, L., & Eng, K. (2016). Virtual Hand Feedback Reduces Reaction Time in an Interactive Finger Reaching Task. *PLOS ONE*, *11*(5), e0154807. https://doi.org/10.1371/journal.pone.0154807

Brandes, J., & Heed, T. (2015). Reach Trajectories Characterize Tactile Localization for Sensorimotor Decision Making. *The Journal of Neuroscience*, *35*(40), 13648–13658. https://doi.org/10.1523/JNEUROSCI.1873-14.2015

Bremmer, F., Duhamel, J.-R., Ben Hamed, S., & Graf, W. (2002). Heading encoding in the macaque ventral intraparietal area (VIP): Heading encoding in area VIP. *European*

Journal of Neuroscience, *16*(8), 1554–1568. https://doi.org/10.1046/j.1460-9568.2002.02207.x

Bremmer, F., Klam, F., Duhamel, J.-R., Ben Hamed, S., & Graf, W. (2002). Visual-vestibular interactive responses in the macaque ventral intraparietal area (VIP): Visual-vestibular interaction in primate parietal cortex. *European Journal of Neuroscience*, *16*(8), 1569–1586. https://doi.org/10.1046/j.1460-9568.2002.02206.x

Bremmer, F., Schlack, A., Shah, N. J., Zafiris, O., Kubischik, M., Hoffmann, K.-P., … Fink, G. R. (2001). Polymodal Motion Processing in Posterior Parietal and Premotor Cortex: A Human fMRI Study Strongly Implies Equivalencies between Humans and Monkeys. *Neuron*, *29*(1), 287–296. https://doi.org/10.1016/S0896-6273(01)00198-2

Bressler, S. L., & Kelso, J. A. S. (2016). Coordination Dynamics in Cognitive Neuroscience. *Frontiers in Neuroscience*, *10*. https://doi.org/10.3389/fnins.2016.00397

Brooks, J. L. (2012). Counterbalancing for serial order carryover effects in experimental condition orders. *Psychological Methods*, *17*(4), 600–614. https://doi.org/10.1037/a0029310

Brooks, S. P., & Gelman, A. (1998). General Methods for Monitoring Convergence of Iterative Simulations. *Journal of Computational and Graphical Statistics*, *7*(4), 434–455. https://doi.org/10.1080/10618600.1998.10474787

Brozzoli, C., Gentile, G., & Ehrsson, H. H. (2012). That's Near My Hand! Parietal and Premotor Coding of Hand-Centered Space Contributes to Localization and Self-Attribution of the Hand. *The Journal of Neuroscience*, *32*(42), 14573–14582. https://doi.org/10.1523/JNEUROSCI.2660-12.2012

Brozzoli, C., Gentile, G., Petkova, V. I., & Ehrsson, H. H. (2011). fMRI Adaptation Reveals a Cortical Mechanism for the Coding of Space Near the Hand. *The Journal of Neuroscience*, *31*(24), 9023–9031. https://doi.org/10.1523/JNEUROSCI.1172-11.2011

Buchanan, J. J., Kelso, J. A. S., DeGuzman, G. C., & Ding, M. (1997). The spontaneous recruitment and suppression of degrees of freedom in rhythmic hand movements. *Human Movement Science*, *16*(1), 1–32. https://doi.org/10.1016/S0167-9457(96)00040-1

Buchholz, V. N., Goonetilleke, S. C., Medendorp, W. P., & Corneil, B. D. (2012). Greater benefits of multisensory integration during complex sensorimotor transformations. *Journal of Neurophysiology*, *107*(11), 3135–3143. https://doi.org/10.1152/jn.01188.2011

Buchholz, V. N., Jensen, O., & Medendorp, W. P. (2011). Multiple Reference Frames in Cortical Oscillatory Activity during Tactile Remapping for Saccades. *The Journal of Neuroscience*, *31*(46), 16864–16871. https://doi.org/10.1523/JNEUROSCI.3404-11.2011

Buchholz, V. N., Jensen, O., & Medendorp, W. P. (2013). Parietal Oscillations Code Nonvisual Reach Targets Relative to Gaze and Body. *The Journal of Neuroscience*, *33*(8), 3492–3499. https://doi.org/10.1523/JNEUROSCI.3208-12.2013

Buckingham, G., & Carey, D. P. (2008). Investigating bimanual coordination in dominant and non-dominant virtual hands. *Laterality: Asymmetries of Body, Brain and Cognition*, *13*(6), 514–526. https://doi.org/10.1080/13576500802257929

Bultitude, J. H., Juravle, G., & Spence, C. (2016). Tactile Gap Detection Deteriorates during Bimanual Symmetrical Movements under Mirror Visual Feedback. *PLoS ONE*, *11*(1), e0146077. https://doi.org/10.1371/journal.pone.0146077

Buneo, C. A., & Andersen, R. A. (2006). The posterior parietal cortex: sensorimotor interface for the planning and online control of visually guided movements. *Neuropsychologia*, *44*(13), 2594–2606. https://doi.org/doi:10.1016/j.neuropsychologia.2005.10.011

Buneo, C. A., Jarvis, M. R., Batista, A. P., & Andersen, R. A. (2002). Direct visuomotor transformations for reaching. *Nature*, *416*(6881), 632. https://doi.org/10.1038/416632a

Burgess, P. R., Wei, J. Y., Clark, F. J., & Simon, J. (1982). Signaling of Kinesthetic Information by Peripheral Sensory Receptors. *Annual Review of Neuroscience*, *5*(1), 171–188. https://doi.org/10.1146/annurev.ne.05.030182.001131

Burk, D., Ingram, J. N., Franklin, D. W., Shadlen, M. N., & Wolpert, D. M. (2014). Motor Effort Alters Changes of Mind in Sensorimotor Decision Making. *PLoS ONE*, *9*(3), e92681. https://doi.org/10.1371/journal.pone.0092681

Burton, H., & Sinclair, R. J. (2000). Attending to and remembering tactile stimuli: a review of brain imaging data and single-neuron responses. *Journal of Clinical Neurophysiology*, *17*(6), 575–591.

Caminiti, R., Innocenti, G. M., & Battaglia-Mayer, A. (2015). Organization and evolution of parieto-frontal processing streams in macaque monkeys and humans. *Neuroscience & Biobehavioral Reviews*, *56*, 73–96. https://doi.org/10.1016/j.neubiorev.2015.06.014

Cappadocia, D. C., Monaco, S., Chen, Y., Blohm, G., & Crawford, J. D. (2016). Temporal Evolution of Target Representation, Movement Direction Planning, and Reach Execution in Occipital–Parietal–Frontal Cortex: An fMRI Study. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhw304

Carson, R. G., & Kelso, J. A. S. (2004). Governing coordination: behavioural principles and neural correlates. *Experimental Brain Research*, *154*(3), 267–274. https://doi.org/10.1007/s00221-003-1726-8

Carson, R. G., & Riek, S. (1998). The influence of joint position on the dynamics of perception-action coupling. *Experimental Brain Research*, *121*(1), 103–114. https://doi.org/10.1007/s002210050442

Chang, C.-C., & Lin, C.-J. (2011). LIBSVM: A library for support vector machines. *ACM Transactions on Intelligent Systems and Technology*, *2*(3), 1–27. https://doi.org/10.1145/1961189.1961199

Chapman, C. S., Gallivan, J. P., Wood, D. K., Milne, J. L., Culham, J. C., & Goodale, M. A. (2010a). Reaching for the unknown: Multiple target encoding and real-time decision-making in a rapid reach task. *Cognition*, *116*(2), 168–176. https://doi.org/10.1016/j.cognition.2010.04.008

Chapman, C. S., Gallivan, J. P., Wood, D. K., Milne, J. L., Culham, J. C., & Goodale, M. A. (2010b). Short-term motor plasticity revealed in a visuomotor decision-making task. *Behavioural Brain Research*, *214*(1), 130–134. https://doi.org/10.1016/j.bbr.2010.05.012

Chen, X., DeAngelis, G. C., & Angelaki, D. E. (2013). Diverse Spatial Reference Frames of Vestibular Signals in Parietal Cortex. *Neuron*, *80*(5), 1310–1321. https://doi.org/10.1016/j.neuron.2013.09.006

Cisek, P. (2012). Making decisions through a distributed consensus. *Current Opinion in Neurobiology*, *22*(6), 927–936. https://doi.org/10.1016/j.conb.2012.05.007

Cisek, P., & Kalaska, J. F. (2010). Neural Mechanisms for Interacting with a World Full of Action Choices. *Annual Review of Neuroscience*, *33*(1), 269–298. https://doi.org/10.1146/annurev.neuro.051508.135409

Cisek, P., Puskas, G. A., & El-Murr, S. (2009). Decisions in Changing Conditions: The Urgency-Gating Model. *The Journal of Neuroscience*, *29*(37), 11560–11571. https://doi.org/10.1523/JNEUROSCI.1844-09.2009

Clemens, I. A. H., De Vrijer, M., Selen, L. P. J., Van Gisbergen, J. A. M., & Medendorp, W. P. (2011). Multisensory Processing in Spatial Orientation: An Inverse Probabilistic Approach. *The*

Journal of Neuroscience, *31*(14), 5365–5377. https://doi.org/10.1523/JNEUROSCI.6472-10.2011

Cléry, J., Guipponi, O., Wardak, C., & Ben Hamed, S. (2015). Neuronal bases of peripersonal and extrapersonal spaces, their plasticity and their dynamics: Knowns and unknowns. *Neuropsychologia*, *70*, 313–326. https://doi.org/10.1016/j.neuropsychologia.2014.10.022

Cohen, L. (1971). Synchronous bimanual movements performed by homologous and non-homologous muscles. *Perceptual and Motor Skills*, *32*(2), 639–644. https://doi.org/10.2466/pms.1971.32.2.639

Cohen, Y. E., & Andersen, R. A. (2000). Reaches to Sounds Encoded in an Eye-Centered Reference Frame. *Neuron*, *27*(3), 647–652. https://doi.org/10.1016/S0896-6273(00)00073-8

Cohen, Y. E., & Andersen, R. A. (2002). A common reference frame for movement plans in the posterior parietal cortex. *Nature Reviews Neuroscience*, *3*(7), 553–562. https://doi.org/10.1038/nrn873

Colby, C. L., Duhamel, J.-R., & Goldberg, M. E. (1993). Ventral intraparietal area of the macaque: anatomic location and visual response properties. *Journal of Neurophysiology*, *69*(3), 902–914.

Connolly, J. D., Andersen, R. A., & Goodale, M. A. (2003). FMRI evidence for a “parietal reach region” in the human brain. *Experimental Brain Research*, *153*(2), 140–145. https://doi.org/10.1007/s00221-003-1587-1

Connolly, J. D., Goodale, M. A., Cant, J. S., & Munoz, D. P. (2007). Effector-specific fields for motor preparation in the human frontal cortex. *NeuroImage*, *34*(3), 1209–1219. https://doi.org/10.1016/j.neuroimage.2006.10.001

Connolly, J. D., Goodale, M. A., Desouza, J. F. X., Menon, R. S., Vilis, T., & Perception), (The Medical Research Council Group for Action and. (2000). A Comparison of Frontoparietal fMRI Activation During Anti-Saccades and Anti-Pointing. *Journal of Neurophysiology*, *84*(3), 1645–1655.

Cooke, D. F., Taylor, C. S. R., Moore, T., & Graziano, M. S. A. (2003). Complex movements evoked by microstimulation of the ventral intraparietal area. *Proceedings of the National Academy of Sciences*, *100*(10), 6163–6168. https://doi.org/10.1073/pnas.1031751100

Craig, A. D. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. *Nature Reviews Neuroscience*, *3*(8), 655–666. https://doi.org/10.1038/nrn894

Craig, A. D. (2004). Human feelings: why are some more aware than others? *Trends in Cognitive Sciences*, *8*(6), 239–241.

Crammond, D. J., & Kalaska, J. F. (1994). Modulation of preparatory neuronal activity in dorsal premotor cortex due to stimulus-response compatibility. *Journal of Neurophysiology*, *71*(3), 1281–1284.

Crawford, J. D., Henriques, D. Y. P., & Medendorp, W. P. (2011). Three-Dimensional Transformations for Goal-Directed Action. *Annual Review of Neuroscience*, *34*(1), 309–331. https://doi.org/10.1146/annurev-neuro-061010-113749

Crevecoeur, F., & Scott, S. H. (2013). Priors Engaged in Long-Latency Responses to Mechanical Perturbations Suggest a Rapid Update in State Estimation. *PLOS Computational Biology*, *9*(8), e1003177. https://doi.org/10.1371/journal.pcbi.1003177

Culham, J. C., Cavina-Pratesi, C., & Singhal, A. (2006). The role of parietal cortex in visuomotor control: What have we learned from neuroimaging? *Neuropsychologia*, *44*(13), 2668–2684. https://doi.org/10.1016/j.neuropsychologia.2005.11.003

Culham, J. C., & Valyear, K. F. (2006). Human parietal cortex in action. *Current Opinion in Neurobiology*, *16*(2), 205–212. https://doi.org/10.1016/j.conb.2006.03.005

Daenen, L., Roussel, N., Cras, P., & Nijs, J. (2010). Sensorimotor incongruence triggers sensory disturbances in professional violinists: an experimental study. *Rheumatology*, *49*(7), 1281–1289. https://doi.org/10.1093/rheumatology/keq067

Davis, T., LaRocque, K. F., Mumford, J. A., Norman, K. A., Wagner, A. D., & Poldrack, R. A. (2014). What do differences between multi-voxel and univariate analysis mean? How subject-, voxel-, and trial-level variance impact fMRI analysis. *NeuroImage*, *97*, 271–283. https://doi.org/10.1016/j.neuroimage.2014.04.037

Davis, T., & Poldrack, R. A. (2013). Measuring neural representations with fMRI: practices and pitfalls. *Annals of the New York Academy of Sciences*, *1296*(1), 108–134. https://doi.org/10.1111/nyas.12156

Day, B. L., & Lyon, I. N. (2000). Voluntary modification of automatic arm movements evoked by motion of a visual target. *Experimental Brain Research*, *130*(2), 159–168.

de Jong, B. M., van der Graaf, F. H. C. E., & Paans, A. M. J. (2001). Brain Activation Related to the Representations of External Space and Body Scheme in Visuomotor Control. *NeuroImage*, *14*(5), 1128–1135. https://doi.org/10.1006/nimg.2001.0911

de Witt, L., Alexander, D., Ekroll, V., & Wagemans, J. (2016). Is neuroimaging measuring information in the brain? *Psychonomic Bulletin & Review*. https://doi.org/10.3758/s13423-016-1002-0

Debaere, F., Swinnen, S. P., Béatse, E., Sunaert, S., Van Hecke, P., & Duysens, J. (2001). Brain Areas Involved in Interlimb Coordination: A Distributed Network. *NeuroImage*, *14*(5), 947–958. https://doi.org/10.1006/nimg.2001.0892

Debaere, F., Wenderoth, N., Sunaert, S., Van Hecke, P., & Swinnen, S. P. (2003). Internal vs external generation of movements: differential neural pathways involved in bimanual coordination performed in the presence or absence of augmented visual feedback. *NeuroImage*, *19*(3), 764–776. https://doi.org/10.1016/S1053-8119(03)00148-4

Deconinck, F. J. A., Smorenburg, A. R. P., Benham, A., Ledebt, A., Feltham, M. G., & Savelsbergh, G. J. P. (2014). Reflections on Mirror Therapy: A Systematic Review of the Effect of Mirror Visual Feedback on the Brain. *Neurorehabilitation and Neural Repair*, *29*(4), 349–361. https://doi.org/10.1177/1545968314546134

Del Gratta, C., Della Penna, S., Ferretti, A., Franciotti, R., Pizzella, V., Tartaro, A., … Rossini, P. M. (2002). Topographic Organization of the Human Primary and Secondary Somatosensory Cortices: Comparison of fMRI and MEG Findings. *NeuroImage*, *17*(3), 1373–1383. https://doi.org/10.1006/nimg.2002.1253

Deneve, S., Latham, P. E., & Pouget, A. (1999). Reading population codes: a neural implementation of ideal observers. *Nature Neuroscience*, *2*(8), 740–745. https://doi.org/10.1038/11205

Denwood, M. J. (2016). runjags: An R package providing interface utilities, model templates, parallel computing methods and additional distributions for MCMC models in JAGS. *Journal of Statistical Software*, *71*(9), 1–25. https://doi.org/doi:http://dx.doi.org/10.18637/jss.v071.i09

Desmurget, M., Epstein, C. M., Turner, R. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience*, *2*, 563–567.

Desmurget, M., & Grafton, S. T. (2000). Forward modeling allows feedback control for fast reaching movements. *Trends in Cognitive Sciences*, *4*(11), 423–431. https://doi.org/10.1016/S1364-6613(00)01537-0

Di Bono, M. G., Begliomini, C., Castiello, U., & Zorzi, M. (2015). Probing the reaching–grasping network in humans through multivoxel pattern decoding. *Brain and Behavior*, *5*(11). https://doi.org/10.1002/brb3.412

Diedrichsen, J. (2007). Optimal Task-Dependent Changes of Bimanual Feedback Control and Adaptation. *Current Biology*, *17*(19), 1675–1679. https://doi.org/10.1016/j.cub.2007.08.051

Diedrichsen, J., & Dowling, N. (2009). Bimanual coordination as task-dependent linear control policies. *Human Movement Science*, *28*(3), 334–347. https://doi.org/10.1016/j.humov.2008.10.003

Diedrichsen, J., Shadmehr, R., & Ivry, R. B. (2010). The coordination of movement: optimal feedback control and beyond. *Trends in Cognitive Sciences*, *14*(1), 31–39. https://doi.org/10.1016/j.tics.2009.11.004

Dietrich, C., Blume, K. R., Franz, M., Huonker, R., Carl, M., Preißler, S., … Weiss, T. (2017). Dermatomal Organization of SI Leg Representation in Humans: Revising the Somatosensory Homunculus. *Cerebral Cortex*. https://doi.org/10.1093/cercor/bhx007

Driver, J., & Noesselt, T. (2008). Multisensory Interplay Reveals Crossmodal Influences on “Sensory-Specific” Brain Regions, Neural Responses, and Judgments. *Neuron*, *57*(1), 11–23. https://doi.org/10.1016/j.neuron.2007.12.013

Driver, J., & Spence, C. (1998). Cross–modal links in spatial attention. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *353*(1373), 1319–1331. https://doi.org/10.1098/rstb.1998.0286

Duffy, F. H., & Burchfiel, J. L. (1971). Somatosensory System: Organizational Hierarchy from Single Units in Monkey Area 5. *Science*, *172*(3980), 273–275. https://doi.org/10.1126/science.172.3980.273

Duhamel, J.-R., Colby, C. L., & Goldberg, M. E. (1998). Ventral intraparietal area of the macaque: congruent visual and somatic response properties. *Journal of Neurophysiology*, *79*, 126–136.

Ehrsson, H. H., Spence, C., & Passingham, R. E. (2004). That’s My Hand! Activity in Premotor Cortex Reflects Feeling of Ownership of a Limb. *Science*, *305*(5685), 875–877. https://doi.org/10.1126/science.1097011

Eickhoff, S. B., Jbabdi, S., Caspers, S., Laird, A. R., Fox, P. T., Zilles, K., & Behrens, T. E. J. (2010). Anatomical and Functional Connectivity of Cytoarchitectonic Areas within the Human Parietal Operculum. *The Journal of Neuroscience*, *30*(18), 6409–6421. https://doi.org/10.1523/JNEUROSCI.5664-09.2010

Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage*, *25*(4), 1325–1335. https://doi.org/10.1016/j.neuroimage.2004.12.034

Ernst, M. O. (2012). Optimal Multisensory Integration: Assumptions and Limits. In B. E. Stein (Ed.), *The New Handbook of Multisensory Processing*. Cambridge, MA, US.

Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(6870), 429–433. https://doi.org/10.1038/415429a

Ezendam, D., Bongers, R. M., & Jannink, M. J. A. (2009). Systematic review of the effectiveness of mirror therapy in upper extremity function. *Disability and Rehabilitation*, *31*(26), 2135–2149. https://doi.org/10.3109/09638280902887768

Fabbri, S., Caramazza, A., & Lingnau, A. (2010). Tuning Curves for Movement Direction in the Human Visuomotor System. *The Journal of Neuroscience*, *30*(40), 13488–13498. https://doi.org/10.1523/JNEUROSCI.2571-10.2010

Fabbri, S., Strnad, L., Caramazza, A., & Lingnau, A. (2014). Overlapping representations for grip type and reach direction. *NeuroImage*, *94*, 138–146. https://doi.org/10.1016/j.neuroimage.2014.03.017

Fabbri, S., Stubbs, K. M., Cusack, R., & Culham, J. C. (2016). Disentangling Representations of Object and Grasp Properties in the Human Brain. *The Journal of Neuroscience*, *36*(29), 7648–7662. https://doi.org/10.1523/JNEUROSCI.0313-16.2016

Farrer, C., Franck, N., Georgieff, N., Frith, C. D., Decety, J., & Jeannerod, M. (2003). Modulating the experience of agency: a positron emission tomography study. *NeuroImage*, *18*(2), 324–333. https://doi.org/10.1016/S1053-8119(02)00041-1

Fattori, P., Gamberini, M., Kutz, D. F., & Galletti, C. (2001). “Arm-reaching” neurons in the parietal area V6A of the macaque monkey. *European Journal of Neuroscience*, *13*(12), 2309–2313. https://doi.org/10.1046/j.0953-816x.2001.01618.x

Fernandez-Ruiz, J., Goltz, H. C., DeSouza, J. F. X., Vilis, T., & Crawford, J. D. (2007). Human Parietal “Reach Region” Primarily Encodes Intrinsic Visual Direction, Not Extrinsic Movement Direction, in a Visual–Motor Dissociation Task. *Cerebral Cortex*, *17*(10), 2283–2292.

Filimon, F. (2010). Human Cortical Control of Hand Movements: Parietofrontal Networks for Reaching, Grasping, and Pointing. *The Neuroscientist*, *16*(4), 388–407. https://doi.org/10.1177/1073858410375468

Filimon, F., Nelson, J. D., Huang, R.-S., & Sereno, M. I. (2009). Multiple Parietal Reach Regions in Humans: Cortical Representations for Visual and Proprioceptive Feedback during On-Line Reaching. *The Journal of Neuroscience*, *29*(9), 2961–2971. https://doi.org/10.1523/JNEUROSCI.3211-08.2009

Flash, T., & Hogan, N. (1985). The coordination of arm movements: an experimentally confirmed mathematical model. *The Journal of Neuroscience*, *5*(7), 1688–1703.

Foell, J., Bekrater-Bodmann, R., McCabe, C. S., & Flor, H. (2013). Sensorimotor Incongruence and Body Perception: An Experimental Investigation. *Frontiers in Human Neuroscience*, *7*. https://doi.org/10.3389/fnhum.2013.00310

Franklin, D. W., & Wolpert, D. M. (2011). Computational Mechanisms of Sensorimotor Control. *Neuron*, *72*(3), 425–442. https://doi.org/10.1016/j.neuron.2011.10.006

Franz, E. A., & Packman, T. (2004). Fooling the brain into thinking it sees both hands moving enhances bimanual spatial coupling. *Experimental Brain Research*, *157*(2), 174–180. https://doi.org/10.1007/s00221-004-1831-3

Franz, E. A., Zelaznik, H. N., Swinnen, S. P., & Walter, C. (2001). Spatial Conceptual Influences on the Coordination of Bimanual Actions: When a Dual Task Becomes a Single Task. *Journal of Motor Behavior*, *33*(1), 103–112. https://doi.org/10.1080/00222890109601906

Friedman, J., Brown, S., & Finkbeiner, M. (2013). Linking cognitive and reaching trajectories via intermittent movement control. *Journal of Mathematical Psychology*, *57*(3–4), 140–151. https://doi.org/10.1016/j.jmp.2013.06.005

Gail, A., & Andersen, R. A. (2006). Neural Dynamics in Monkey Parietal Reach Region Reflect Context-Specific Sensorimotor Transformations. *The Journal of Neuroscience*, *26*(37), 9376–9384. https://doi.org/10.1523/JNEUROSCI.1570-06.2006

Gallace, A., Soto-Faraco, S., Dalton, P., Kreukniet, B., & Spence, C. (2008). Response requirements modulate tactile spatial congruency effects. *Experimental Brain Research*, *191*(2), 171–186. https://doi.org/10.1007/s00221-008-1510-x

Gallace, A., & Spence, C. (2014). *In Touch with the Future: The Sense of Touch from Cognitive Neuroscience to Virtual Reality*. Oxford University Press.

Galletti, C., Kutz, D. F., Gamberini, M., Breveglieri, R., & Fattori, P. (2003). Role of the medial parieto-occipital cortex in the control of reaching and grasping movements. *Experimental Brain Research*, *153*(2), 158–170. https://doi.org/10.1007/s00221-003-1589-z

Gallivan, J. P., Barton, K. S., Chapman, C. S., Wolpert, D. M., & Flanagan, J. R. (2015). Action plan co-optimization reveals the parallel encoding of competing reach movements. *Nature Communications*, *6*. https://doi.org/10.1038/ncomms8428

Gallivan, J. P., & Chapman, C. S. (2014). Three-dimensional reach trajectories as a probe of real-time decision-making between multiple competing targets. *Frontiers in Neuroscience*, *8*. https://doi.org/10.3389/fnins.2014.00215

Gallivan, J. P., & Culham, J. C. (2015). Neural coding within human brain areas involved in actions. *Current Opinion in Neurobiology*, *33*, 141–149. https://doi.org/10.1016/j.conb.2015.03.012

Gallivan, J. P., Johnsrude, I. S., & Flanagan, J. R. (2015). Planning Ahead: Object-Directed Sequential Actions Decoded from Human Frontoparietal and Occipitotemporal Networks. *Cerebral Cortex*, bhu302. https://doi.org/10.1093/cercor/bhu302

Gallivan, J. P., Logan, L., Wolpert, D. M., & Flanagan, J. R. (2016). Parallel specification of competing sensorimotor control policies for alternative action options. *Nature Neuroscience*, *19*(2), 320–326. https://doi.org/10.1038/nn.4214

Gallivan, J. P., McLean, D. A., Flanagan, J. R., & Culham, J. C. (2013). Where One Hand Meets the Other: Limb-Specific and Action-Dependent Movement Plans Decoded from Preparatory Signals in Single Human Frontoparietal Brain Areas. *The Journal of Neuroscience*, *33*(5), 1991–2008. https://doi.org/10.1523/JNEUROSCI.0541-12.2013

Gallivan, J. P., McLean, D. A., Smith, F. W., & Culham, J. C. (2011). Decoding Effector-Dependent and Effector-Independent Movement Intentions from Human Parieto-Frontal Brain Activity. *The Journal of Neuroscience*, *31*(47), 17149–17168. https://doi.org/10.1523/JNEUROSCI.1058-11.2011

Gardner, E. P. (2017). Neural pathways for cognitive command and control of hand movements. *Proceedings of the National Academy of Sciences*, *114*(16), 4048–4050. https://doi.org/10.1073/pnas.1702746114

Gentile, G., Petkova, V. I., & Ehrsson, H. H. (2011). Integration of Visual and Tactile Signals From the Hand in the Human Brain: An fMRI Study. *Journal of Neurophysiology*, *105*(2), 910–922. https://doi.org/10.1152/jn.00840.2010

Gertz, H., & Fiehler, K. (2015). Human posterior parietal cortex encodes the movement goal in a pro-/anti-reach task. *Journal of Neurophysiology*, jn.01039.2014. https://doi.org/10.1152/jn.01039.2014

Gertz, H., Lingnau, A., & Fiehler, K. (2017). Decoding Movement Goals from the Fronto-Parietal Reach Network. *Frontiers in Human Neuroscience*, *11*. https://doi.org/10.3389/fnhum.2017.00084

Ghazanfar, A. A., & Schroeder, C. E. (2006). Is neocortex essentially multisensory? *Trends in Cognitive Sciences*, *10*(6), 278–285. https://doi.org/10.1016/j.tics.2006.04.008

Gherri, E., & Forster, B. (2012). Crossing the hands disrupts tactile spatial attention but not motor attention: Evidence from event-related potentials. *Neuropsychologia*, *50*(9), 2303–2316. https://doi.org/10.1016/j.neuropsychologia.2012.05.034

Gill, J. (2010). Critical Differences in Bayesian and Non-Bayesian Inference and why the Former is Better. In *Statistics in the Social Sciences: Current Methodological Developments* (pp. 135–157). John Wiley & Sons, Inc.

Gilron, R., Rosenblatt, J., Koyejo, O., Poldrack, R. A., & Mukamel, R. (2017). What's in a pattern? Examining the type of signal multivariate analysis uncovers at the group level. *NeuroImage*, *146*, 113–120. https://doi.org/10.1016/j.neuroimage.2016.11.019

Gold, J. I., Law, C.-T., Connolly, P., & Bennur, S. (2008). The Relative Influences of Priors and Sensory Evidence on an Oculomotor Decision Variable During Perceptual Learning. *Journal of Neurophysiology*, *100*(5), 2653–2668. https://doi.org/10.1152/jn.90629.2008

Gold, J. I., & Shadlen, M. N. (2000). Representation of a perceptual decision in developing oculomotor commands. *Nature*, *404*(6776), 390–394. https://doi.org/10.1038/35006062

Gold, J. I., & Shadlen, M. N. (2001). Neural computations that underlie decisions about sensory stimuli. *Trends in Cognitive Sciences*, *5*(1), 10–16.

Gold, J. I., & Shadlen, M. N. (2007). The Neural Basis of Decision Making. *Annual Review of Neuroscience*, *30*(1), 535–574. https://doi.org/10.1146/annurev.neuro.29.051605.113038

Göschl, F., Friese, U., Daume, J., König, P., & Engel, A. K. (2015). Oscillatory signatures of crossmodal congruence effects: An EEG investigation employing a visuotactile pattern matching paradigm. *NeuroImage*, *116*, 177–186. https://doi.org/10.1016/j.neuroimage.2015.03.067

Graziano, M. S. ., Taylor, C. S. ., Moore, T., & Cooke, D. F. (2002). The Cortical Control of Movement Revisited. *Neuron*, *36*(3), 349–362. https://doi.org/10.1016/S0896-6273(02)01003-6

Graziano, M. S. A., & Aflalo, T. N. (2007). Rethinking Cortical Organization Moving Away from Discrete Areas Arranged in Hierarchies. *The Neuroscientist*, *13*(2), 138–147. https://doi.org/10.1177/1073858406295918

Graziano, M. S. A., & Botvinick, M. M. (2002). How the brain represents the body: insights from neurophysiology and psychology. In W. Prinz & B. Hommel (Eds.), *Common mechanisms in perception and action: Attention and performance XIX*.

Graziano, M. S. A., & Cooke, D. F. (2006). Parieto-frontal interactions, personal space, and defensive behavior. *Neuropsychologia*, *44*(6), 845–859. https://doi.org/10.1016/j.neuropsychologia.2005.09.009

Graziano, M. S. A., Yap, G., & Gross, C. (1994). Coding of visual space by premotor neurons. *Science*, *266*(5187), 1054–1057. https://doi.org/10.1126/science.7973661

Grefkes, C., & Fink, G. R. (2005). The functional organization of the intraparietal sulcus in humans and monkeys. *Journal of Anatomy*, *207*(1), 3–17.

Grefkes, C., Ritzl, A., Zilles, K., & Fink, G. R. (2004). Human medial intraparietal cortex subserves visuomotor coordinate transformation. *NeuroImage*, *23*(4), 1494–1506. https://doi.org/10.1016/j.neuroimage.2004.08.031

Grünert-Plüss, N., Hufschmid, U., Santschi, L., & Grünert, J. (2008). Mirror Therapy in Hand Rehabilitation: A Review of the Literature, the St Gallen Protocol for Mirror Therapy and Evaluation of a Case Series of 52 Patients. *The British Journal of Hand Therapy*, *13*(1), 4–11.

Hagler, D. J., Riecke, L., & Sereno, M. I. (2007). Parietal and superior frontal visuospatial maps activated by pointing and saccades. *NeuroImage*, *35*(4), 1562–1577. https://doi.org/10.1016/j.neuroimage.2007.01.033

Hagura, N., Haggard, P., & Diedrichsen, J. (2017). Perceptual decisions are biased by the cost to act. *eLife*, *6*, e18422. https://doi.org/10.7554/eLife.18422

Haith, A. M., & Krakauer, J. W. (2013). Theoretical models of motor control and motor learning. *Routledge Handbook of Motor Control and Motor Learning. London: Routledge*, 7–28.

Haken, H., Kelso, J. A. S., & Bunz, H. (1985). A theoretical model of phase transitions in human hand movements. *Biological Cybernetics*, *51*(5), 347–356. https://doi.org/10.1007/BF00336922

Hanes, D. P., & Carpenter, R. H. S. (1999). Countermanding saccades in humans. *Vision Research*, *39*(16), 2777–2791. https://doi.org/10.1016/S0042-6989(99)00011-5

Harrell Jr, F. E. with contributions from C. D. and many others. (2016). *Hmisc: Harrell Miscellaneous. R package version 4.0-2*. Retrieved from https://CRAN.R-project.org/package=Hmisc

Hastie, T., & Tibshirani, R. J. (1990). *Generalized additive models*. London: Chapman and Hall.

Haxby, J. V., Connolly, A. C., & Guntupalli, J. S. (2014). Decoding Neural Representational Spaces Using Multivariate Pattern Analysis. *Annual Review of Neuroscience*, *37*(1), 435–456. https://doi.org/10.1146/annurev-neuro-062012-170325

Haxby, J. V., Gobbini, M. I., Furey, M. L., Ishai, A., Schouten, J. L., & Pietrini, P. (2001). Distributed and Overlapping Representations of Faces and Objects in Ventral Temporal Cortex. *Science*, *293*(5539), 2425–2430. https://doi.org/10.1126/science.1063736

Hay, J. C., Pick, H. L. J., & Ikeda, K. (1965). Visual capture produced by prism spectacles. *Psychonomic Science*, *2*(1–12), 215–216. https://doi.org/10.3758/BF03343413

Haynes, J.-D. (2015). A Primer on Pattern-Based Approaches to fMRI: Principles, Pitfalls, and Perspectives. *Neuron*, *87*(2), 257–270. https://doi.org/10.1016/j.neuron.2015.05.025

Haynes, J.-D., & Rees, G. (2006). Decoding mental states from brain activity in humans. *Nature Reviews Neuroscience*, *7*(7), 523–534. https://doi.org/10.1038/nrn1931

Haynes, J.-D., Sakai, K., Rees, G., Gilbert, S., Frith, C., & Passingham, R. E. (2007). Reading Hidden Intentions in the Human Brain. *Current Biology*, *17*(4), 323–328. https://doi.org/10.1016/j.cub.2006.11.072

Hebart, M. N., Görgen, K., & Haynes, J.-D. (2015). The Decoding Toolbox (TDT): a versatile software package for multivariate analyses of functional imaging data. *Frontiers in Neuroinformatics*, *8*. https://doi.org/10.3389/fninf.2014.00088

Heed, T., & Azañón, E. (2014). Using time to investigate space: a review of tactile temporal order judgments as a window onto spatial processing in touch. *Frontiers in Psychology*, *5*. https://doi.org/10.3389/fpsyg.2014.00076

Heed, T., Backhaus, J., & Röder, B. (2012). Integration of hand and finger location in external spatial coordinates for tactile localization. *Journal of Experimental Psychology: Human Perception and Performance*, *38*(2), 386–401. https://doi.org/10.1037/a0024059

Heed, T., Backhaus, J., Röder, B., & Badde, S. (2016). Disentangling the External Reference Frames Relevant to Tactile Localization. *PLOS ONE*, *11*(7), e0158829. https://doi.org/10.1371/journal.pone.0158829

Heed, T., Beurze, S. M., Toni, I., Röder, B., & Medendorp, W. P. (2011). Functional Rather than Effector-Specific Organization of Human Posterior Parietal Cortex. *The Journal of Neuroscience*, *31*(8), 3066–3076. https://doi.org/10.1523/JNEUROSCI.4370-10.2011

Heed, T., Buchholz, V. N., Engel, A. K., & Röder, B. (2015). Tactile remapping: from coordinate transformation to integration in sensorimotor processing. *Trends in Cognitive Sciences*, *19*(5), 251–258. https://doi.org/10.1016/j.tics.2015.03.001

Heed, T., Leoné, F. T. M., Toni, I., & Medendorp, W. P. (2016). Functional versus effector-specific organization of the human posterior parietal cortex: revisited. *Journal of Neurophysiology*, *116*(4), 1885–1899. https://doi.org/10.1152/jn.00312.2014

Heed, T., Möller, J., & Röder, B. (2015). Movement Induces the Use of External Spatial Coordinates for Tactile Localization in Congenitally Blind Humans. *Multisensory Research*, *28*(1–2), 173–194. https://doi.org/10.1163/22134808-00002485

Heed, T., & Röder, B. (2010). Common anatomical and external coding for hands and feet in tactile attention: evidence from event-related potentials. *Journal of Cognitive Neuroscience*, *22*(1), 184–202. https://doi.org/10.1162/jocn.2008.21168

Heed, T., & Röder, B. (2014). Motor coordination uses external spatial coordinates independent of developmental vision. *Cognition*, *132*(1), 1–15. https://doi.org/10.1016/j.cognition.2014.03.005

Heekeren, H. R., Marrett, S., Bandettini, P. A., & Ungerleider, L. G. (2004). A general mechanism for perceptual decision-making in the human brain. *Nature*, *431*(7010), 859–862. https://doi.org/10.1038/nature02966

Henriques, D. Y. P., Klier, E. M., Smith, M. A., Lowy, D., & Crawford, J. D. (1998). Gaze-Centered Remapping of Remembered Visual Space in an Open-Loop Pointing Task. *The Journal of Neuroscience*, *18*(4), 1583–1594.

Hermosillo, R., Ritterband-Rosenbaum, A., & van Donkelaar, P. (2011). Predicting Future Sensorimotor States Influences Current Temporal Decision Making. *The Journal of Neuroscience*, *31*(27), 10019–10022. https://doi.org/10.1523/JNEUROSCI.0037-11.2011

Hillis, J. M., Ernst, M. O., Banks, M. S., & Landy, M. S. (2002). Combining Sensory Information: Mandatory Fusion Within, but Not Between, Senses. *Science*, *298*(5598), 1627–1630. https://doi.org/10.1126/science.1075396

Hogan, N., & Sternad, D. (2007). On rhythmic and discrete movements: reflections, definitions and implications for motor control. *Experimental Brain Research*, *181*(1), 13–30. https://doi.org/10.1007/s00221-007-0899-y

Hogan, N., & Sternad, D. (2012). Dynamic primitives of motor behavior. *Biological Cybernetics*, *106*(11–12), 727–739. https://doi.org/10.1007/s00422-012-0527-1

Holmes, A. P., & Friston, K. J. (1998). Generalisability, Random Effects & Population Inference. *Neuroimage*, *7*, S754.

Holmes, N. P., Crozier, G., & Spence, C. (2004). When mirrors lie: “Visual capture” of arm position impairs reaching performance. *Cognitive, Affective, & Behavioral Neuroscience*, *4*(2), 193–200. https://doi.org/10.3758/CABN.4.2.193

Holmes, N. P., Snijders, H. J., & Spence, C. (2006). Reaching with alien limbs: Visual exposure to prosthetic hands in a mirror biases proprioception without accompanying illusions of ownership. *Perception & Psychophysics*, *68*(4), 685–701. https://doi.org/10.3758/BF03208768

Holmes, N. P., & Spence, C. (2004). The body schema and the multisensory representation(s) of peripersonal space. *Cognitive Processing*, *5*(2), 94–105. https://doi.org/10.1007/s10339-004-0013-3

Holmes, N. P., & Spence, C. (2005). Visual bias of unseen hand position with a mirror: spatial and temporal factors. *Experimental Brain Research*, *166*(3–4), 489–497. https://doi.org/10.1007/s00221-005-2389-4

Howard, I. S., Ingram, J. N., & Wolpert, D. M. (2011). Separate representations of dynamics in rhythmic and discrete movements: evidence from motor learning. *Journal of Neurophysiology*, *105*(4), 1722–1731. https://doi.org/10.1152/jn.00780.2010

Huang, R.-S., Chen, C., Tran, A. T., Holstein, K. L., & Sereno, M. I. (2012). Mapping multisensory parietal face and body areas in humans. *Proceedings of the National Academy of Sciences*, *109*(44), 18114–18119. https://doi.org/10.1073/pnas.1207946109

Huang, R.-S., & Sereno, M. I. (2007). Dodecapus: An MR-compatible system for somatosensory stimulation. *NeuroImage*, *34*(3), 1060–1073. https://doi.org/10.1016/j.neuroimage.2006.10.024

Huys, R. (2010). The Dynamical Organization of Limb Movements. In R. Huys & V. K. Jirsa (Eds.), *Nonlinear Dynamics in Human Behavior* (pp. 69–90). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-16262-6_3

Huys, R., Studenka, B. E., Rheaume, N. L., Zelaznik, H. N., & Jirsa, V. K. (2008). Distinct Timing Mechanisms Produce Discrete and Continuous Movements. *PLOS Computational Biology*, *4*(4), e1000061. https://doi.org/10.1371/journal.pcbi.1000061

Inui, K., Wang, X., Tamura, Y., Kaneoke, Y., & Kakigi, R. (2004). Serial Processing in the Human Somatosensory System. *Cerebral Cortex*, *14*(8), 851–857. https://doi.org/10.1093/cercor/bhh043

Iwamura, Y., Iriki, A., & Tanaka, M. (1994). Bilateral hand representation in the postcentral somatosensory cortex. *Nature*, *369*(6481), 554. https://doi.org/10.1038/369554a0

Jager, G., & Postma, A. (2003). On the hemispheric specialization for categorical and coordinate spatial relations: A review of the current evidence. *Neuropsychologia*, *41*(4), 504–515.

Jeannerod, M. (1988). *The neural and behavioural organization of goal-directed movements* (Vol. xii). New York, NY, US: Clarendon Press/Oxford University Press.

Jones, S. A. H., & Henriques, D. Y. P. (2010). Memory for proprioceptive and multisensory targets is partially coded relative to gaze. *Neuropsychologia*, *48*(13), 3782–3792. https://doi.org/10.1016/j.neuropsychologia.2010.10.001

Kalaska, J. F. (2009). From Intention to Action: Motor Cortex and the Control of Reaching Movements, 139–178. https://doi.org/10.1007/978-0-387-77064-2_8

Kalaska, J. F., Scott, S. H., Cisek, P., & Sergio, L. E. (1997). Cortical control of reaching movements. *Current Opinion in Neurobiology*, *7*(6), 849–859. https://doi.org/10.1016/S0959-4388(97)80146-8

Kaplan, J. T., Man, K., & Greening, S. G. (2015). Multivariate cross-classification: applying machine learning techniques to characterize abstraction in neural representations. *Frontiers in Human Neuroscience*, *9*. https://doi.org/10.3389/fnhum.2015.00151

Karhu, J., & Tesche, C. D. (1999). Simultaneous Early Processing of Sensory Input in Human Primary (SI) and Secondary (SII) Somatosensory Cortices. *Journal of Neurophysiology*, *81*(5), 2017–2025.

Karnath, H.-O., Baier, B., & Nägele, T. (2005). Awareness of the Functioning of One's Own Limbs Mediated by the Insular Cortex? *The Journal of Neuroscience*, *25*(31), 7134–7138. https://doi.org/10.1523/JNEUROSCI.1590-05.2005

Kastner, S., Chen, Q., Jeong, S. K., & Mruczek, R. E. B. (2017). A brief comparative review of primate posterior parietal cortex: A novel hypothesis on the human toolmaker. *Neuropsychologia. Advance Online Publication*. https://doi.org/10.1016/j.neuropsychologia.2017.01.034

Kelso, J. A. S. (1984). Phase transitions and critical behavior in human bimanual coordination. *American Journal of Physiology - Regulatory, Integrative and Comparative Physiology*, *246*(6), R1000–R1004.

Kelso, J. A. S., Buchanan, J. J., DeGuzman, G. C., & Ding, M. (1993). Spontaneous recruitment and annihilation of degrees of freedom in biological coordination. *Physics Letters A*, *179*(4–5), 364–371. https://doi.org/10.1016/0375-9601(93)90692-S

Kelso, J. A. S., Holt, K. G., Rubin, P., & Kugler, P. N. (1981). Patterns of human interlimb coordination emerge from the properties of non-linear, limit cycle oscillatory processes: theory and data. *Journal of Motor Behavior*, *13*(4), 226–261.

Kelso, J. A. S., Scholz, J. P., & Schöner, G. (1986). Nonequilibrium phase transitions in coordinated biological motion: critical fluctuations. *Physics Letters A*, *118*(6), 279–284. https://doi.org/10.1016/0375-9601(86)90359-2

Khan, A. Z., Crawford, J. D., Blohm, G., Urquizar, C., Rossetti, Y., & Pisella, L. (2007). Influence of initial hand and target position on reach errors in optic ataxic and normal subjects. *Journal of Vision*, *7*(5), 8. https://doi.org/10.1167/7.5.8

Kim, D.-H., & Cruse, H. (2001). Two kinds of body representation are used to control hand movements following tactile stimulation. *Experimental Brain Research*, *139*(1), 76–91. https://doi.org/10.1007/s002210100741

Kitazawa, S. (2002). Where conscious sensation takes place. *Consciousness and Cognition*, *11*(3), 475–477.

Klam, F., & Graf, W. (2003). Vestibular Signals of Posterior Parietal Cortex Neurons during Active and Passive Head Movements in Macaque Monkeys. *Annals of the New York Academy of Sciences*, *1004*(1), 271–282. https://doi.org/10.1196/annals.1303.024

Knill, D. C., & Saunders, J. A. (2003). Do humans optimally integrate stereo and texture information for judgments of surface slant? *Vision Research*, *43*(24), 2539–2558. https://doi.org/10.1016/S0042-6989(03)00458-9

Konen, C. S., Mruczek, R. E. B., Montora, J. L., & Kastner, S. (2013). Functional organization of human posterior parietal cortex: grasping- and reaching-related activations relative to topographically organized cortex. *Journal of Neurophysiology*. https://doi.org/10.1152/jn.00657.2012

Körding, K. P., & Wolpert, D. M. (2006). Bayesian decision theory in sensorimotor control. *Trends in Cognitive Sciences*, *10*(7), 319–326. https://doi.org/10.1016/j.tics.2006.05.003

Kovacs, A. J., Buchanan, J. J., & Shea, C. H. (2008). Bimanual 1:1 with 90° continuous relative phase: difficult or easy! *Experimental Brain Research*, *193*(1), 129–136. https://doi.org/10.1007/s00221-008-1676-2

Kovacs, A. J., Buchanan, J. J., & Shea, C. H. (2009). Impossible is nothing: 5:3 and 4:3 multi-frequency bimanual coordination. *Experimental Brain Research*, *201*(2), 249–259. https://doi.org/10.1007/s00221-009-2031-y

Kovacs, A. J., Buchanan, J. J., & Shea, C. H. (2010). Perceptual and attentional influences on continuous 2:1 and 3:2 multi-frequency bimanual coordination. *Journal of Experimental Psychology: Human Perception and Performance*, *36*(4), 936–954. https://doi.org/10.1037/a0019259

Kovacs, A. J., & Shea, C. H. (2011). The learning of 90° continuous relative phase with and without Lissajous feedback: External and internally generated bimanual coordination. *Acta Psychologica*, *136*(3), 311–320. https://doi.org/10.1016/j.actpsy.2010.12.004

Krampe, R. T., Engbert, R., & Kliegl, R. (2002). Representational Models and Nonlinear Dynamics: Irreconcilable Approaches to Human Movement Timing and Coordination or Two Sides of the Same Coin? Introduction to the Special Issue on Movement Timing and Coordination. *Brain and Cognition*, *48*(1), 1–6. https://doi.org/10.1006/brcg.2001.1300

Krasovsky, A., Gilron, R., Yeshurun, Y., & Mukamel, R. (2014). Differentiating Intended Sensory Outcome from Underlying Motor Actions in the Human Brain. *The Journal of Neuroscience*, *34*(46), 15446–15454. https://doi.org/10.1523/JNEUROSCI.5435-13.2014

Kriegeskorte, N. (2009). Relating Population-Code Representations between Man, Monkey, and Computational Models. *Frontiers in Neuroscience*, *3*(3), 363–373. https://doi.org/10.3389/neuro.01.035.2009

Kriegeskorte, N., Goebel, R., & Bandettini, P. (2006). Information-based functional brain mapping. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(10), 3863–3868. https://doi.org/10.1073/pnas.0600244103

Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational Similarity Analysis - Connecting the Branches of Systems Neuroscience. *Frontiers in Systems Neuroscience*, *2*. https://doi.org/10.3389/neuro.06.004.2008

Kruschke, J. K. (2015). *Doing Bayesian data analysis: a tutorial with R, JAGS, and Stan* (Edition 2). Boston: Academic Press.

Kruschke, J. K., Aguinis, H., & Joo, H. (2012). The Time Has Come Bayesian Methods for Data Analysis in the Organizational Sciences. *Organizational Research Methods*, *15*(4), 722–752. https://doi.org/10.1177/1094428112457829

Leconte, P., Xivry, J.-J. O. de, Stoquart, G., Lejeune, T., & Ronsse, R. (2016). Rhythmic arm movements are less affected than discrete ones after a stroke. *Experimental Brain Research*, *234*(6), 1403–1417. https://doi.org/10.1007/s00221-015-4543-y

Lee, T. D., Blandin, Y., & Proteau, L. (1996). Effects of task instructions and oscillation frequency on bimanual coordination. *Psychological Research*, *59*(2), 100–106. https://doi.org/10.1007/BF01792431

Lenth, R. V. (2015). *lsmeans: Least-squares means. R package version 2.19.* Retrieved from http://CRAN.R-project.org/package=lsmeans.

Leoné, F. T. M., Heed, T., Toni, I., & Medendorp, W. P. (2014). Understanding Effector Selectivity in Human Posterior Parietal Cortex by Combining Information Patterns and Activation Measures. *The Journal of Neuroscience*, *34*(21), 7102–7112. https://doi.org/10.1523/JNEUROSCI.5242-13.2014

Lewis, J. W., & Van Essen, D. C. (2000). Corticocortical connections of visual, sensorimotor, and multimodal processing areas in the parietal lobe of the macaque monkey. *The Journal of Comparative Neurology*, *428*(1), 112–137. https://doi.org/10.1002/1096-9861(20001204)428:1<112::AID-CNE8>3.0.CO;2-9

Liddell, T. M., & Kruschke, J. K. (2014). Ostracism and fines in a public goods game with accidental contributions: The importance of punishment type. *Judgment and Decision Making*, *9*(6), 523–547.

Limanowski, J., & Blankenburg, F. (2016). Integration of Visual and Proprioceptive Limb Position Information in Human Posterior Parietal, Premotor, and Extrastriate Cortex. *The Journal of Neuroscience*, *36*(9), 2582–2589. https://doi.org/10.1523/JNEUROSCI.3987-15.2016

Lloyd, D. M., Shore, D. I., Spence, C., & Calvert, G. A. (2003). Multisensory representation of limb position in human premotor cortex. *Nature Neuroscience*, *6*(1), 17–18. https://doi.org/10.1038/nn991

Logothetis, N. K. (2007). The ins and outs of fMRI signals. *Nature Neuroscience*, *10*(10), 1230–1232. https://doi.org/10.1038/nn1007-1230

Logothetis, N. K. (2008). What we can do and what we cannot do with fMRI. *Nature*, *453*(7197), 869–878. https://doi.org/10.1038/nature06976

Longo, M. R., Azañón, E., & Haggard, P. (2010). More than skin deep: body representation beyond primary somatosensory cortex. *Neuropsychologia*, *48*(3), 655–668.

Macaluso, E., Frith, C. D., & Driver, J. (2007). Delay activity and sensory-motor translation during planned eye or hand movements to visual or tactile targets. *Journal of Neurophysiology*, *98*(5), 3081–3094.

Makin, J. G., Fellows, M. R., & Sabes, P. N. (2013). Learning Multisensory Integration and Coordinate Transformation via Density Estimation. *PLoS Computational Biology*, *9*(4), e1003035. https://doi.org/10.1371/journal.pcbi.1003035

Makin, T. R., Holmes, N. P., & Zohary, E. (2007). Is That Near My Hand? Multisensory Representation of Peripersonal Space in Human Intraparietal Sulcus. *The Journal of Neuroscience*, *27*(4), 731–740. https://doi.org/10.1523/JNEUROSCI.3653-06.2007

Marcos, E., Cos, I., Girard, B., & Verschure, P. F. (2015). Motor cost influences perceptual decisions. *PloS One*, *10*(12), e0144841.

McCabe, C. S. (2011). Mirror Visual Feedback Therapy. A Practical Approach. *Journal of Hand Therapy*, *24*(2), 170–179. https://doi.org/10.1016/j.jht.2010.08.003

McCabe, C. S., Haigh, R. C., Halligan, P. W., & Blake, D. R. (2005). Simulating sensory–motor incongruence in healthy volunteers: implications for a cortical model of pain. *Rheumatology*, *44*(4), 509–516. https://doi.org/10.1093/rheumatology/keh529

McGlone, F., Kelly, E. F., Trulsson, M., Francis, S. T., Westling, G., & Bowtell, R. (2002). Functional neuroimaging studies of human somatosensory cortex. *Behavioural Brain Research*, *135*(1), 147–158.

McGuire, L. M. M., & Sabes, P. N. (2009). Sensory transformations and the use of multiple reference frames for reach planning. *Nature Neuroscience*, *12*(8), 1056–1061. https://doi.org/10.1038/nn.2357

Mechsner, F. (2004). A psychological approach to human voluntary movements. *Journal of Motor Behavior*, *36*(4), 355–370. https://doi.org/10.1080/00222895.2004.11007993

Mechsner, F., Kerzel, D., Knoblich, G., & Prinz, W. (2001). Perceptual basis of bimanual coordination. *Nature*, *414*(6859), 69–73. https://doi.org/10.1038/35102060

Medendorp, W. P. (2004). Integration of Target and Effector Information in Human Posterior Parietal Cortex for the Planning of Action. *Journal of Neurophysiology*, *93*(2), 954–962. https://doi.org/10.1152/jn.00725.2004

Medendorp, W. P., Buchholz, V. N., Van Der Werf, J., & Leoné, F. T. M. (2011). Parietofrontal circuits in goal-oriented behaviour. *European Journal of Neuroscience*, *33*, 2017–2027.

Medendorp, W. P., Goltz, H. C., Vilis, T., & Crawford, J. D. (2003). Gaze-centered updating of visual space in human parietal cortex. *The Journal of Neuroscience*, *23*(15), 6209–6214.

Medina, J., Khurana, P., & Coslett, H. B. (2015). The influence of embodiment on multisensory integration using the mirror box illusion. *Consciousness and Cognition*, *37*, 71–82. https://doi.org/10.1016/j.concog.2015.08.011

Meredith, M. A. (2002). On the neuronal basis for multisensory convergence: a brief overview. *Cognitive Brain Research*, *14*(1), 31–40. https://doi.org/10.1016/S0926-6410(02)00059-9

Meredith, M. A., Nemitz, J. W., & Stein, B. E. (1987). Determinants of multisensory integration in superior colliculus neurons. I. Temporal factors. *The Journal of Neuroscience*, *7*(10), 3215–3229.

Meredith, M. A., & Stein, B. E. (1983). Interactions among converging sensory inputs in the superior colliculus. *Science*, *221*(4608), 389–391. https://doi.org/10.1126/science.6867718

Meredith, M. A., & Stein, B. E. (1986). Spatial factors determine the activity of multisensory neurons in cat superior colliculus. *Brain Research*, *365*(2), 350–354. https://doi.org/10.1016/0006-8993(86)91648-3

Miall, R. C., & Ivry, R. B. (2004). Moving to a different beat. *Nature Neuroscience*, *7*(10), 1025–1026. https://doi.org/10.1038/nn1004-1025

Mirpour, K., & Bisley, J. W. (2015). Remapping, Spatial Stability, and Temporal Continuity: From the Pre-Saccadic to Postsaccadic Representation of Visual Space in LIP. *Cerebral Cortex*, bhv153. https://doi.org/10.1093/cercor/bhv153

Morasso, P. (1981). Spatial control of arm movements. *Experimental Brain Research*, *42*(2), 223–227.

Morgan, M. L., DeAngelis, G. C., & Angelaki, D. E. (2008). Multisensory Integration in Macaque Visual Cortex Depends on Cue Reliability. *Neuron*, *59*(4), 662–673. https://doi.org/10.1016/j.neuron.2008.06.024

Moseley, L. G., Gallace, A., & Spence, C. (2008). Is mirror therapy all it is cracked up to be? Current evidence and future directions: *Pain*, *138*(1), 7–10. https://doi.org/10.1016/j.pain.2008.06.026

Müller, S., & Fiehler, K. (2014a). Effector movement triggers gaze-dependent spatial coding of tactile and proprioceptive-tactile reach targets. *Neuropsychologia*, *62*, 184–193. https://doi.org/10.1016/j.neuropsychologia.2014.07.025

Müller, S., & Fiehler, K. (2014b). Gaze-dependent spatial updating of tactile targets in a localization task. *Cognition*, *5*, 66. https://doi.org/10.3389/fpsyg.2014.00066

Müller, S., & Fiehler, K. (2016). Mixed body- and gaze-centered coding of proprioceptive reach targets after effector movement. *Neuropsychologia*, *87*, 63–73. https://doi.org/10.1016/j.neuropsychologia.2016.04.033

Mulliken, G. H., Musallam, S., & Andersen, R. A. (2008). Forward estimation of movement state in posterior parietal cortex. *Proceedings of the National Academy of Sciences*, *105*(24), 8170–8177.

Murray, M. M., Thelen, A., Thut, G., Romei, V., Martuzzi, R., & Matusz, P. J. (2016). The multisensory function of the human primary visual cortex. *Neuropsychologia*, *83*, 161–169. https://doi.org/10.1016/j.neuropsychologia.2015.08.011

Nashed, J. Y., Crevecoeur, F., & Scott, S. H. (2012). Influence of the behavioral goal and environmental obstacles on rapid feedback responses. *Journal of Neurophysiology*, *108*(4), 999–1009. https://doi.org/10.1152/jn.01089.2011

Nichols, T. E., & Holmes, A. P. (2002). Nonparametric permutation tests for functional neuroimaging: A primer with examples. *Human Brain Mapping*, *15*(1), 1–25. https://doi.org/10.1002/hbm.1058

Nili, H., Wingfield, C., Walther, A., Su, L., Marslen-Wilson, W., & Kriegeskorte, N. (2014). A Toolbox for Representational Similarity Analysis. *PLOS Computational Biology*, *10*(4), e1003553. https://doi.org/10.1371/journal.pcbi.1003553

Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, *10*(9), 424–430. https://doi.org/10.1016/j.tics.2006.07.005

Oldfield, R. C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*(1), 97–113. https://doi.org/10.1016/0028-3932(71)90067-4

Oliveira, F. T., & Ivry, R. B. (2008). The Representation of Action: Insights From Bimanual Coordination. *Current Directions in Psychological Science*, *17*(2), 130–135. https://doi.org/10.1111/j.1467-8721.2008.00562.x

Oosterhof, N. N., Tipper, S. P., & Downing, P. E. (2012). Viewpoint (in) dependence of action representations: an MVPA study. *Journal of Cognitive Neuroscience*, *24*(4), 975–989.

Oostwoud Wijdenes, L., Brenner, E., & Smeets, J. B. J. (2014). Analysis of methods to determine the latency of online movement adjustments. *Behavior Research Methods*, *46*(1), 131–139. https://doi.org/10.3758/s13428-013-0349-7

Orban, G. A. (2016). Functional definitions of parietal areas in human and non-human primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *283*(1828), 20160118. https://doi.org/10.1098/rspb.2016.0118

O'Regan, J. K., & Noë, A. (2001). A sensorimotor account of vision and visual consciousness. *Behavioral and Brain Sciences*, *24*(05), 939–973. https://doi.org/10.1017/S0140525X01000115

Overvliet, K. E., Azañón, E., & Soto-Faraco, S. (2011). Somatosensory saccades reveal the timing of tactile spatial remapping. *Neuropsychologia*, *49*(11), 3046–3052. https://doi.org/10.1016/j.neuropsychologia.2011.07.005

Pasalar, S., Ro, T., & Beauchamp, M. S. (2010). TMS of posterior parietal cortex disrupts visual tactile multisensory integration. *European Journal of Neuroscience*, *31*(10), 1783–1790. https://doi.org/10.1111/j.1460-9568.2010.07193.x

Pélisson, D., Prablanc, C., Goodale, M. A., & Jeannerod, M. (1986). Visual control of reaching movements without vision of the limb. *Experimental Brain Research*, *62*(2), 303–311. https://doi.org/10.1007/BF00238849

Pellijeff, A., Bonilha, L., Morgan, P. S., McKenzie, K., & Jackson, S. R. (2006). Parietal updating of limb posture: An event-related fMRI study. *Neuropsychologia*, *44*(13), 2685–2690. https://doi.org/10.1016/j.neuropsychologia.2006.01.009

Penfield, W., & Boldrey, E. (1937). Somatic Motor and Sensory Representation in the Cerebral Cortex of Man as Studied by Electrical Stimulation. *Brain*, *60*(4), 389–443. https://doi.org/10.1093/brain/60.4.389

Pesaran, B., Nelson, M. J., & Andersen, R. A. (2006). Dorsal Premotor Neurons Encode the Relative Position of the Hand, Eye, and Goal during Reach Planning. *Neuron*, *51*(1), 125–134. https://doi.org/10.1016/j.neuron.2006.05.025

Pinheiro, J. C., & Bates, D. M. (2000). *Mixed-Effects Models in S and S-PLUS*. New York: Springer. https://doi.org/10.1007/b98882

Plummer, M. (2015). *JAGS Version 4.0. 0 user manual*. Retrieved from http://freebsd.csie.nctu.edu.tw/distfiles/mcmc-jags/jags_user_manual.pdf

Pouget, A., Dayan, P., & Zemel, R. S. (2000). Information processing with population codes. *Nature Reviews Neuroscience*, *1*(2), 125–132. https://doi.org/10.1038/35039062

Pouget, A., Dayan, P., & Zemel, R. S. (2003). Computation and inference with population codes. *Annual Review of Neuroscience*, *26*(1), 381–410. https://doi.org/10.1146/annurev.neuro.26.041002.131112

Pouget, A., Deneve, S., & Duhamel, J.-R. (2002). A computational perspective on the neural basis of multisensory spatial representations. *Nature Reviews Neuroscience*, *3*(9), 741–747. https://doi.org/10.1038/nrn914

Pouget, A., Ducom, J.-C., Torri, J., & Bavelier, D. (2002). Multisensory spatial representations in eye-centered coordinates for reaching. *Cognition*, *83*(1), B1–B11. https://doi.org/10.1016/S0010-0277(01)00163-9

Pritchett, L. M., Carnevale, M. J., & Harris, L. R. (2012). Reference frames for coding touch location depend on the task. *Experimental Brain Research*, *222*(4), 437–445. https://doi.org/10.1007/s00221-012-3231-4

Pruszynski, J. A., Kurtzer, I., Nashed, J. Y., Omrani, M., Brouwer, B., & Scott, S. H. (2011). Primary motor cortex underlies multi-joint integration for fast feedback control. *Nature*, *478*(7369), 387–390. https://doi.org/10.1038/nature10436

Pruszynski, J. A., & Scott, S. H. (2012). Optimal feedback control and the long-latency stretch response. *Experimental Brain Research*, *218*(3), 341–359. https://doi.org/10.1007/s00221-012-3041-8

R Core Team. (2015). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

R Core Team. (2016). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Raizada, R. D. S., & Kriegeskorte, N. (2010). Pattern-information fMRI: New questions which it opens up and challenges which face it. *International Journal of Imaging Systems and Technology*, *20*(1), 31–41. https://doi.org/10.1002/ima.20225

Raizada, R. D. S., Tsao, F.-M., Liu, H.-M., Holloway, I. D., Ansari, D., & Kuhl, P. K. (2010). Linking brain-wide multivoxel activation patterns to behaviour: Examples from language and math. *NeuroImage*, *51*(1), 462–471. https://doi.org/10.1016/j.neuroimage.2010.01.080

Ramachandran, V. S., & Altschuler, E. L. (2009). The use of visual feedback, in particular mirror visual feedback, in restoring brain function. *Brain*, *132*(7), 1693–1710. https://doi.org/10.1093/brain/awp135

Ramsay, J. O., Hooker, G., & Graves, S. (2009). *Functional Data Analysis with R and MATLAB*. New York, NY, USA: Springer.

Ramsay, J. O., & Silverman, B. W. (2005). *Functional data analysis*. New York, NY, USA: Springer.

Ratcliff, R., & Rouder, J. N. (1998). Modeling Response Times for Two-Choice Decisions. *Psychological Science*, *9*(5), 347–356. https://doi.org/10.1111/1467-9280.00067

Rathelot, J.-A., Dum, R. P., & Strick, P. L. (2017). Posterior parietal cortex contains a command apparatus for hand movements. *Proceedings of the National Academy of Sciences*, *114*(16), 4255–4260. https://doi.org/10.1073/pnas.1608132114

Reichenbach, A., Bresciani, J.-P., Peer, A., Bulthoff, H. H., & Thielscher, A. (2010). Contributions of the PPC to Online Control of Visually Guided Reaching Movements Assessed with fMRI-Guided TMS. *Cerebral Cortex*, *21*(7), 1602–1612. https://doi.org/10.1093/cercor/bhq225

Reichenbach, A., Franklin, D. W., Zatka-Haas, P., & Diedrichsen, J. (2014). A Dedicated Binding Mechanism for the Visual Control of Movement. *Current Biology*, *24*(7), 780–785. https://doi.org/10.1016/j.cub.2014.02.030

Renzi, C., Ricciardi, E., Bonino, D., Handjaras, G., Vecchi, T., & Pietrini, P. (2013). The Effects of Visual Control and Distance in Modulating Peripersonal Spatial Representation. *PLoS ONE*, *8*(3). https://doi.org/10.1371/journal.pone.0059460

Resulaj, A., Kiani, R., Wolpert, D. M., & Shadlen, M. N. (2009). Changes of mind in decision-making. *Nature*, *461*(7261), 263–266.

Riek, S., Carson, R. G., & Byblow, W. D. (1992). Spatial and muscular dependencies in bimanual coordination. *Journal of Human Movement Studies*, *23*(6), S. 251-265.

Riek, S., & Woolley, D. (2005). Hierarchical organisation of neuro-anatomical constraints in interlimb coordination. *Human Movement Science*, *24*(5–6), 798–814. https://doi.org/10.1016/j.humov.2005.10.002

Rigato, S., Bremner, A. J., Mason, L., Pickering, A., Davis, R., & van Velzen, J. (2014). The electrophysiological time course of somatosensory spatial remapping: vision of the hands modulates effects of posture on somatosensory evoked potentials. *European Journal of Neuroscience*, *39*(4), 703–703. https://doi.org/10.1111/ejn.12528

Rincon-Gonzalez, L., Buneo, C. A., & Helms Tillery, S. I. (2011). The Proprioceptive Map of the Arm Is Systematic and Stable, but Idiosyncratic. *PLoS ONE*, *6*(11), e25214. https://doi.org/10.1371/journal.pone.0025214

Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981a). Afferent properties of periarcuate neurons in macaque monkeys. I. Somatosensory responses. *Behavioural Brain Research*, (2), 125–146.

Rizzolatti, G., Scandolara, C., Matelli, M., & Gentilucci, M. (1981b). Afferent properties of periarcuate neurons in macaque monkeys. II. Visual responses. *Behavioural Brain Research*, (2), 147–163.

Röder, B., Rösler, F., & Spence, C. (2004). Early Vision Impairs Tactile Perception in the Blind. *Current Biology*, *14*(2), 121–124. https://doi.org/10.1016/j.cub.2003.12.054

Ronsse, R., Sternad, D., & Lefèvre, P. (2008). A Computational Model for Rhythmic and Discrete Movements in Uni- and Bimanual Coordination. *Neural Computation*, *21*(5), 1335–1370. https://doi.org/10.1162/neco.2008.03-08-720

Rosenthal, R., Rosnow, R. L., & Rubin, D. B. (1999). *Contrasts and Effect Sizes in Behavioral Research: A Correlational Approach*. Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9780511804403

Ruben, J., Schwiemann, J., Deuchert, M., Meyer, R., Krause, T., Curio, G., … Villringer, A. (2001). Somatotopic Organization of Human Secondary Somatosensory Cortex. *Cerebral Cortex*, *11*(5), 463–473. https://doi.org/10.1093/cercor/11.5.463

Ruzzoli, M., & Soto-Faraco, S. (2014). Alpha Stimulation of the Human Parietal Cortex Attunes Tactile Perception to External Space. *Current Biology*, *24*(3), 329–332. https://doi.org/10.1016/j.cub.2013.12.029

Salesse, R., Oullier, O., & Temprado, J.-J. (2005). Plane of Motion Mediates the Coalition of Constraints in Rhythmic Bimanual Coordination. *Journal of Motor Behavior*, *37*(6), 454–464. https://doi.org/10.3200/JMBR.37.6.454-464

Sarlegna, F. R., Blouin, J., Bresciani, J.-P., Bourdin, C., Vercher, J.-L., & Gauthier, G. M. (2003). Target and hand position information in the online control of goal-directed arm movements. *Experimental Brain Research*, *151*(4), 524–535. https://doi.org/10.1007/s00221-003-1504-7

Sarlegna, F. R., & Sainburg, R. L. (2009). The Roles of Vision and Proprioception in the Planning of Reaching Movements. In D. Sternad (Ed.), *Progress in Motor Control* (pp. 317–335). Springer US.

Saunders, J. A., & Knill, D. C. (2003). Humans use continuous visual feedback from the hand to control fast reaching movements. *Experimental Brain Research*, *152*(3), 341–352. https://doi.org/10.1007/s00221-003-1525-2

Schaal, S., Sternad, D., Osu, R., & Kawato, M. (2004). Rhythmic arm movement is not discrete. *Nature Neuroscience*, *7*(10), 1136–1143. https://doi.org/10.1038/nn1322

Schicke, T., & Röder, B. (2006). Spatial remapping of touch: confusion of perceived stimulus order across hand and foot. *Proceedings of the National Academy of Sciences*, *103*(31), 11808–11813.

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology*, *20*(2), 416–420. https://doi.org/10.1093/beheco/arn145

Schlack, A., Hoffmann, K.-P., & Bremmer, F. (2002). Interaction of linear vestibular and visual stimulation in the macaque ventral intraparietal area (VIP): Linear vestibular and visual responses in area VIP. *European Journal of Neuroscience*, *16*(10), 1877–1886. https://doi.org/10.1046/j.1460-9568.2002.02251.x

Schlack, A., Sterbing-D'Angelo, S. J., Hartung, K., Hoffmann, K.-P., & Bremmer, F. (2005). Multisensory Space Representations in the Macaque Ventral Intraparietal Area. *The Journal of Neuroscience*, *25*(18), 4616–4625. https://doi.org/10.1523/JNEUROSCI.0455-05.2005

Schmidt, R. C., Carello, C., & Turvey, M. T. (1990). Phase transitions and critical fluctuations in the visual coordination of rhythmic movements between people. *Journal of Experimental Psychology: Human Perception and Performance*, *16*(2), 227. https://doi.org/10.1037/0096-1523.16.2.227

Schroeder, C. E., & Foxe, J. (2005). Multisensory contributions to low-level, "unisensory" processing. *Current Opinion in Neurobiology*, *15*(4), 454–458. https://doi.org/10.1016/j.conb.2005.06.008

Schubert, J. T. W., Buchholz, V. N., Föcker, J., Engel, A. K., Röder, B., & Heed, T. (2015). Oscillatory activity reflects differential use of spatial reference frames by sighted and blind individuals in tactile attention. *NeuroImage*, *117*, 417–428. https://doi.org/10.1016/j.neuroimage.2015.05.068

Scott, S. H. (2002). Optimal strategies for movement: success with variability. *Nature Neuroscience*, *5*(11), 1110–1111.

Scott, S. H. (2003). The role of primary motor cortex in goal-directed movements: insights from neurophysiological studies on non-human primates. *Current Opinion in Neurobiology*, *13*(6), 671–677. https://doi.org/10.1016/j.conb.2003.10.012

Scott, S. H. (2004). Optimal feedback control and the neural basis of volitional motor control. *Nature Reviews Neuroscience*, *5*(7), 532–546. https://doi.org/10.1038/nrn1427

Scott, S. H. (2012). The computational and neural basis of voluntary motor control and planning. *Trends in Cognitive Sciences*, *16*(11), 541–549. https://doi.org/10.1016/j.tics.2012.09.008

Scott, S. H. (2016). A Functional Taxonomy of Bottom-Up Sensory Feedback Processing for Motor Actions. *Trends in Neurosciences*, *39*(8), 512–526. https://doi.org/10.1016/j.tins.2016.06.001

Selen, L. P. J., Shadlen, M. N., & Wolpert, D. M. (2012). Deliberation in the Motor System: Reflex Gains Track Evolving Evidence Leading to a Decision. *The Journal of Neuroscience*, *32*(7), 2276–2286. https://doi.org/10.1523/JNEUROSCI.5273-11.2012

Semjen, A., Summers, J. J., & Cattaert, D. (1995a). Hand coordination in bimanual circle drawing. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(5), 1139.

Semjen, A., Summers, J. J., & Cattaert, D. (1995b). Hand coordination in bimanual circle drawing. *Journal of Experimental Psychology: Human Perception and Performance*, *21*(5), 1139. https://doi.org/10.1037/0096-1523.21.5.1139

Sereno, M. I., & Huang, R.-S. (2006). A human parietal face area contains aligned head-centered visual and tactile maps. *Nature Neuroscience*, *9*(10), 1337–1343. https://doi.org/10.1038/nn1777

Sereno, M. I., & Huang, R.-S. (2014). Multisensory maps in parietal cortex. *Current Opinion in Neurobiology*, *24*, 39–46. https://doi.org/10.1016/j.conb.2013.08.014

Sereno, M. I., Pitzalis, S., & Martinez, A. (2001). Mapping of Contralateral Space in Retinotopic Coordinates by a Parietal Cortical Area in Humans. *Science*, *294*(5545), 1350–1354. https://doi.org/10.1126/science.1063695

Shadlen, M. N., & Kiani, R. (2013). Decision Making as a Window on Cognition. *Neuron*, *80*(3), 791–806. https://doi.org/10.1016/j.neuron.2013.10.047

Shadlen, M. N., & Newsome, W. T. (1996). Motion perception: seeing and deciding. *Proceedings of the National Academy of Sciences*, *93*(2), 628–633.

Shadlen, M. N., & Newsome, W. T. (2001). Neural Basis of a Perceptual Decision in the Parietal Cortex (Area LIP) of the Rhesus Monkey. *Journal of Neurophysiology*, *86*(4), 1916–1936.

Shadmehr, R., & Mussa-Ivaldi, S. (2012). *Biological Learning and Control: How the Brain Builds Representations, Predicts Events, and Makes Decisions*. Cambridge, MA, US: The MIT Press.

Shea, C. H., Buchanan, J. J., & Kennedy, D. M. (2016). Perception and action influences on discrete and reciprocal bimanual coordination. *Psychonomic Bulletin & Review*, *23*(2), 361–386. https://doi.org/10.3758/s13423-015-0915-3

Shore, D. I., Spry, E., & Spence, C. (2002). Confusing the mind by crossing the hands. *Cognitive Brain Research*, *14*(1), 153–163. https://doi.org/http://dx.doi.org/10.1016/S0926-6410(02)00070-8

Silver, M. A., & Kastner, S. (2009). Topographic maps in human frontal and parietal cortex. *Trends in Cognitive Sciences*, *13*(11), 488–495. https://doi.org/10.1016/j.tics.2009.08.005

Singmann, H. (2015). *afex: Analysis of Factorial Experiments. R package version 0.13–145.* Retrieved from https://r-forge.r-project.org/R/?group_id=1450

Snapp-Childs, W., Wilson, A. D., & Bingham, G. P. (2011). The stability of rhythmic movement coordination depends on relative speed: the Bingham model supported. *Experimental Brain Research*, *215*(2), 89–100. https://doi.org/10.1007/s00221-011-2874-x

Snyder, L. H. (2000). Coordinate transformations for eye and arm movements in the brain. *Current Opinion in Neurobiology*, *10*(6), 747–754.

Snyder, L. H., Batista, A. P., & Andersen, R. A. (1997). Coding of intention in the posterior parietal cortex. *Nature*, *386*(6621), 167–70. https://doi.org/http://dx.doi.org/10.1038/386167a0

Sober, S. J., & Sabes, P. N. (2003). Multisensory Integration during Motor Planning. *The Journal of Neuroscience*, *23*(18), 6982–6992.

Sober, S. J., & Sabes, P. N. (2005). Flexible strategies for sensory integration during motor planning. *Nature Neuroscience*, *8*(4), 490–497. https://doi.org/10.1038/nn1427

Soechting, J. F., & Flanders, M. (1989). Sensorimotor representations for pointing to targets in three-dimensional space. *Journal of Neurophysiology*, *62*(2), 582–594.

Soechting, J. F., & Flanders, M. (1992). Moving in Three-Dimensional Space: Frames of Reference, Vectors, and Coordinate Systems. *Annual Review of Neuroscience*, *15*(1), 167–191. https://doi.org/10.1146/annurev.ne.15.030192.001123

Soechting, J. F., & Lacquaniti, F. (1983). Modification of trajectory of a pointing movement in response to a change in target location. *Journal of Neurophysiology*, *49*(2), 548–564.

Song, J.-H., & Nakayama, K. (2009). Hidden cognitive states revealed in choice reaching tasks. *Trends in Cognitive Sciences*, *13*(8), 360–366.

Soto-Faraco, S., & Azañón, E. (2013). Electrophysiological correlates of tactile remapping. *Neuropsychologia*, *51*(8), 1584–1594. https://doi.org/10.1016/j.neuropsychologia.2013.04.012

Spence, C. (2012). Multisensory Perception, Cognition, and Behavior: Evaluating the Factors Modulating Multisensory Integration. In B. E. Stein (Ed.), *The New Handbook of Multisensory Processing* (pp. 241–264). Cambridge, MA, US.

Spencer, R. M. C., & Ivry, R. B. (2007). The temporal representation of in-phase and anti-phase movements. *Human Movement Science*, *26*(2), 226–234. https://doi.org/10.1016/j.humov.2007.01.002

Spencer, R. M. C., Zelaznik, H. N., Diedrichsen, J., & Ivry, R. B. (2003). Disrupted Timing of Discontinuous But Not Continuous Movements by Cerebellar Lesions. *Science*, *300*(5624), 1437–1439. https://doi.org/10.1126/science.1083661

Spivey, M. J., Grosjean, M., & Knoblich, G. (2005). Continuous attraction toward phonological competitors. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(29), 10393–10398. https://doi.org/10.1073/pnas.0503903102

Stein, B. E., Burr, D., Constantinidis, C., Laurienti, P. J., Meredith, M. A., Perrault, T. J., … Lewkowicz, D. J. (2010). Semantic confusion regarding the development of multisensory integration: a practical solution. *European Journal of Neuroscience*, *31*(10), 1713–1720. https://doi.org/10.1111/j.1460-9568.2010.07206.x

Stein, B. E., Huneycutt, W. S., & Meredith, M. A. (1988). Neurons and behavior: the same rules of multisensory integration apply. *Brain Research*, *448*(2), 355–358. https://doi.org/10.1016/0006-8993(88)91276-0

Stein, B. E., Meredith, M. A., Huneycutt, W. S., & McDade, L. (1989). Behavioral indices of multisensory integration: orientation to visual cues is affected by auditory stimuli. *Journal of Cognitive Neuroscience*, *1*(1), 12–24.

Stein, B. E., & Stanford, T. R. (2008). Multisensory integration: current issues from the perspective of the single neuron. *Nature Reviews Neuroscience*, *9*(4), 255–266. https://doi.org/10.1038/nrn2331

Sternad, D. (2008). Towards a Unified Theory of Rhythmic and Discrete Movements — Behavioral, Modeling and Imaging Results. In A. Fuchs & V. K. Jirsa (Eds.), *Coordination: Neural, Behavioral and Social Dynamics* (pp. 105–133). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-540-74479-5_6

Sternad, D., Dean, W. J., & Schaal, S. (2000). Interaction of rhythmic and discrete pattern generators in single-joint movements. *Human Movement Science*, *19*(4), 627–664. https://doi.org/10.1016/S0167-9457(00)00028-2

Sternad, D., Saltzman, E. L., & Turvey, M. T. (1998). Interlimb coupling in a simple serial behavior: A task dynamic approach. *Human Movement Science*, *17*(3), 393–433.

Sterzi, R., Bottini, G., Celani, M. G., Righetti, E., Lamassa, M., Ricci, S., & Vallar, G. (1993). Hemianopia, hemianaesthesia, and hemiplegia after right and left hemisphere damage. A hemispheric difference. *Journal of Neurology, Neurosurgery & Psychiatry*, *56*(3), 308–310.

Swinnen, S. P. (2002). Intermanual coordination: From behavioural principles to neural-network interactions. *Nature Reviews Neuroscience*, *3*(5), 348–359. https://doi.org/10.1038/nrn807

Swinnen, S. P., Jardin, K., & Meulenbroek, R. (1996). Between-limb asynchronies during bimanual coordination: Effects of manual dominance and attentional cueing. *Neuropsychologia*, *34*(12), 1203–1213. https://doi.org/10.1016/0028-3932(96)00047-4

Swinnen, S. P., Jardin, K., Verschueren, S., Meulenbroek, R., Franz, L., Dounskaia, N., & Walter, C. . (1998). Exploring interlimb constraints during bimanual graphic performance: effects of muscle grouping and direction. *Behavioural Brain Research*, *90*(1), 79–87. https://doi.org/10.1016/S0166-4328(97)00083-1

Swinnen, S. P., Lee, T. D., Verschueren, S., Serrien, D. J., & Bogaerds, H. (1997). Interlimb coordination: Learning and transfer under different feedback conditions. *Human Movement Science*, *16*(6), 749–785. https://doi.org/10.1016/S0167-9457(97)00020-1

Szczepanski, S. M., Konen, C. S., & Kastner, S. (2010). Mechanisms of Spatial Attention Control in Frontal and Parietal Cortex. *The Journal of Neuroscience*, *30*(1), 148–160. https://doi.org/10.1523/JNEUROSCI.3862-09.2010

Tagliabue, M., & McIntyre, J. (2014). A modular theory of multisensory integration for motor control. *Frontiers in Computational Neuroscience*, *8*, 1. https://doi.org/10.3389/fncom.2014.00001

Takahashi, T., Kansaku, K., Wada, M., Shibuya, S., & Kitazawa, S. (2013). Neural Correlates of Tactile Temporal-Order Judgment in Humans: an fMRI Study. *Cerebral Cortex*, *23*(8), 1952–1964. https://doi.org/10.1093/cercor/bhs179

Tal, N., & Amedi, A. (2009). Multisensory visual–tactile object related network in humans: insights gained using a novel crossmodal adaptation approach. *Experimental Brain Research*, *198*(2–3), 165–182. https://doi.org/10.1007/s00221-009-1949-4

Tame, L., Moles, A., & Holmes, N. P. (2014). Within, but not between hands interactions in vibrotactile detection thresholds reflect somatosensory receptive field organization. *Frontiers in Psychology*, *5*. https://doi.org/10.3389/fpsyg.2014.00174

Teasdale, N., Bard, C., Fleury, M., Young, D. E., & Proteau, L. (1993). Determining Movement Onsets from Temporal Series. *Journal of Motor Behavior*, *25*(2), 97–106. https://doi.org/10.1080/00222895.1993.9941644

Temprado, J.-J., Swinnen, S. P., Carson, R. G., Tourment, A., & Laurent, M. (2003). Interaction of directional, neuromuscular and egocentric constraints on the stability of preferred bimanual coordination patterns. *Human Movement Science*, *22*(3), 339–363. https://doi.org/10.1016/S0167-9457(03)00049-6

Temprado, J.-J., Zanone, P.-G., Monno, A., & Laurent, M. (1999). Attentional load associated with performing and stabilizing preferred bimanual patterns. *Journal of Experimental Psychology: Human Perception and Performance*, *25*(6), 1579.

Todorov, E. (2004). Optimality principles in sensorimotor control. *Nature Neuroscience*, *7*(9), 907–915. https://doi.org/10.1038/nn1309

Todorov, E., & Jordan, M. I. (2002). Optimal feedback control as a theory of motor coordination. *Nature Neuroscience*, *5*(11), 1226–1235. https://doi.org/10.1038/nn963

Toni, I., Thoenissen, D., Zilles, K., & Niedeggen, M. (2002). Movement preparation and working memory: a behavioural dissociation. *Experimental Brain Research*, *142*(1), 158–162. https://doi.org/10.1007/s00221-001-0933-4

Tramper, J. J., & Medendorp, W. P. (2015). Parallel updating and weighting of multiple spatial maps for visual stability during whole-body motion. *Journal of Neurophysiology*, jn.00576.2015. https://doi.org/10.1152/jn.00576.2015

Tresch, M. C., Saltiel, P., & Bizzi, E. (1999). The construction of movement by the spinal cord. *Nature Neuroscience*, *2*(2), 162–167.

Trommershäuser, J., Maloney, L. T., & Landy, M. S. (2008). Decision making, movement planning and statistical decision theory. *Trends in Cognitive Sciences*, *12*(8), 291–297. https://doi.org/10.1016/j.tics.2008.04.010

Uno, Y., Kawato, M., & Suzuki, R. (1989). Formation and control of optimal trajectory in human multijoint arm movement. *Biological Cybernetics*, *61*(2), 89–101.

Vallar, G. (1997). Spatial frames of reference and somatosensory processing: a neuropsychological perspective. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *352*(1360), 1401.

van Beers, R. J., Sittig, A. C., & Denier van der Gon, J. J. (1998). The precision of proprioceptive position sense. *Experimental Brain Research*, *122*(4), 367–377. https://doi.org/10.1007/s002210050525

van Beers, R. J., Sittig, A. C., & Denier van der Gon, J. J. (1999). Integration of Proprioceptive and Visual Position-Information: An Experimentally Supported Model. *Journal of Neurophysiology*, *81*(3), 1355–1364.

Van Essen, D. C. (2012). Cortical Cartography and Caret Software. *NeuroImage*, *62*(2), 757–764. https://doi.org/10.1016/j.neuroimage.2011.10.077

Van Essen, D. C., Glasser, M. F., Dierker, D. L., Harwell, J., & Coalson, T. (2012). Parcellations and Hemispheric Asymmetries of Human Cerebral Cortex Analyzed on Surface-Based Atlases. *Cerebral Cortex*, *22*(10), 2241–2262. https://doi.org/10.1093/cercor/bhr291

Veilleux, L.-N., & Proteau, L. (2010). Suboptimal online control of aiming movements in virtual contexts. *Experimental Brain Research*, *208*(3), 345–358. https://doi.org/10.1007/s00221-010-2487-9

Vesia, M., & Crawford, J. D. (2012). Specialization of reach function in human posterior parietal cortex. *Experimental Brain Research*, *221*(1), 1–18. https://doi.org/10.1007/s00221-012-3158-9

Vesia, M., Prime, S. L., Yan, X., Sergio, L. E., & Crawford, J. D. (2010). Specificity of Human Parietal Saccade and Reach Regions during Transcranial Magnetic Stimulation. *The Journal of Neuroscience*, *30*(39), 13053–13065. https://doi.org/10.1523/JNEUROSCI.1644-10.2010

Vignemont, F. de, Majid, A., Jola, C., & Haggard, P. (2009). Segmenting the body into parts: Evidence from biases in tactile perception. *The Quarterly Journal of Experimental Psychology*, *62*(3), 500–512. https://doi.org/10.1080/17470210802000802

Wada, M., Takano, K., Ikegami, S., Ora, H., Spence, C., & Kansaku, K. (2012). Spatio-Temporal Updating in the Left Posterior Parietal Cortex. *PLoS ONE*, *7*(6), e39800. https://doi.org/10.1371/journal.pone.0039800

Wann, J. P., & Ibrahim, S. F. (1992). Does limb proprioception drift? *Experimental Brain Research*, *91*(1), 162–166. https://doi.org/10.1007/BF00230024

Weigelt, C., & Cardoso de Oliveira, S. (2002). Visuomotor transformations affect bimanual coupling. *Experimental Brain Research*, *148*(4), 439–450. https://doi.org/10.1007/s00221-002-1316-1

Weigelt, M., Rieger, M., Mechsner, F., & Prinz, W. (2007). Target-related coupling in bimanual reaching movements. *Psychological Research*, *71*(4), 438–447. https://doi.org/10.1007/s00426-005-0043-1

Whitwell, R. L., & Goodale, M. A. (2013). Grasping without vision: Time normalizing grip aperture profiles yields spurious grip scaling to target size. *Neuropsychologia*, *51*(10), 1878–1887. https://doi.org/10.1016/j.neuropsychologia.2013.06.015

Wickham, H. (2009). *ggplot2: Elegant Graphics for Data Analysis*. New York: Springer.

Wilson, A. D., & Bingham, G. P. (2008). Identifying the information for the visual perception of relative phase. *Perception & Psychophysics*, *70*(3), 465–476. https://doi.org/10.3758/PP.70.3.465

Wilson, A. D., Collins, D. R., & Bingham, G. P. (2005a). Human movement coordination implicates relative direction as the information for relative phase. *Experimental Brain Research*, *165*(3), 351–361. https://doi.org/10.1007/s00221-005-2301-2

Wilson, A. D., Collins, D. R., & Bingham, G. P. (2005b). Perceptual coupling in rhythmic movement coordination: stable perception leads to stable action. *Experimental Brain Research*, *164*(4), 517–528. https://doi.org/10.1007/s00221-005-2272-3

Wilson, A. D., Snapp-Childs, W., & Bingham, G. P. (2010). Perceptual learning immediately yields new stable motor coordination. *Journal of Experimental Psychology: Human Perception and Performance*, *36*(6), 1508. https://doi.org/10.1037/a0020412

Wimmers, R. H., Beek, P. J., & van Wieringen, P. C. W. (1992). Phase transitions in rhythmic tracking movements: A case of unilateral coupling. *Human Movement Science*, *11*(1–2), 217–226. https://doi.org/10.1016/0167-9457(92)90062-G

Wolpert, D. M., & Ghahramani, Z. (2000). Computational principles of movement neuroscience. *Nature Neuroscience*, *3*, 1212–1217. https://doi.org/10.1038/81497

Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). Are arm trajectories planned in kinematic or dynamic coordinates? An adaptation study. *Experimental Brain Research*, *103*(3), 460–470. https://doi.org/10.1007/BF00241505

Wolpert, D. M., Goodbody, S. J., & Husain, M. (1998). Maintaining internal representations: the role of the human superior parietal lobe. *Nature Neuroscience*, *1*(6), 529–533.

Wolpert, D. M., & Landy, M. S. (2012). Motor control is decision-making. *Current Opinion in Neurobiology*, *22*(6), 996–1003. https://doi.org/10.1016/j.conb.2012.05.003

Wuyts, I. J., Summers, J. J., Carson, R. G., Byblow, W. D., & Semjen, A. (1996). Attention as a mediating variable in the dynamics of bimanual coordination. *Human Movement Science*, *15*(6), 877–897.

Yamamoto, S., & Kitazawa, S. (2001). Reversal of subjective temporal order due to arm crossing. *Nature Neuroscience*, *4*(7), 759–765. https://doi.org/10.1038/89559

Zaal, F. T. J. M., Bingham, G. P., & Schmidt, R. C. (2000). Visual perception of mean relative phase and phase variability. *Journal of Experimental Psychology: Human Perception and Performance*, *26*(3), 1209–1220. https://doi.org/10.1037//0096-1523.26.3.1209

Appendix

Supplemental results accompanying Chapter 4

In the supplemental results, we report analyses that address several potential confounds and alternative interpretations of the results presented in the main text:

1. The sine waves fit to the data may not describe the shape of raw data well.
2. The arbitrary classification of phase differences as correct and incorrect at a cut-off of +/-50° may influence the results, given that the largest differences between conditions appear to be present in a smaller phase interval of about +/-20°.
3. The results reported in the main text may reflect a switch from horizontal (left-right) to vertical (up-down) finger movements rather than a reduction of overall movement accuracy.

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1. Sine waves capture the velocity pattern of the raw data

Phase information can be readily retrieved, when a sine wave is fit to the data. The main advantage of fitting sine waves is that there is a unique high and low point in the sine pattern, allowing unequivocal identification of the relevant movement parameters. Furthermore, movements usually do indeed follow a sinusoidal velocity pattern, which is made explicit with our approach.

To demonstrate that sine fitting is appropriate with the present data, see *Figure S1*, which plots true movement (solid) vs. fitted sines (dashed) for an example set of movement cycles. Note, that high and low points are well captured.

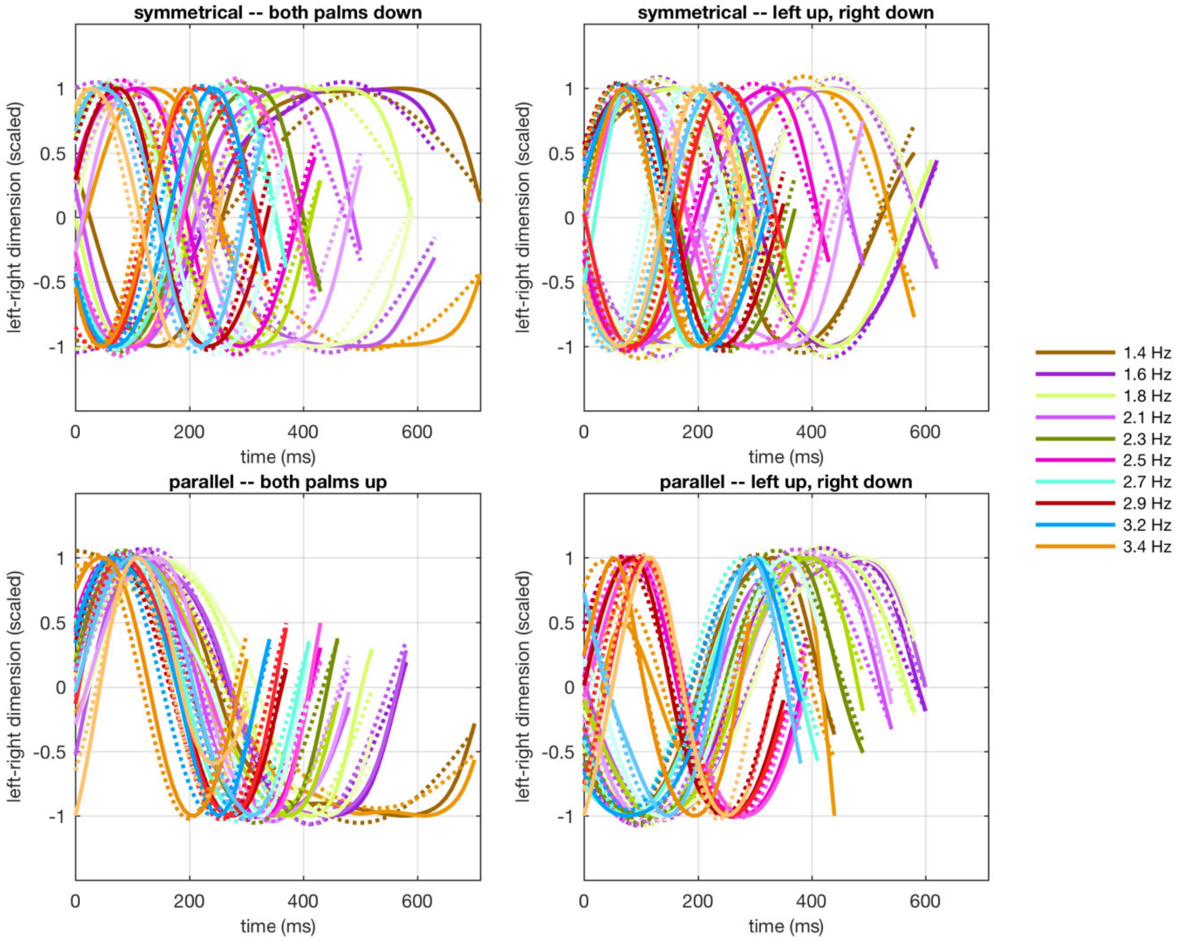

Figure S1. Illustration of exemplar sine wave fit to raw data of a single participant. One movement cycle is plotted per speed level (color-coded) and hand orientation across movement instructions (panels). Solid lines indicate raw data, whereas fitted sine waves are plotted as dashed lines. Dark and bright shades of the same color indicate left and right hand traces respectively.

2. The reported results are qualitatively similar when phase differences are dichotomized according to different criteria

By using a phase range of +/- 50° to determine of movements were performed correctly, we adopted an analysis strategy that has been introduced by others (Mechsner et al., 2001) and that we have used previously in the finger oscillation task (Heed & Röder, 2014). Using this strategy also in the present study allows comparison across studies, which is important because we draw direct comparisons to these previous studies.

Furthermore, the histograms displayed in *Figure 4.2* in Chapter 4 illustrate that a +/- 50° relative phase range (grey shading) is appropriate to capture the major part of the distributions that center around the correct phase difference at slow movement speeds (180° for symmetrical and 0° for parallel movements). Choosing a smaller relative phase range artificially cuts off large proportions of these distributions that describe the variation of relative phase at higher movement speeds in the present experiment. Nonetheless, to demonstrate that our central results are invariant to the threshold used to dichotomize the data into correct and false responses, *Figure S2* shows accuracy using a relative phase range of +/-20° in correspondence to *Figure 4.3* in Chapter 4. Note, that the results are similar for both analyses (cut-off at 50° and at 20°).

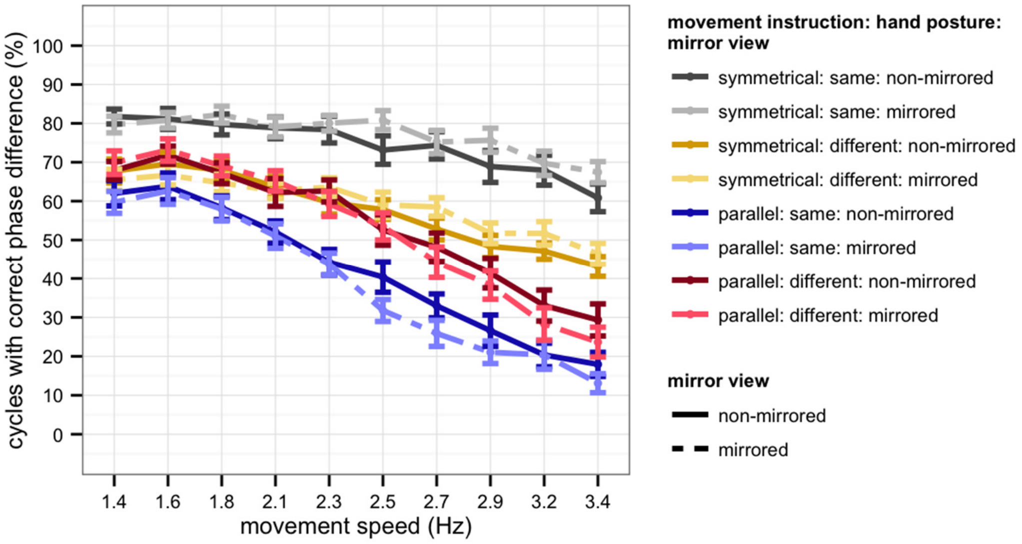

Figure S2. Illustration of accuracy in the finger oscillation task. Percentage of movement cycles with the correct phase difference (+/-20°) between the two index fingers. Line colors represent the interaction of movement instruction (symmetrical vs. parallel) and hand orientation (same vs. different). Dark colors and solid lines represent non-mirrored conditions, and bright colors and dashed lines indicate mirrored feedback conditions. Error bars represent standard errors of the mean.

3. There is no trade-off between movements in the horizontal and vertical planes

Participants were required to perform abduction and adduction movements in the horizontal plane. Previous studies have shown that the motor system can spontaneously recruit additional degrees of freedom when high movement speed is required. For finger oscillations, motion can transition from the horizontal (left-right) toward the vertical (up-down) dimension. We note, that if such trade-offs were evident in our study, they would still reflect condition-specific modulations, and, thus, lead to similar conclusions as the ones we draw in the main text. Nevertheless, we conducted several analyses to test whether participants produced the instructed abduction and adduction movements in the horizontal plane at high speeds in the present study, and whether the effects we report reflect a trade-off between movements in the horizontal and vertical planes.

We analyzed movement velocity, because this variable best reflects the variability of the finger movements over time and is also the basis of the sine waves analyzed in the present study. First, *Figure S3* illustrates density distributions fitted to the absolute number of movement cycles identified per participant at the four highest speed levels (ranging from 2.5. to 3.4 Hz), pooled across movement instructions and hand orientations. At high speeds, participants tend to get out of rhythm and reduce movement amplitude, and this often leads to a moderate decline of the number of performed movement cycles that can be identified in motion data. For simplicity, data are collapsed across mirror view conditions. The grand mean of movement cycles across participants is displayed as black horizontal bars; the instructed number of movement cycles is displayed as a red dashed line. It is evident from the shape of the density distributions that the number of produced movement cycles generally matched the target number of movements well for all participants, even in the most difficult condition, that is, parallel movements at high speeds with hands oriented differently (bottom right panel).

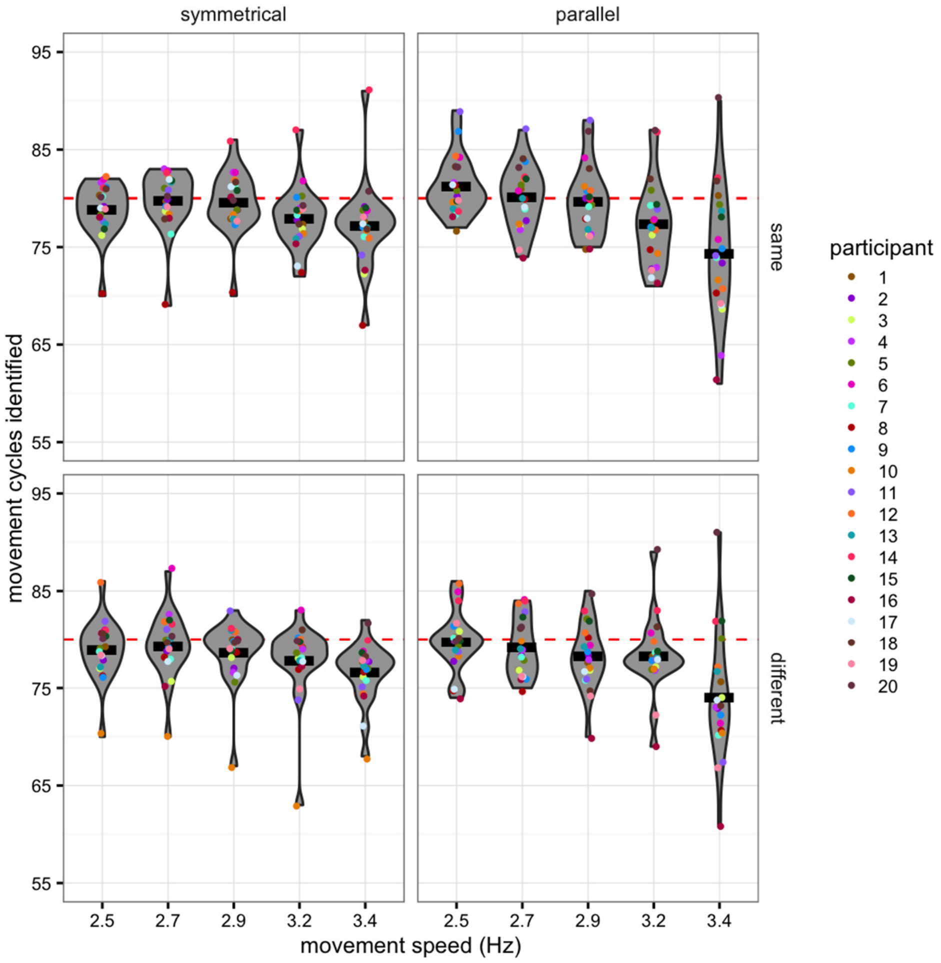

Figure S3. Illustration of the absolute number of movement cycles identified per participant at high speed levels (2.5 to 3.4 Hz).

Second, to demonstrate that movements were primarily executed in the horizontal plane at all times, *Figure S4* shows numerically differentiated movement velocities of a single participants' left (blue) and right hand (red) in the left-right (horizontal) dimension across all hand orientations. Example data is taken from the most difficult condition, that is, parallel movements executed with mirrored visual feedback. If one presumes that systematic trade-offs occur between horizontal and vertical movements due to our experimental conditions, a switch to the vertical motion plane should be especially evident when performance is most difficult. *Figure S5* shows the corresponding velocities in the up-down (vertical) dimension. It is apparent that amplitudes were highest in the left-right dimension, even at high frequencies and when executing parallel movements with hands oriented differently (two bottom panels), as well as in a supine orientation (two top panels).

Third, to illustrate this finding on a group level, *Figure S6* shows the standard deviation of velocity per participant and speed level (ranging from 1.4 to 3.4 Hz) for all three movement dimensions, averaged across trials and the two hands. Standard deviations should be highest in the instructed movement plane, that is, the left-right dimension, while standard deviations in the other dimensions should be considerably smaller. For simplicity, data are collapsed across mirror view conditions. The grand mean of standard deviations across participants is displayed as horizontal bars that are color-coded according to movement dimension. Critically, the standard deviation of velocity increases in all three dimensions with rising movement speed. This result pattern does not support the suggestion that a trade-off from one to the other dimension has taken place, but instead reflects a general increase in movement variablilty with higher speed. Furthermore, amplitude in the horizontal dimension exceeded that of the other two dimensions even at high speeds in all participants. This finding holds also when considering each hand separately (data not shown).

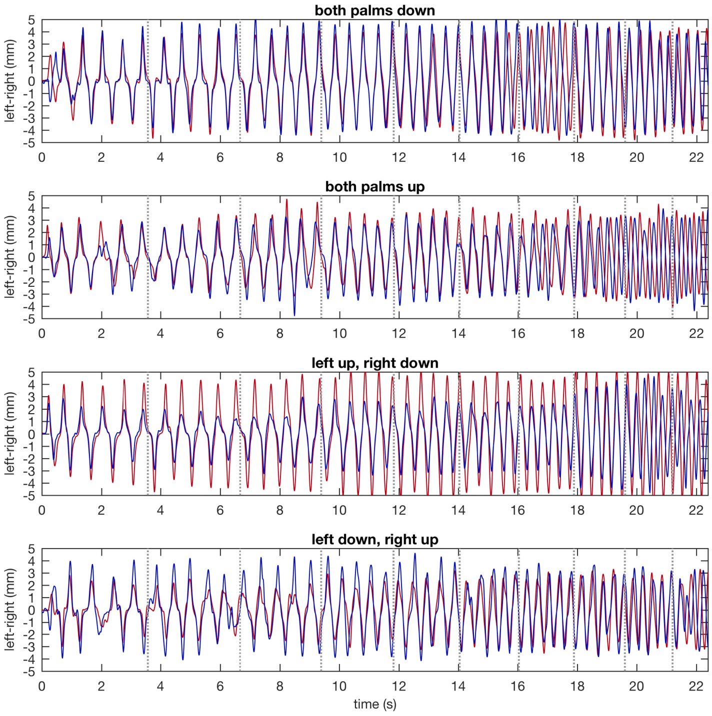

Figure S4. Left-right (horizontal) velocity traces of a single participant across hand orientations. Data are from the most difficult experimental condition, that is, parallel movements executed while receiving mirrored visual feedback. See *Figure S5* for the corresponding traces in the up-down (vertical) dimension.

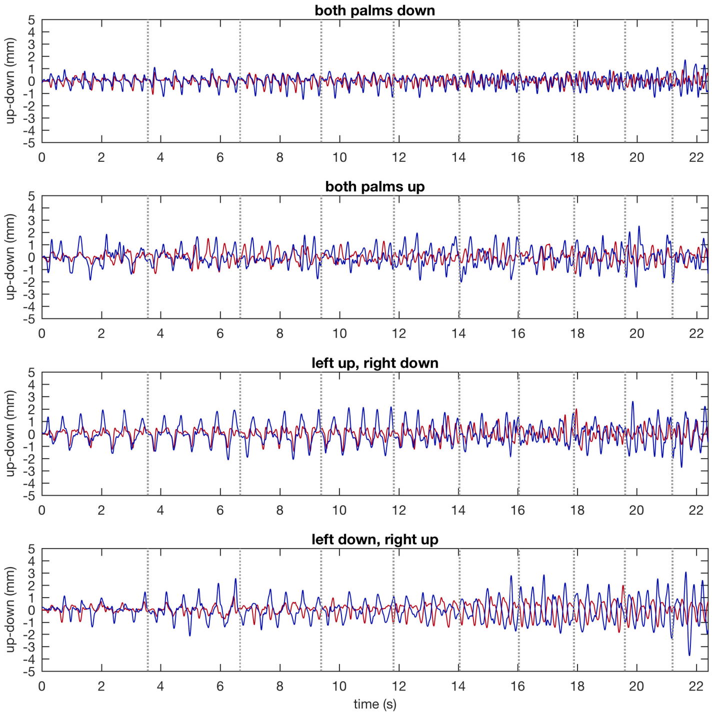

Figure S5. Up-down (vertical) velocity traces of the same participant and conditions as *Figure S4*.

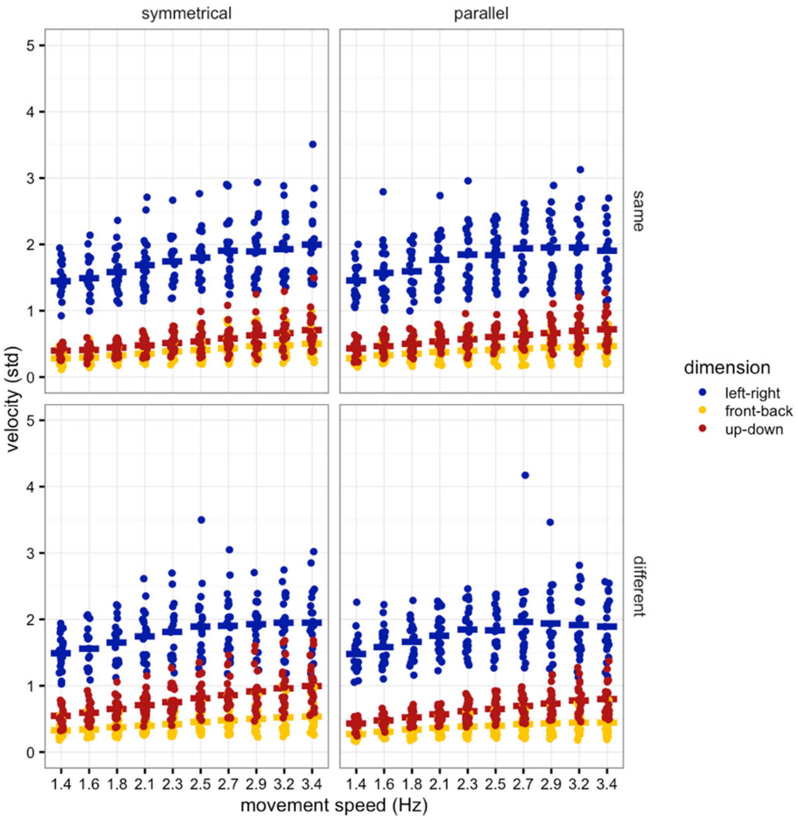

Figure S6. Illustration of the standard deviation of velocity per participant and speed level (1.4 to 3.4 Hz) for all three movement dimensions, averaged across trials and hands. The grand mean of standard deviations across participants is displayed as horizontal bars color-coded according to movement dimension.

Note, that a switch to vertical instead of horizontal movement patterns does not appear to have been an issue, as demonstrated above. However, some transitions from parallel to symmetrical coordination patterns occurred at high movement frequencies. This is a well-described phenomenon shown by numerous previous investigations (e.g., L. Cohen, 1971; Kelso, 1984; Kelso et al., 1986). In the present study, these transitions were evident in an increased number of movements that were generated with relative phase differences centered around 180° when a phase difference around 0° characterizing parallel movements would have been appropriate (see *Figure 4.2* in Chapter 4 for illustration of observed phase differences). Crucially, the question central to the present study was to test whether visual reafferent information is relevant for bimanual coordination. Our approach is to test whether the percentage of correctly performed movements decreases with speed. It is not essential for the current research question to further qualify whether or not pattern transitions occurred. Consequently, we dichotomized relative phases into correct and false responses instead of analyzing actual phase differences (see above, comparability with previous studies).

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