The Role of Social Contextual Factors in Instrumental and Communicative Action Understanding in Infancy

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AE	Action execution
ANOVA	Analysis of variance
AO	Action observation
ASD	Autism spectrum disorder
ASL	Associative sequential learning
CWT	Continuous wavelet transform
EEG	Electroencephalography
ERD	Event-related desynchronization
ERO(s)	Event-related oscillation(s)
ERP(s)	Event-related potential(s)
ERS	Event-related synchronization
fMRI	Functional magnetic resonance imaging
fNIRS	Function near-infrared spectroscopy
FT	Fourier transform
ICA	Independent component analysis
IFC	Inferior frontal cortex
IFG	Inferior frontal gyrus
IIR	Infinite impulse response
IPL	Inferior parietal lobule
ISI	Inter-stimulus interval
LCD	Liquid crystal display
LCP	Left centro-parietal
LFC	Left fronto-central
MEG	Magnetoencephalography
MEPs	Motor-evoked potentials
MNS	Mirror neuron system

Nc	Negative central
OCC	Occipital
PET	Positron emission tomography
PPC	Posterior parietal cortex
RCP	Right centro-parietal
RFC	Right fronto-central
SD	Standard deviation
SE	Standard error
STFT	Short time Fourier transform
STS	Superior temporal sulcus
TMS	Transcranial magnetic stimulation
vPMC	Ventral premotor cortex
WT	Wavelet transform

Abstract

Humans' ability to predict the goals of others' actions is extensively shaped throughout life by varying social contexts and experiences. However, research has identified basic mechanisms of such an ability already in infancy. The mirror system has been implicated in this skill for goal prediction and action understanding. Similar to adults (8-13Hz), recent electroencephalography (EEG) research with infants has shown mu rhythm desynchronization (6-9Hz), which is considered the EEG signature of the mirror system functions, around the centrally located channels (corresponding to the sensorimotor cortex) for actions performed by the self and to those observed or expected from others (Cuevas et al., 2014; Fox et al., 2016; Marshall & Meltzoff, 2011).

The interpretation of what the mirror system does, however, has remained equivocal. On the classic direct-matching account (Rizzolatti et al., 2001), the observation of actions directly activates an understanding of the goals qua one's own action repertoire. The action reconstruction account (Csibra, 2008) suggests that the motor activation in the observer is only a consequence, not the cause, of predicting action goals, however, limiting this mechanism only to instrumental actions. The recently proposed social responding account (Hamilton, 2016) suggests that the mirror system activates due to one's anticipation of an appropriate response to the observed action.

Goal predictions occur in the context and service of social interaction and cooperation, which in turn, shape our predictions. Under this assumption, I conducted three EEG studies to investigate how actions and goal attribution may be interlinked with distinct social and spatial contexts that may render interpretations of actions, whether instrumental or communicative, as meaningful and goal-oriented.

In studies 1 and 2, the target action that was observed by one group of adults (only in study 1) and several groups of 9-month-old infants comprised of the back-of-hand action (palm-up). The back-of-hand action has been frequently incorporated as a control condition in studies of action understanding, with the expectation that this action

is not instrumental in obtaining goals (objects) when compared to more typical actions such as grasping (For example, Southgate et al., 2010). However, in the current studies, the participants watched videos of the back-of-hand action being unfolded under varying social, nonsocial and spatial contexts, as third-party observers. The findings, as evident by means of significant mu desynchronization, revealed that the back-of-hand action was interpreted as meaningful only in the congruent social setting, where the observed back-of-hand action could be associated with a requestive goal. Similarly, the pointing action, which was previously shown to not elicit mu desynchronization (Pomiechowska & Csibra, 2017), was incorporated in study 3. In this study, 12-month-old infants exhibited significant mu desynchronization when observing the pointing action in social situations, either for a requestive purpose or to share attention.

The significant findings in this thesis, particularly from the infant samples, were elicited in the right hemisphere, i.e., the right centro-parietal and the right fronto-central regions, providing further support to the social functions of the right hemisphere. Further, the findings provided substantial evidence that processing communicative actions and attributing communicative goals also exhibited mu rhythm desynchronization, suggesting that the function of the mirror system is not limited to instrumental actions alone. Finally, the findings also bring to light the limitations of existing theories of action understanding and suggest that a broader, composite perspective may be better suited that offers more flexibility for one’s interpretation of the association between actions, context and goals.

1 Introduction

As social beings, humans engage in extensive collaboration with conspecifics for most part of their lifespan. Cultural learning and cooperation are fundamental to human cognition (Tomasello, 2014). We understand other people, make joint plans, offer advice and learn from others' experiences. We share our opinions, display emotions, and possess different ideologies and values. Our unique ability to infer and share goals, beliefs and intentions lays the foundation for successful action understanding. This unique ability has been attributed to the functions of the mirror neuron system (MNS) or the mirror system, as it is referred to in humans[1].

The MNS contains neurons that are activated when one executes goal-directed actions and when observing another individual perform the same action. The discovery of the MNS towards the end of the 20th century inspired a range of diverse investigations over the past two decades, suggesting that mirroring functions may have far-reaching implications beyond action understanding. Several theories have been put forth, focusing on the origins and mechanisms of the MNS, however, with little consensus. Recently, the focus has been extended to also include social interactions and communicative parameters that facilitate action understanding.

While speech and language are predominant mediums enabling our inferences, prelinguistic infants are already able to engage in social events, thereby also accurately encoding action goals and understanding them. However, what mechanisms facilitate their action understanding? Is it the motor representation of the action or inferential processes? Further, if infants are able to engage with other people socially from early on, then they should also perceive communicative (referential) gestures such as back-

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[1] As it is ethically implausible (although there may be exceptions) to conduct experiments at the cellular level with human participants, we cannot refer to neuronal activation while discussing similarities with the monkey MNS or functions relating to humans and hence the use of the term mirror system is preferred while referring to humans (Hickok, 2014).

of-hand (palm-up configuration) or pointing as meaningful in a similar manner as instrumental actions, such as grasping. Moreover, considering the complexity of human behaviour, action understanding may encompass a flexible system that takes into account the available contextual factors.

In the following introduction, I provide a brief overview of the discovery of the MNS, the evidence for the existence of an analogous mirror system in humans and its far-reaching implications and criticisms. Next, I delve into the details of the extant theories and claims, while also placing emphasis on the evidence from infant action understanding studies, and on EEG and its signature for the mirror system functions, mu rhythm desynchronization.

1.1 Discovery of the Mirror Neuron System

In 1988, a group of scientists in Parma, Italy, began to investigate the role of neurons in area F5 of the macaque's premotor cortex (located within the frontal lobe) for grasping actions (Rizzolatti et al., 1988). In this single-cell study, they found that viewing different types of objects activated specific sets of neurons that fired for a specific type of grasping not only when producing the action but also in anticipation of the action that the object afforded. For example, on seeing a raisin, the neurons that code for a pincer grasp began to fire even before the monkey moved its arm. In a successive study, the researchers also found another subsection of the F5 neurons that not only fired when the monkey performed goal-directed movements but also when it observed the experimenter act in a goal-directed manner, for example while grasping objects in order to replace them in between trials. This led to the discovery of the new set of functions in the F5 region (di Pellegrino et al., 1992) and these neurons were later referred to as the mirror neurons (Rizzolatti, Fadiga, Gallese et al., 1996).

Subsequent studies also demonstrated that specific neurons selectively activated for specific observed actions such as grasping, placing, manipulating, or for other properties such as hand preference or action direction (Gallese et al., 1996), or in response to the observed grasping hand alone or when the agent is also visible while executing the action (Nelissen et al., 2006). In general, mirror neurons have been found in both the left and right hemispheres (Gallese et al., 1996).

Additional data revealed that mirror neurons also activated when monkeys executed or observed ingestive mouth actions such as picking, sucking or breaking food or performing intransitive actions such as lip smacking and tongue protrusions (Ferrari et al., 2003). The functions extended to perceiving occluded goals, such as when monkeys observed an experimenter reach for an object hidden behind an occluder (Umiltà et al., 2001) and observing and executing grasping actions with the help of tools (Ferrari et al., 2005; Umiltà et al., 2008).

Parallel monkey experiments revealed that the neurons in the superior temporal sulcus (STS) of the temporal lobe played a role in perceiving biological motion (Nelissen et al., 2006) and observing hand-object interactions and other gross movements. However, these neurons are not endowed with motor properties (Perrett et al., 1990). In other words, these neurons do not fire in response to self-produced actions but possibly relay visual information related to both self-produced and observed actions. The STS neurons are reciprocally connected with neurons of the inferior parietal lobule (IPL) of the posterior parietal cortex (PPC) (Pandya & Seltzer, 1982; Seltzer & Pandya, 1986), which are in turn reciprocally connected to area F5 of the premotor cortex, (Rizzolatti et al., 1998; Rizzolatti et al., 1997), as depicted in Figure 1. The neurons in the STS communicate with those of area F5 through two possible routes via the PPC, one coding for visual information that facilitates intention understanding and the other relaying information about the object that enables congruent motor acts (Nelissen et al., 2011).

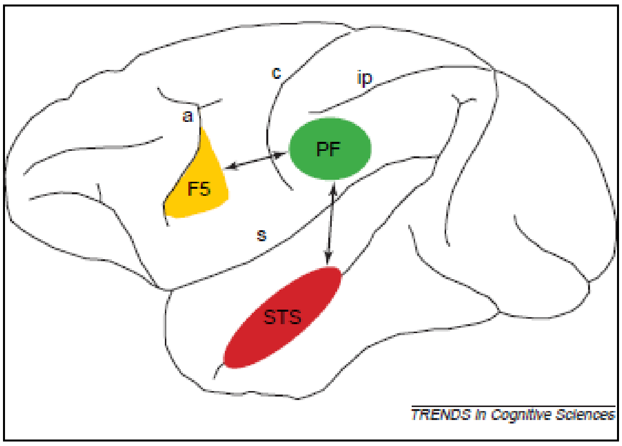

Figure 1: The macaque MNS

Lateral view of the macaque brain showing the areas of the mirror neuron system – area F5 of the monkey premotor cortex, PF of the inferior parietal lobule (IPL) and the superior temporal sulcus (STS). The arrows indicate reciprocal connections. (a: arcuate sulcus; c: central sulcus; ip: intraparietal sulcus; s: sylvian sulcus).

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In addition, there is evidence that the PPC, especially area PF, forms an extension of the mirror neuron system, where a considerable percentage of neurons fire for both execution and observation of goal-directed hand-object interactions (Gallese et al., 2002). Moreover, these neurons also code for the intention of observed actions, and not just the kinematics, as shown by Fogassi et al. (2005). In this study, the researchers showed that a subset of neurons fired with stronger intensity for 'grasping-to-eat' actions but with lesser intensity for 'grasping-to-place' actions and vice versa for both executed and observed actions. The discharge pattern of these neurons was attributed to the "*chained motor organization of the IPL*" (Fogassi et al. (2005), p.665), where the final goal (possibly determined by context and object type) is embedded within successive motor acts and not due to a simple temporal association between these motor acts. In other words, these neurons possibly belong to the so called logically-related neurons, where the observation of one motor act (such as grasping) elicits the activation of neurons, which are triggered by the execution of functionally related motor acts (such as eating) (di Pellegrino et al., 1992). This finding is relevant in the context of complex human (social) collaborations, which are replete with such logically chained motor acts.

About a decade after its initial discovery, the function of the MNS was seemingly promoted from coding ‘what’ the agent was doing to a more complex ability of anticipating ‘why’ an action would be done. Understanding intentions requires more than just following the kinematics of an action. One has to anticipate ahead, differentiate between goals of identical actions and draw inferences. Based on the initial data, it was considered plausible that there was more to mirror neurons beyond action understanding.

1.2 The Mirror System in Humans

The mirror system is also alternatively referred to as the parieto-frontal mirror circuit (Fabbri-Destro & Rizzolatti, 2008). Similar to the monkey sites, the mirror system, comprises of the inferior frontal cortex (IFC) (including the ventral premotor cortex (vPMC) and the inferior frontal gyrus (IFG)) and the IPL in humans (Rizzolatti et al., 2001; Rizzolatti & Craighero, 2004; See Caspers et al., 2010 for a meta-analysis), as shown in Figure 2. While some researchers consider the STS region as part of the mirror system (for example, Keysers & Perrett, 2004), other researchers do not (for example, Fabbri-Destro & Rizzolatti, 2008). Further, there is no consensus on whether the functions of the mirror system are lateralized in humans (Aziz-Zadeh et al., 2006; Shillcock et al., 2019).

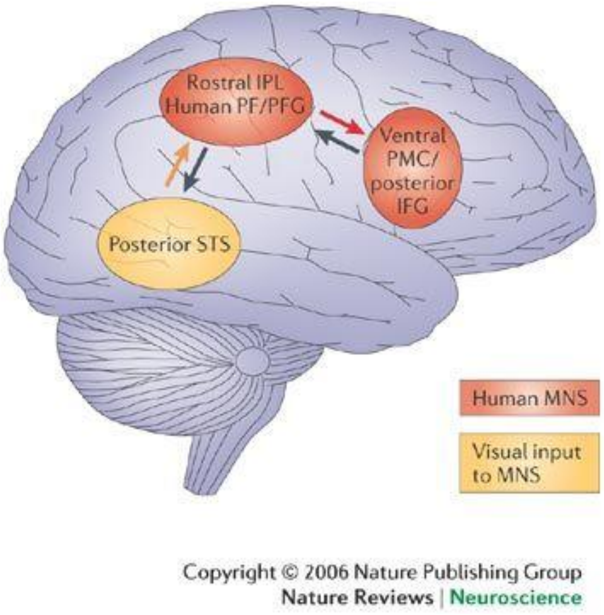

Figure 2: The human mirror system

Lateral view of the human brain showing the mirror system areas and their interconnections. (STS: superior temporal sulcus; IPL: inferior parietal lobule; PMC: premotor cortex; IFG: inferior frontal gyrus).

Reprinted by permission from Springer Nature: Nature Reviews Neuroscience, Vol. 7, the mirror neuron system and the consequences of its dysfunction, Marco Iacoboni & Mirella Dapretto, 2006

With the exception of one study at the neuronal level (Mukamel et al., 2010), most evidence for the mirror system in humans comes indirectly from non-invasive measures[2] such as functional magnetic resonance imagining (fMRI), positron emission tomography (PET), transcranial magnetic stimulation (TMS) or EEG. In this section, I provide a short overview of the early findings that implicated the mirror system in action understanding in humans.

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[2] It is interesting to note that the initial experiments using the PET method conducted by the Parma group in Italy with human participants did not exhibit a cortical correspondence between the executed and observed actions, and between the executed and imagined actions. Observed and imagined actions but not executed actions activated the inferior frontal cortex, left STS and left parietal area 40 (Grafton et al., 1996; Rizzolatti, Fadiga, Matelli et al., 1996). Further, the sites activated during executed grasping in humans were not similar to those activated in the monkey.

Stimulating the motor cortex using TMS facilitated an increase in motor evoked potentials (MEPs) from the muscles involved in the observed actions such as grasping objects of different sizes (Fadiga et al., 1995), writing movements (Strafella & Paus, 2000) and also when observing intransitive hand or finger flexions and extensions (Maeda, Kleiner-Fisman, et al., 2002; Maeda, Mazziotta, et al., 2002). TMS stimulation during observation of ongoing grasping or flicking actions resulted in a greater motor facilitation when compared to directly watching the end position of the same actions, suggesting an anticipatory role of the mirror system functions (Urgesi et al., 2010).

fMRI investigations using observation/execution paradigms around the turn of the century also provided the initial evidence for the existence of a mirror system in humans. These studies showed mirror system activation for hand-object manipulations (Binkofski, Buccino, Posse, et al., 1999; Binkofski, Buccino, Stephan, et al., 1999), for object- and non-object-related motor acts using different effectors (Buccino et al., 2001), and for the imitation of intransitive actions (Iacoboni et al., 1999) or guitar chord movements (Binkofski & Buccino, 2006; Buccino, Binkofski, et al., 2004; Buccino, Vogt, et al., 2004). Further, the mirror system exhibited a stronger activation when participants watched grasping actions embedded with intentions such as ‘grasping to drink’ or ‘grasping to clean’ as opposed to the context alone or the action alone (Iacoboni et al., 2005).

Another source of evidence for the mirror system came from investigations with apraxia patients. These patients, with damage to the left IFG, demonstrated difficulties in executing transitive and intransitive actions, in judging the correctness of the same actions they observed (Pazzaglia, Smania, et al., 2008) and in recognizing sounds associated with actions (such as cutting paper or hand clapping) (Pazzaglia, Pizzamiglio, et al., 2008).

Mu rhythm desynchronization is considered as the EEG signature of the mirror system functions (Fox et al., 2016; Pineda, 2005, 2008), despite some recent reservations (Coll et al., 2015, 2017; Hobson & Bishop, 2017)[3]. Mu rhythm refers to brain oscillations typically between 8-13Hz in adults and 6-9Hz in infants, generated over the central sites corresponding to the location of the sensorimotor cortex (Cuevas et al., 2014; Fox et al., 2016; Marshall & Meltzoff, 2011).

The neurons that fire together synchronously in a resting state desynchronize when executing and/or observing goal-directed actions (Pfurtscheller, 2003; Pfurtscheller & Lopes Da Silva, 1999; Pineda, 2005). This desynchronization is typically represented by negative amplitudes or as reduced power values compared to a neutral baseline. The terms mu desynchronization, mu suppression or mu attenuation have been used in the existing literature interchangeably to describe this phenomenon.

According to Pineda (2005), "*mu rhythms reflect downstream modulation of motor neurons by cells in the premotor cortex, some of which are mirror neurons*" and "*when action observation/comprehension occurs, then mu rhythms reflect primarily mirror neuron modulation*" (p.63). Evidence from source localization has revealed that mu desynchronization during action execution and action observation is indeed elicited from the regions included in the mirror system circuit (Arnstein et al., 2011; Thorpe et al., 2016).

Gastaut & Bert (1954) published one of the earliest papers associating the mu rhythm with action understanding. In this study, the participants exhibited mu rhythm desynchronization when they watched scenes of boxers in action. This was followed by a rebound activity when the boxers were absent from the screen. Similar to the other methods, EEG research also provided early evidence associating mu rhythm

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[3] According to Coll et al. (2015, 2017) and Hobson & Bishop (2017), mu desynchronization may reflect sensory but not motor process or is possibly confounded by other non-mirror processes that are not specific to observing actions and may involve regions other than the sensorimotor cortex (and therefore, not always elicited by the central regions).

desynchronization with the functions of the mirror system. For example, mu desynchronization was elicited for executing and observing hand-object actions (Cochin, 1999; Hari et al., 1998; Muthukumaraswamy et al., 2004; Muthukumaraswamy & Johnson, 2004) and also for imagining aimless movements (Babiloni et al., 2002).

Recent research has not only confirmed these early findings (for example, Llanos et al., 2013) but also provided further evidence that execution and observation of a wide range of actions elicit mu desynchronization, for example, when participant pairs perform actions in synchrony (Naeem et al., 2012); recognition of handgrip-object congruency (Kumar et al., 2013); observing sports-related or dance actions (Denis et al., 2017; Nota et al., 2017); and observing pantomimes (Oberman, McCleery, et al., 2007). In addition, the method has also proven successful to investigate infants' action understanding abilities (Marshall & Meltzoff, 2011; Cuevas et al., 2014). With concurrent findings comparable from different methods, the mirror system was proven to play an integral role in human action/intention understanding.

1.3 Critical Views on the Mirror System

Besides action understanding, the mirror system found its biggest implications in speech perception and language (Rizzolatti & Arbib, 1998; for a recent review see Pulvermüller, 2018) due to the homological similarity between area F5 in the macaque brain and the Broca's area[4] in the humans (Rizzolatti, Fadiga, Gallese et al., 1996). In the following years, the functions of the mirror system were implicated in the domains of emotions, including empathy, disgust and pain (additionally with the insula and cingulate areas) (Bastiaansen et al., 2009; Gallese et al., 2004; Wicker et al., 2003) and mind

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[4] The inferior frontal area comprises of Broadmann areas 44 (pars opercularis) & 45 (pars triangularis), which make up the Broca's area. Cytoarchitechtonically, monkey area F5 corresponds to human area 44 (Hickok, 2014).

reading (Gallese & Goldman, 1998). Autism spectrum disorders (ASD) (Iacoboni & Dapretto, 2006; Oberman et al., 2005) have been linked with mirror system dysfunction.

However, recent reports have questioned the basis on which the aforementioned functions have been attributed to the mirror system. For instance, the functions of the mirror system in being able to process executed and observed actions do not contribute anything more than the theory-theory approach[5] to mind reading (Borg, 2007; Spaulding, 2012) or they may be representing contingent visual and motor associations (Heyes, 2010b, 2010a). Similarly, evidence associating impairments related to ASD with a possible dysfunction of the mirror system has been challenged (Hamilton, 2013b; Southgate, Gergely, et al., 2008; Southgate & Hamilton, 2008) as not all individuals with ASD symptoms display deficits in their perception of the observed instrumental actions.

Hickok (2009, 2013, 2014, 2015; Hickok & Hauser, 2010) has repeatedly refuted the action understanding claims on various grounds. His main contentions include: 1) a lack of conclusive evidence for a human mirror system; 2) other non-mirror areas such as the STS also facilitate action understanding (also see Kosonogov, 2012); 3) a lack of one-to-one correspondence between the monkey MNS and the human mirror system; 4) action execution and action observation need not co-exist. He has also raised profound criticisms regarding the role of the mirror system in language because damage to the Broca's area does not cause speech recognition deficits. Further, previous research has shown that syllable discrimination is not the same as speech recognition and the two abilities are processed through different cortical streams (Hickok & Poeppel, 2000, 2004, 2007). However, these criticisms have been viewed as harsh and illogical (Glenberg, 2015; Kemmerer, 2015). While the debates surrounding the mirror system are quite fascinating in themselves, an effort to explore these details in depth is beyond the scope

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[5] According to the theory-theory approach, the ability to understand what another person does or thinks is based on applying common sense and general knowledge of how things are done when observing the actions of the other person. In contrast, mirroring functions reflect the ability to relate one's own intentional mechanisms to that of the other person (Borg, 2007).

of this thesis. Nevertheless, human beings generally understand and appropriately respond to observed actions in social situations. Therefore, based on the extant research over the past two decades, it may be reasonable to associate the mirror system to a capacity that enables such goal-directed action understanding, even though consensus needs to be achieved regarding the specific functions and the broader implications.

Up until now, I have reviewed evidence on the discovery of the MNS, and some early evidence for an analogous system in humans using different methods and its manifestations. In the following subsections, I provide a brief overview of the theories focusing on the origins of the mirror system and the mechanisms enabling its functions and in doing so I place more emphasis on the evidence from infant literature, where available, as infant research is of highest relevance for this thesis.

1.4 The Mirror System: Origins and Mechanisms

There is little consensus on whether the mirror system constitutes an innate basis (Lepage & Théoret, 2006), involves lower order associations (Heyes, 2010b, 2010a; Paulus, 2014) or demands higher-level top-down processes (Csibra, 2008). For ease of understanding, I classify the theories proposed thus far into two categories. The first category involves the roots of the mirror neurons. These theories seek to understand how the mirror system came into existence in humans. The second category of theories pursues the mechanisms of the mirror system, i.e., the processes that facilitate goal attribution and action understanding.

1.4.1 Origins of the Mirror System

According to the Frame/content theory of evolution of speech production (MacNeilage, 1998), the systematic opening-and-closing of the mouth typical for chewing actions is also used as communicative gestures such as ‘lip smacks’ or ‘teeth chatters’ by other mammals including nonhuman primates. These gestures were initially visual but came to be associated with sounds through evolution, which were further refined in primate communication and finally appeared as speech in humans. Deriving from this theory and their experimental findings delineating the homological similarity between the monkey area F5 and the Broca's area in humans, Rizzolatti et al. (1996) emphasized on the evolutionary basis of mirror neurons, thereby proposing the **adaptation hypothesis** or the **genetic perspective**[6]. In other words, humans adapted the early mechanism facilitating the execution and understanding of actions as an extension towards higher-order functions such as producing and understanding (verbal) gestures and signals.

The **Hebbian learning** account (Keysers & Gazzola, 2014; Keysers & Perrett, 2004) does not deny the evolutionary perspective but suggests that the neurons of the three cortical areas, STS, IPL and IFG are interconnected in an anticipatory manner. In other words, while viewing an object may already activate neurons that code for grasping it, this anticipatory activation is also dynamic, in the sense that prediction errors are computed by incorporating feedback in the loop.

In contrast, the **associative hypothesis**, also referred to as the **associative sequential learning (ASL) hypothesis** (Cook, 2012; Cook et al., 2014; Heyes, 2010b; Heyes, 2001) advocates that humans possess an innate ability for associative learning by means of contiguity (two events occur closer in time) and contingency (the two events are correlated). This predisposition enables lower level associations between co-occurring sensory and motor events, resulting in co-activation of the sensory and motor regions, thereby shaping the mirror neurons. The mirror neurons are, therefore, a product of sensorimotor experience and not of evolution.

The **epigenetic perspective** (Ferrari et al., 2013) proposes that humans acquire mirror neurons through evolution and their functions remain homogenous at birth. However, environmental differences during development or the intensity of sensorimotor

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[6] These terms were originally not used by Rizzolatti et al. (1996) but have been mentioned in other publications (such as Cook et al., 2014; Heyes, 2010b) to refer to the evolutionary perspective of the mirror neurons.

training may render their functions plastic, giving rise to variations in the capacity for action understanding and social cognition.

Given the complexity of human behaviour and development, it may be reasonable to posit that mirror neurons could be products of combined innate and environmental factors. However, despite a lack of consensus on its origins, researchers largely agree that the ability to process others' actions and goals is central to the mirror system and the different theories describing this mechanism and the corresponding evidence are reviewed in the following subsection.

1.4.2 Mechanisms of Action Understanding

The focus in this subsection encompasses the cognitive mechanisms that facilitate action understanding. For example, when does goal detection happen? How important are the kinematics of a particular action? Does action familiarity play a role? What factors influence action understanding in infants? In the following, I provide an overview of the theories proposed thus far with evidence to substantiate the different claims. The first three accounts of action understanding described i.e., direct-matching, predictive coding and ideomotor accounts, subsume that action understanding is automatic and requires a motor representation of the observed action. The last two theories i.e., action reconstruction and social responding, take into account factors beyond motor representation that possibly aid action understanding.

According to the **direct-matching** theory (Rizzolatti et al., 2001), understanding actions as goal-directed is facilitated by one's own prior experience with an action, consequently, limiting this capacity only to those actions, which are already present in our motor repertoire. Evidence for direct-matching comes from different categories of research. Attributing meaning to species-specific actions, the difference between experts and novices, the association between one's own emerging or competent motor skills and action understanding, or the role of active training versus observational learning have been investigated to date.

In an fMRI study, Buccino, Lui, et al. (2004) demonstrated that the mirror system activated when human adults observed mouth actions such as biting performed by a human agent, monkey and a dog. However, when observing species-specific oral communicative movements, the participants exhibited the strongest mirror system activation for their observation of silent speech, specifically in the frontal area, followed by a weaker activation for lip smacking but no activation for barking. However, the posterior areas remained active for all three observed movements. Therefore, the researchers concluded that observing barking could be interpreted on a visual basis but not due to a match in the motor repertoire.

fMRI studies have also demonstrated differential motor activation between experts and novices when observing dancing moves (Calvo-Merino et al., 2006), playing a musical instrument (Haslinger et al., 2005) or in the field of sports (Aglioti et al., 2008; Balser, Lorey, Pilgramm, Naumann, et al., 2014; Balser, Lorey, Pilgramm, Stark, et al., 2014; Wimshurst et al., 2016; see Yang, 2015 for a review). In all these studies, the experts exhibited significantly greater mirror system activation, suggesting that repeated practice with specific movements provides an additional advantage to the experts during their observation of the same, when compared to the novices.

Evidence for an underlying motor competency comes from infant studies as infant groups naturally differ in their (developing) motor ability. For example, 14-month-old infants, who were proficient crawlers but had relatively little experience with walking, predicted observed crawling actions accurately as opposed to walking (Stapel et al., 2016). Following a similar pattern, 14- and 16-month-old infants displayed greater mu (and beta rhythm) desynchronization when they observed videos of other crawling infants when compared to walking, due to their greater experience with crawling (van Elk et al., 2008). Further, reach competence in 9-month-old infants (Cannon et al., 2016), or grip strength at 12 months (Upshaw et al., 2016) were associated with the magnitude of mu desynchronization. Specifically, infants who exhibited greater reach competency also demonstrated greater mu desynchronization for the observation of reaching and grasping actions (Cannon et al., 2016). Similarly, infants with greater grip strength demonstrated significant mu desynchronization during the observation of lifting actions, when compared to infants with a lower grip strength (Upshaw et al., 2016). In addition, significant mu desynchronization exhibited by 12-month-old infants during action observation correlated with their reach-grasp competence during action execution but the same relationship was not evident in 9-month-old infants (Yoo et al., 2016). All this evidence taken together suggested that the degree of experience with a particular action correlated with the subsequent understanding of the same action.

There is evidence suggesting that active experience with an action is superior to observational learning and facilitates greater action understanding when compared to the latter. For example, a group of adults displayed significant mu desynchronization when they re-observed an unfamiliar action (drawing letters from the Cham Alphabet of South-east Asia) after having imitated the same (Marshall et al., 2009). Further, the group of adults, who received prior visual and motor training in producing these letters exhibited greater mu desynchronization than the group of adults, who received visual training alone (Quandt et al., 2011). Another study provided evidence that prior motor experience with the weight of the objects as opposed to just the information about the weights resulted in greater mu desynchronization when adults observed the same objects being lifted (Quandt & Marshall, 2014). These findings could also be extended to using tools in a goal-directed manner. For example, active experience with using a mechanical claw as a tool to pick up objects as opposed to prior observational learning resulted in greater mu desynchronization in a group of adults when the same action was observed during the test session (Cannon et al., 2014).

Analogous to the adult findings, evidence for active training has also been reported in infant studies using behavioural methods, eye tracking or EEG. In a behavioural study, 3-month-old infants wearing sticky mittens while exploring objects ‘accidentally’ grasped them due to the attached Velcro, thus acquiring active experience for this action. Subsequently, these infants paid more attention to the goal object of the observed grasping action compared to the group of infants with no prior active experience (Sommerville et al., 2005). These findings were recently confirmed in an EEG study, in which a group of 4-month-old infants, after receiving active training with sticky mittens, subsequently exhibited larger P400 ERP (event-related potential) component[7] compared to those who passively observed the action during the training period (Bakker et al., 2016). Further, training with non-sticky mittens resulted in reduced exploratory behaviours when compared to training with sticky mittens (Needham et al., 2017; Wiesen et al., 2016; but see Williams et al., 2015 for opposing results). Following active training but not observational learning, 8-month-old infants were able to assess the purpose of observed means-to-end action sequences to achieve distal goals (such as pulling a cloth closer to obtain an object placed on the far end of the cloth) (Gerson, Mahajan, et al., 2015). Similarly after active training, 6-month-old infants preferred to watch videos depiciting audio-visual synchrony between the tapping action on the drum using drumsticks and its associated sounds as opposed to when the videos depicted audio-visual asynchrony (Gerson, Schiavio, et al., 2015). After receiving first-hand experience in a collaborative activity with an experimenter, 10-month-old infants were better able to perceive common goals when observing the same collaborative activity from a third-person perspective (Henderson & Woodward, 2011).

The effect of active experience on action understanding has also been demonstrated in other modalities as well. For instance, 8- and 9-month-old infants displayed significant mu desynchronization when they heard the sound of a rattle they received prior active training with when compared to sounds that were not related to the object that the infants previously trained with (Paulus et al., 2012, 2013). 10-month-old

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[7] The P400 component is considered as the infant ERP signature for (social) gesture understanding (Gredebäck et al., 2015).

infants were familiarized with the operation of two novel objects at home, where for one object they received active training but they passively watched the second action being operated by the caregiver. Subsequent EEG measures revealed significant mu desynchronization when infants heard the sounds related to the actively trained novel object when compared to the passively observed operation of the second novel object (Gerson, Bekkering, et al., 2015).

Successful action understanding, according to the direct-matching theory, relies on an automatic, simulative process, activating the same motor program required for executing the same action, without the need for complex inferences. If this was the case, then human beings let alone infants should by no means be able to comprehend actions that cannot belong to their motor repertoire, such as dogs wagging their tail or birds flapping their wings and yet, these actions are not interpreted as meaningless and do not always require complex inferences. When observing an eagle swoop down on its prey, the goal as well as the action is considered goal-directed even though the actions of swooping down or hunting a prey are not part of the human motor or action vocabulary. Therefore, during infant development, it seems plausible to expect that infants perceive actions that they do not yet execute. Nevertheless, according to Rizzolatti & Sinigaglia (2010), the comprehension of observed inexecutable actions or of actions that are not part of the motor repertoire, are based on visual experience but not as a possible motor activity from within an individual (see Hickok, 2014, for a critical view on this claim).

What processes, both at the functional and cortical level, entail automatic action understanding? The **predictive coding** account (Kilner et al., 2007) points out that understanding an action available in the motor repertoire involves different levels of hierarchy – intention, goal, kinematics, muscle – with only the kinematics being represented visually. The mirror system, with the interconnections between the IFG and IPL, and the IPL and STS functions in a top-down manner. In other words, the ability to understand an action as goal-directed is predictive. Inferences are first made regarding the intention or the goal of an action before predicting the motor commands or the kinematics required to fulfill them. During this process, one's predictions are constantly compared with the ongoing action to reduce prediction error and update action representation. Further, action understanding also depends on two separate pathways, one coding for intentions and the other coding for immediate goals and may encompass regions outside the mirror system (Kilner, 2011; Kilner & Frith, 2008).

Conversely, the **ideomotor** account (Paulus, 2012) proposes a 'lean' approach to action understanding, without ascribing higher order intentions to others. Repeated experience with bidirectional action-effect associations generate corresponding motor programs. For example, when I extend my arm to reach towards an object, the effect of this action would be to eventually grasp the object. Such associations result in predictions regarding the goal or effects of the observed actions, modulated by attentional mechanisms. Evidence for such predictions comes from eye tracking studies, where anticipatory eye gazes towards the effect of an action (for example, goal object or location) suggest goal understanding (Gredebäck & Falck-Ytter, 2015).

Nevertheless, is action understanding limited to an available motor representation? How does one construe goals of unfamiliar actions? Alternatively, what happens to actions that may not be associated with an effect? Sometimes, we observe actions that were not intended, for example in the case of a 'motor slip' and yet our motor representation does not update in the wake of new visual information and alter its goal or render the action as meaningless (Buccino et al., 2007). It is likely that such flexibility of action perception cannot occur simply due to an available motor repertoire, especially with reference to infant action understanding.

The **action reconstruction** framework (Csibra, 2008; see also Southgate, 2013) is similar to predictive coding (Kilner et al., 2007) on many grounds. Firstly, both theories lay emphasis on the top-down functions of mirroring where goal inferences determine action perception. Secondly, both theories suggest that such inferences incorporate areas beyond the mirror system. Finally, both theories suggest that top-down higher-order functions of mirroring allow for verification and revision of goals along the hierarchy, when necessary. However, the two theories differ in terms of the actual mirroring processes. According to the action reconstruction account, action mirroring is '*emulative'*, does not depend on an available motor repertoire, and the outcome is more significant than the means to achieve it (Csibra, 2008). For example, the goal of drinking water may be achieved through a sequence of motor acts, the specifics of which may differ among different people. While one individual may pick up the glass with one's hand and bring it towards the mouth, the same person may observe another individual insert a straw in to the glass and move his or her mouth towards it. Therefore, whether one prefers to sip water from a glass or suck water from a straw, the outcome of drinking water remains the same. As a result, action understanding does not require a direct match between the observed and executed actions because the process of emulation still enables this capacity. Such action mirroring incorporating emulation and action anticipation also plays a vital role for action coordination, which human beings frequently engage in.

Robust evidence for the action reconstruction framework comes from infant studies. For example, infants as young as 6 months were able to attribute meaning when observing a hand touching an object by poking at it with the index finger, and 12- and 9-month-old infants encoded goals of self-propelled objects despite having no prior experience or motor programs for these actions (Biro & Leslie, 2007). 13-month-old infants displayed predictive gazes towards the goal of a self-propelled ball, even when the goal location was occluded (Biro, 2013). In addition, these gaze shifts were faster for efficient actions (when the ball jumped over an obstacle) than non-efficient actions (when the ball jumped in the absence of an obstacle). Further 6- and 12-month-old infants were able to anticipate the goal of feeding actions from a third-party perspective and demonstrated greater pupil dilation for irrational feeding actions, such as when the food approached the hand of the receiver instead of the mouth (Gredebäck & Melinder, 2010). At the age of 6 months, infants displayed accurate goal-directed predictive looks suggesting that they already encoded object-action associations (such as cup-to-mouth or phone-to-ear) (Hunnius & Bekkering, 2010). In another study, pre-walking 8-month-old infants displayed significantly longer looking time when their observation of infant stepping actions, briefly interrupted by an occluder, were followed by incoherent continuation of the same action (from the last watched frame) compared to a coherent continuation of the stepping actions (de Klerk et al., 2016). Further, 9-month-old infants displayed significant mu desynchronization irrespective of whether they watched a hand or a claw reach for the object or the object move in a self-propelled action (Southgate & Begus, 2013). In a study using functional near-infrared spectroscopy (fNIRS), 4-month-old infants displayed greater premotor cortex activation when observing robot-like rigid movements compared to human-like motion (Grossmann et al., 2013). All these findings suggest that infants were able to construe goals of actions that they possibly had no experience with and had no motor programs to recruit or compare. Therefore, as a theory of action understanding, the action reconstruction account offers some flexibility and takes into account factors beyond the motor repertoire, when compared to the direct-matching account.

The **social responding** theory (Hamilton, 2016) suggests that the function of the mirror system is not to understand or predict ongoing actions, instead it activates in preparation to respond to ongoing actions, implying that the mirror system works in a prospective manner. Evidence for this theory is derived from the findings of automatic imitation (Heyes, 2011). Automatic imitation refers to a behavioural tendency, where movement execution for congruent responses are faster when compared to incongruent stimulus-response associations. For example, extending one’s right hand in response to observing a social partner’s similar action while greeting, would be a faster response than when asked to inhibit this (socially) correct response and respond by folding hands instead. Congruent stimulus-response associations are crucial in real situations where ongoing action observations may call for appropriate (social) responses. For example, when adults were asked to imitate grasp or handshake actions, where the agent used his right hand, they were faster to grasp with their left hand (mirror image) but were faster to extend their right hand to fulfill a handshake response (Liepelt et al., 2010). While watching a video of an agent preparing coffee, adults displayed large MEPs, when they observed the agent extend her hand to reach out for a cup away from her but virtually closer to the participant. Although the action was incomplete, it still induced MEPs possibly because the participants prepared themselves to hand over the out-of-reach cup to the agent, as they would have done in a real, interactive situation (Sartori et al., 2013). Further, infants and young children seem to share and anticipate collaborative goals and actions (Henderson & Woodward, 2011; Warneken et al., 2014) and their success is contingent upon their perception of compatible action-response associations. The ability to anticipate and reciprocate appropriately, as postulated by the social responding theory, may also implicate the role of the mirror system in the development of helping behaviour and prosociality.

Comparing the various theories in terms of their relevance for infant action understanding and the limited motor development of infants, the direct-matching account seems to be restrictive, even though training studies provide some support. However, training studies do not take into account the possible effects of temporal association within the experimental setting between the ‘trained’ executed action and its later observation. In the absence of training, would infants have recognized the goals for the same unknown actions in the presence of other cues? Clearly, infants do not possess a wide motor repertoire but I have reviewed some evidence to show that they understand and anticipate goals of unfamiliar and inexecutable actions. The evidence indicates that infants use other sources of information or cues beyond the action itself to infer the goals.

Taking a closer look at the different experimental paradigms of action understanding studies, with the exception of some studies on intransitive actions, hand-object interactions seem to play a crucial role. For instance, when we grasp a mug, we also displace its location – to drink or place it in a cupboard. The grasping action here is not only a hand-object interaction but it also brings about a change in the environment. However, in real situations, our use of actions is neither always object-oriented (for example, gestures used as a co-expressive modality) nor brings about changes in the environment directly or immediately. In addition, one’s observation of actions is not always governed by a need to respond. We also use many meaningful actions simply to convey information, for example, when using sign language or gestures. Therefore, the critical question is whether action understanding is limited to some actions or action sequences but not the others.

In the following section, I provide an overview of the two main action categories, instrumental and referential actions, and I briefly elaborate on infants’ teleological understanding (Csibra, 2003). Further, I challenge the view that instrumental but not referential actions may be perceived as goal-oriented.

1.5 What Type of Actions are Goal-directed?

Infants in the first year of life possess a teleological representation of actions (Csibra, 2003; Csibra & Gergely, 2013). In other words, in any given environment, an observed **action** is perceived as goal-directed only if it affords an efficient means to achieve the end state or the **goal** after considering the **situational constraints**. Therefore, the relationship among action, goal and the situational constraints (i.e., context) plays an important role in goal attribution and action understanding. For example, in order to reach the end (goal) position, an agent may move in a straight line from the starting position and then jump over a barrier on the way before continuing along the trajectory. The jumping action in this case is perceived as efficient by 12-month-old infants due to the constraints imposed by the environment, which otherwise may be inefficient (Csibra et al., 2003; Gergely et al., 1995). Numerous studies have confirmed these early findings that infants consider the principle of efficiency while evaluating actions. For example, 6- to 8-month-old infants interpreted their observation of biomechanically impossible events such as extreme elasticity in stretching and twisting an arm along obstacles to obtain an object as efficient (Southgate, Johnson, et al., 2008).

In a modified paradigm, Liu & Spelke (2017) demonstrated that 6-month-old infants not only expect an agent to be efficient while jumping over barriers, such as executing shorter and quicker jumps for lower barriers, they also assume an overhypothesis[8] that the agent will continue to take the shorter path because of such occurrences in the previous trials. Further, Scott & Baillargeon (2013) demonstrated that 16-month-old infants also expect an agent to grasp an object that is more easily accessible to her than expend additional energy to grasp an object that requires more effort to obtain.

Such teleological representation of actions is suggested to be appropriate for instrumental actions but not referential actions (Csibra, 2003). Instrumental actions are those that help achieve the end state and bring about an immediate effect in the environment, such as grasping. Grasping is an example of a transitive action, which enables direct manipulation or attainment of goals. The fulfillment of a grasping action always requires an object to complete the goal but failed or incomplete grasps do not elicit significant mu desynchronization (Nyström, 2008; Nyström et al., 2011; Pomiechowska & Csibra, 2017). However, an exception was reported in a recent study, where a group of adults, 8- and 14-month-old infants did not demonstrate a significant difference in mu desynchronization when observing completed and failed pincer grasps (Meyer et al., 2016).

Conversely, the purpose of referential actions such as the back-of-hand (palm-up configuration) or pointing is to inform or communicate and are not considered goal-directed (Pomiechowska & Csibra, 2017) because these actions do not lead to an immediate change in the environment. However, in real-life situations, this is not always true. What would happen if the most efficient means to achieve a goal were to communicate about it instead of acting on it? In this case, one is not simply providing information; instead, communication acts as the means to achieve the goal indirectly.

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[8] Overhypothesis refers to a mechanism of inferential ability by which multiple levels of generalizations are formed based on inferences drawn from similar events. These inferences take into account features beyond direct experience. The concept was originally proposed by Nelson Goodman in 1955 (Dewar & Xu, 2010).

This could pertain to situations where, for example, the goal is unreachable due to shortness of height or mobility issues or simply when acting on it may take longer and is, as a result, inefficient. When viewed critically, the three features (action, goal, context) that render an instrumental action as efficient and goal-directed may also be applicable to the interpretation of communicative actions.

As social beings, humans always communicate with one another, either with the help of language, gestures or both and under some circumstances, indirectly. Simply observing a colleague shiver on a cold, windy day may result in the observer infer the colleague’s current state and possibly lead to the act of shutting the window, although the goal action was not explicitly requested. Humans also resort to the use of gestures or signs, if the situation demands it, for example, in instances of deafness or if someone wishes to pass on a message out of the range of audible limits. Therefore, actions, which represent communicative intentions that enable the attainment of end-states indirectly, may also be construed as goal-oriented. Specifically, if perception of instrumental actions takes into account the physical and spatial factors, understanding referential actions may then depend on appropriate social and communicative factors. In addition, going by the action reconstruction account, which limits its application to instrumental actions (Pomiechowska & Csibra, 2017), emulative processes may also be relevant to perceiving communicative actions as well, thereby construing communicative goals for such actions.

fMRI studies with adult samples confirm that communicative actions are indeed goal-oriented and that the mirror system plays a role in our understanding of such actions. For example, the mirror system areas were activated when observing and imitating communicative hand actions such as ‘wave a greeting’ or ‘look up’ (Mainieri et al., 2013), ‘thumbs up/down’ and pantomimes such as ‘turning a key’ and ‘tossing a coin’ (Montgomery et al., 2007), but not for facial expressions such as ‘happy’ or ‘anger’ (Montgomery & Haxby, 2008). Observing pictures of cooperative actions also elicited activation in the mirror system areas when compared to observing affective pictures

(Canessa et al., 2012) and also in differentiating between communicative and private intentions both in the second-person and third-person perspectives (Ciaramidaro et al., 2014).

Recent EEG studies with adults also support influences of social factors on action understanding, specifically sensorimotor mu rhythm desynchronization. For instance, Oberman, Pineda, et al. (2007) reported that participants displayed significant mu desynchronization when they observed an interactive tossing of the ball (such that the agent on the screen tossed the ball towards the participant virtually) as opposed to passively watching agents tossing the ball at each other or tossing ball in the air without any interaction. A recent study also reported significant mu desynchronization when participants observed culturally appropriate social reciprocal actions such as folding hands or touching a person’s feet to seek blessing both in the third-person and second-person situations (Tikka et al., 2016). Significant mu desynchronization was also reported when participants observed communicative gestures such as ‘thumbs up’ and ‘social grasping’, where an agent reached for and grasped objects placed on the palm of another (Streltsova et al., 2010) and when actively engaged in a Rock-Scissor-Paper game (Perry et al., 2011). Further, mu desynchronization was also modulated by the observer’s emotional connection with the agent or by the consequence of an action. For example, previously elicited mu desynchronization while observing grasping actions, both goal-directed (with object) and purely kinematic (without object) in the pre-manipulation observation phase, ceased to exist in the post-manipulation execution task (after the emotional connect with the agent was manipulated) when the agent was judged to be unfair (Aragón et al., 2014). When participants watched an agent place coins in the reward, punish or neutral bowl, significant mu desynchronization was demonstrated for the rewarding actions when compared to the punishing or neutral actions (Brown et al., 2013).

While there is some evidence that social factors modulate mu desynchronization in infants, such studies are only beginning to surface. Stroganova et al. (1998) provided evidence that 7- to 8-month-old infants exhibited significant decrease in mu activity when participating in the peek-a-boo game, specifically during phases when they anticipated the reappearance of the hiding experimenter and after she reappeared and socially engaged with the infants. Further, compared to observing non-interactive movements such as hopping and skipping, 14-month-old infants exhibited greater mu desynchronization when observing interactive actions such as when the experimenter initiated turn-taking sequences such as imitating infants' spontaneous hand actions (Reid et al., 2011). Recently St. John et al. (2016) conducted a live study by combining EEG and eye tracking methods, where 12-month-old infants observed four conditions comprising of nonsocial, joint attention, language-only and social engagement events. The conditions differed in terms of the level of engagement the agent had with the infants or objects. In the joint attention condition, the agent (seated opposite to the infant) directed the infant's attention towards objects by pointing to them and talking to the infant. In the social engagement condition, the agent directed the infant's attention to herself as opposed to the objects. In the language-only condition, infants heard the agent's voice from behind the curtain and in the nonsocial condition, they simply watched two objects without the agent being present. The results showed significant frontal mu desynchronization for joint attention compared to the language-only and nonsocial conditions and significant temporal mu desynchronization for joint attention and social engagement compared to the nonsocial condition. In addition, 30-month-old infants exhibited significant mu desynchronization when observing and executing facial expressions (Rayson et al., 2016). However, more research directly comparing the influence of social factors on infants' action understanding seems to be lacking. What we know is that infants use communicative gestures even before speech develops (Goldin-Meadow, 1999) and therefore, one could expect infants to comprehend the meaning of such gestures even before they begin to produce them.

All this evidence put together seems to suggest that action understanding need not be limited to instrumental actions alone. In real situations, humans use actions for numerous other purposes than for only instrumental ones. If communicative gestures play an integral role for the development of speech and language (Lüke et al., 2020), then they need to be construed as meaningful and goal-oriented. Therefore, context plays a fundamental role in our understanding of actions and is equally applicable to instrumental and referential actions because real life scenarios comprise of both these actions abundantly.

1.6 Rationality of Goal Attribution

In the evidence described to this point, starting with the discovery of the MNS to the recent action understanding studies, the presence of visible goals has been the most prominent feature. Specifically, action understanding of object-directed actions were ascribed to fulfilled goals but not to incomplete ones. Although Fogassi et al. (2005) and Iacoboni et al. (2005) provided evidence that both monkeys and human adults, respectively, encode embedded goals within an appropriate context, more research in this area is lacking. Further, both these studies incorporated fulfilled goals, where the outcome was shown. Therefore, this raises an important question of whether action understanding is also involved in encoding embedded goals and pertains to action sequences, where the goal is unfulfilled or is implied and indirect but the outcome is not shown. This question is applicable to both instrumental and communicative actions alike.

Behavioural studies have shown that infants perceive goals of failed and incomplete instrumental actions (For example, Brandone et al., 2014; Hamlin et al., 2008). To elaborate, 10-month-old infants produced anticipatory looks to the goal object even when the agent's attempts to obtain the object over a barrier were unsuccessful (Brandone et al., 2014). Similarly, 7-month-old infants chose the toy (between two toys present on the table) that the experimenter attempted to reach for but was unable to obtain (Hamlin et al., 2008). Considering that infants in these behavioural studies perceived the observed unfulfilled actions as goal-directed, it may be plausible that similar inferences may also elicit significant mu desynchronization. If the context provides sufficient cues allowing for goal attribution, failure in attaining the end state should not alter the subsequent mu activity. In other words, even if the goal object is not obtained or not touched, action understanding should still manifest due to the contextual factors that suggest the presence of a goal.

Observing communicative actions such as pointing generates a referential expectation (Gredebäck et al., 2010) and do not typically involve touching objects with the extended index finger. Similarly, while the back-of-hand action may be indicative of a request, this action does not result in the direct attainment of the object. Such communicative actions possibly lead to reciprocal action sequences or responses to attain goals indirectly, as explained in the previous section. Therefore, in this case, the purpose of the initial communicative action is not directly evident when compared to instrumental actions, but is embedded and contingent upon the available contextual cues and the observer's inferential processes. Bearing in mind my reasoning from the previous section, attributing embedded communicative goals should also exhibit mu desynchronization similar to when attributing direct instrumental goals. However, research in this area, especially with infants, seems to be lacking.

1.7 Mu Rhythm and Action Understanding

Infant EEG research for over the past decade has investigated several factors that modulate mu rhythm activity, ranging from observing simple grasping actions to complex social dynamics. There is also some evidence from infant data that action execution and action observation paradigms exhibit overlapping cortical activation. In this section, I provide an outline of the development of the infant mu rhythm and the prevailing evidence for action understanding, as determined by the mu rhythm activity. Finally, I briefly provide an overview of some questions that remain to be addressed.

1.7.1 Development of the Mu Rhythm

In their investigation of mu desynchronization over the central region elicited from 7- to 8-month-old infants participating in a peek-a-boo game, Stroganova et al. (1998) analyzed mu activity in the 6-9Hz range by separating the activity into single 6-7, 7-8, and 8-9Hz frequency bands. The results revealed the strongest decrease in mu activity in the 6-7 and 7-8Hz frequencies. The researchers noted that while mu activity in the 8-9Hz band decreased significantly when compared to the baseline, this decrease was lower compared to the other bands, suggesting that this band could be nearing the higher limit of the mu frequency band for infants of this age group. In a subsequent study, Stroganova et al. (1999) recorded EEG from 8- and 11-month-old infants during periods of sustained attention towards an agent blowing soap bubbles and while being placed in a dark room. The findings revealed a decrease in bilateral mu activity in the precentral region during sustained attention and an increase in bilateral occipital alpha activity during darkness. The peak of the individual mu activity varied from 6.2 to 8.4Hz at 8 months and increased to 6.6 to 8.8Hz at 11 months. A similar increase in the peak of the occipital alpha activity was also reported. Importantly, the study concluded that mu and alpha activity differ in their topographical distribution and represent different functions.

In a systematic longitudinal study, Marshall et al. (2002) investigated the development of the mu spectrum from early infancy to early childhood (at 5 months, 10 months, 14 months, 24 months, and 4 years). EEG was recorded during the observation of the bingo wheel with varied number of balls, being spun across several trials. The researchers found that with increasing age, the dominant peak frequency increased across the cortical sites (frontal, central, parietal & occipital). Specifically, a low frequency peak of 4-7Hz at 5 months increased to 7-8Hz at 10 months and 14 months, 8Hz at 24 months and 8-9Hz at 4 years. Moreover, the data also revealed an increase in the activity between 6-9Hz with increasing age. However, this increase was restricted to the central and parietal regions, which did not differ significantly from each other but the activity in both regions was found to be significantly greater than the relative power in the frontal and occipital regions.

In a recent cross-sectional study using the magnetoencephalography (MEG) method, groups of infants, children, and adults were directed to squeeze a pipette with their right hand, while recording data from electrodes in the central region of the left hemisphere (Berchicci et al., 2011). The investigators reported that the peak mu frequency increased significantly during the first year of life that is, from 2.75Hz at 3 months, to 6.25Hz at 7 months, and 8.6Hz at around 10 months but was found be consistently around 8Hz after the second year of life and during early childhood. The reason for this increase in the peak frequency over the age has been attributed to the subsequent maturation of the sensorimotor cortex and the enhancement of the functional cortical connections in this region (Berchicci et al., 2015). Similarly, Thorpe et al. (2016) revealed an increase in peak mu frequency spectrum, with 7-8Hz at 12 months, 8.5-10Hz at 4 years when participants executed goal-directed grasping actions. Moreover, the authors were able to confirm from source localization analyses that this mu activity was generated mostly from the central and parietal regions encompassing the mirror system regions of both hemispheres.

In keeping with the above evidence, mu rhythm frequency spectrum has been established to oscillate between 6-9Hz during infancy, which is slower than the normal adult range of 8-13Hz and usually corresponds to the activation of the centrally located EEG channels C3 and C4 (Fox et al., 2016; Hobson & Bishop, 2017; Marshall & Meltzoff, 2011) as shown in Figure 3. Due to its spectral overlap with the occipital alpha range (Marshall & Meltzoff, 2011; Cuevas et al., 2014), EEG studies typically also analyze data from the occipital region to examine possible confounding processes. Research with infants using EEG has incorporated various paradigms over the past decade and has revealed diverse findings as elaborated in the following subsection.

1.7.2 Obtaining the Goal 'Hands Down'

In this subsection, I focus on the various paradigms incorporating hand actions, hand-object interactions[9] or the involvement of hands in infant EEG studies of action understanding and the consequent findings for both action execution and action observation phases. To avoid redundancy, details regarding methodological differences and inconsistencies are summarized in section 2.5.

The most widely investigated hand action in infant EEG studies of action understanding comprises of the reach and grasp action. Recent investigations have focused on whether executing and observing grasping actions elicited sensorimotor mu desynchronization and examined whether a topographical overlap in mu activity was evident. For example, 9-month-old infants exhibited significant mu desynchronization over the left sensorimotor cortex (central channels) while observing fulfilled grasping (Southgate et al., 2009) or when the goal was implied behind an occluder (Southgate et al., 2010). During the execution of the goal-directed grasping action, infants exhibited either right-lateralized (Southgate et al., 2010) or bilateral sensorimotor mu desynchronization (Southgate et al., 2009). Similarly, de Klerk et al. (2015) provided evidence for a bilateral central activation for execution but a left-lateralized activation for observation of grasping actions in their investigation with a sample 12-month-old infants. Younger infants at 7 months exhibited greater mu desynchronization when reproducing, or in other words, grasping the same goal object as that of the experimenter (Filippi et al., 2016). In this study, action execution elicited bilateral central and occipital activation and action observation elicited bilateral central activation. Reach and grasp competence also modulated the magnitude of mu desynchronization for 9- and 12-month-old infants

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[9] While foot movements may facilitate goal attainment similar to hand movements, observing and executing foot movements differ in their somatotopical activation (Pfurtscheller et al., 1997). Specifically, the medial region corresponding to the location Cz and the lateral regions, C3 and C4, are activated for foot and hand actions, respectively. The same pattern has been reported in infant EEG studies, where hand and foot actions are shown to attain the same goal of grasping or button press (de Klerk et al., 2015; Marshall et al., 2013a; Saby et al., 2013).

(Cannon et al., 2016; Upshaw et al., 2016; Yoo et al., 2016). While Upshaw et al. (2016) reported right hemisphere central activation for action execution, Cannon et al. (2016) and Yoo et al. (2016) reported activation across the bilateral frontal, central, parietal and occipital cortical sites. For action observation, Cannon et al. (2016) reported greater desynchronization in the right frontal and bilateral occipital regions; Upshaw et al (2016) reported greater desynchronization in the right central region and Yoo et al. (2016) reported greater desynchronization in the occipital region compared to the frontal and centro-parietal regions. Observing an agent lifting objects that 14-month-old infants' previously experienced as heavier also elicited greater mu desynchronization at the central region of the right hemisphere, which differed from a more distributed bilateral central activation and right-lateralized frontal, parietal and occipital activation for action execution (Marshall et al., 2013b).

Studies incorporating a button press goal-directed action also similarly reported significant mu desynchronization not only over the central region for 14-month-old infants for action execution but also over a more distributed network including frontal, central and parietal areas for action observation (Marshall et al., 2011). In another study, observing button press actions that infants previously executed also facilitated significant mu desynchronization when compared to observing actions that the infants did not execute in the previous trial. However, action execution and action observation phases did not reveal a topographical overlap in this study. While action observation elicited bilateral central activation, action execution elicited mu desynchronization across the frontal, central and parietal sites in the right hemisphere (Saby et al., 2012). Subsequent studies using the button press paradigm provided evidence of a bilateral central activation for both action execution and action observation (Marshall et al., 2013a; Saby et al., 2013)[10].

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[10] It should be noted that the studies by Marshall et al. (2013a) and Saby et al. (2013) focused only on the activity elicited in the central region, averaged across the two hemispheres, and did not include other regions for the analysis.

Further, Montirosso et al. (2019) recorded data from groups of 14-month-old full-term and pre-term infants when they executed and observed button press actions. The findings demonstrated a global pattern of desynchronization across all regions (frontal, central, parietal and occipital) for action execution in both the groups. Interestingly, the groups exhibited differential activity during action observation. While the full-term infants displayed significant desynchronization in the right frontal, bilateral parietal and occipital regions for action observation, the pre-term infants exhibited desynchronization only in the right parietal region. Based on the findings from the action observation data, the authors suggested that pre-term births could result in an inadequate development of networks among cortical areas that facilitate action perception and imitation.

Recent research has provided evidence that observing actions beyond the conventional grasping and button press actions are also perceived as goal-directed. For example, 9-month-old infants exhibited significant mu desynchronization in the left central region while observing grasping actions carried out by a mechanical claw by itself or while observing self-propelled actions (Southgate & Begus, 2013). Unusual actions such as observing an agent place a cup to the ear elicited significant bilateral fronto-central mu desynchronization in a sample of 12-month-old infants (Stapel et al., 2010). Observing an agent turning on a lamp or a sound box with his head (despite when his hands were free) exhibited significant bilateral frontal mu desynchronization in a group of 12- to 14-month-old infants, when compared to observing the conventional hand action to achieve the same goal. Interestingly, the infants did not exhibit significant mu desynchronization when they observed the agent turning on a lamp or a sound box with his head, especially when his hands were restrained to achieve the same goal (Langeloh et al., 2018).

Infants between 18 and 36 months revealed significant mu desynchronization when observing and imitating complex hand-object action sequences from the beginning to the end position (Ruysschaert et al., 2013; Warreyn et al., 2013). The objects in these studies were playfully moved from their starting position (i.e., from one side of the box) to the goal position (i.e., the other side of the box) and included some bouncing movements along the trajectory. Warreyn et al. (2013) found significant bilateral central and parietal mu desynchronization for both action execution and action observation, however, additionally, significant occipital alpha desynchronization for action observation was also evident. Ruysschaert et al. (2013) provided evidence that action observation conditions presented under live settings elicited significantly greater activation when compared to presenting videos. Specifically, infants in the live group exhibited significant mu desynchronization in the left central and bilateral frontal and parietal regions for action execution. Action observation results revealed a similar pattern with bilateral activation across these three regions.

In a false belief paradigm, 6-month-old infants showed significant left central mu desynchronization when they anticipated an agent to reach for an object due to her false belief of its presence inside a box but not otherwise (Southgate & Vernetti, 2014). Moreover, 18-month-old infants displayed bilateral central activation when they were able to anticipate actions based on statistical learning of action pairs than when such actions were presented randomly (Monroy et al., 2019).

Some recent investigations have revealed that manipulating social factors also modulate mu desynchronization. For example, 14-month-old infants exhibited greater mu desynchronization in the right central region for observing interactive actions such as when the experimenter initiated turn-taking sequences such as imitating infants' spontaneous hand actions when compared to observing non-interactive movements such as hopping and skipping (Reid et al., 2011). Moreover, as elaborated in section 1.5 of this thesis, 12-month-old infants showed greater mu desynchronization across the bilateral frontal and temporal sites for observing actions such as pointing that resulted in joint attention but not when observing nonsocial events (St. John et al., 2016). As social factors also include aspects beyond hand actions, it may be notable to mention that observing and executing facial expressions such as 'happy' and 'sad' elicited right central mu desynchronization in 30-month-old infants (Rayson et al., 2016).

To summarize, not all infant EEG studies provided evidence of activity in the occipital region or cortical areas beyond the central region (For example, De Klerk et al., 2015; Gerson, Bekkering, et al., 2015; Paulus et al., 2013; Southgate et al., 2009, 2010; Southgate & Vernetti, 2014; van Elk et al., 2008). However, the tendency has shifted recently to also include other regions. This shift is in line with the recent recommendations to include the overall cortical pattern of mu and/or alpha desynchronization (Cuevas et al., 2014; Marshall & Meltzoff, 2011). Further, recent functional connectivity analyses with infant EEG data revealed that central mu and occipital alpha desynchronization elicited during execution and observation of goal-directed actions represent distinct but coherent functions that allocate both motor and attentional processes (Debnath et al., 2019).

The above overview of the existing evidence indicates a range of behaviours and actions that elicit action understanding in infants, specifically mu desynchronization. While some studies reveal a close overlap of topographical activity between action execution and action observation, this is not always the case. In addition, some studies report activity beyond the central areas or global mu desynchronization for action execution but localized activity for action observation, however, the pattern is reversed in other studies. Furthermore, there are variations in the regions that elicited significant mu desynchronization for both these phases, as elaborated above. Considering these variations, it is not possible to deduce whether one or more regions specifically encode goals and the means to fulfill different goals or whether specific types of actions or action sequences elicit unilateral or bilateral activation. Nevertheless, the existing literature provides robust evidence that observing goal-directed actions elicits mu desynchronization in infant samples, despite the disparities in topography and lateralization.

Overall, infant research thus far has largely investigated fulfilled actions in the action observation phase, i.e., actions that result in obtaining the intended goal. EEG research on implied goal fulfillment, where the hand does not touch the object or obtain the object is scarce. Similarly, most actions comprised of typical instrumental actions, where the goals were not distant or embedded. Further, the actions represented immediate changes in the action-goal contingency or hand-object interactions. In other words, the means to fulfill a goal and the outcome of the means were both revealed to the infants. Therefore, the question of whether infants perceive distant and embedded goals remains to be investigated. In the same way, the actions that infants observed were also the same actions that they executed. Thus, it is not clear whether a topographical overlap between action execution and action observation could also be expected if an exact match between the executed and observed actions is not achieved.

Finally, investigations on social factors modulating mu activation during infancy are still at the early stages and require further investigation considering the importance of social factors during infant development. However, there seems to be an inclination, although preliminary, towards a right hemisphere lateralization (Rayson et al., 2016; Reid et al., 2011) when processing social factors and social-related information, which may be of interest for future studies investigating neurophysiological correlates of infants' social action understanding.

2 The Method of EEG

The discovery of EEG has been credited to the German neuropsychiatrist, Hans Berger, who began using the method to test human patients in 1924. Despite technological advances in the past century with other noninvasive measures, EEG continues to remain important for diagnostic and research purposes, owing to its low cost, comparatively easy application procedures and high temporal resolution (Niedermeyer & Schomer, 2011). In this chapter, I focus on the principles of EEG, the analysis parameters, the challenges of conducting EEG with infant population and the methodological disparities in infant mu studies.

2.1 Basic Principles

The brain is a treasure house of billions of neurons, controlling and conducting everyday activities from simple limb movements to higher order cognitive capacities. Typically, the electrical activity measured by EEG is generated by pyramidal neurons, a type of multipolar neuron with long apical dendrites reaching the cortical surface. An important mechanism than enables neurons to communicate is referred to as the action potential, where electric signals, received from the dendrite are propagated along the axon and finally transmitted to nearby neurons through synaptic interconnections. These synaptic transmissions may be excitatory or inhibitory, either increasing or decreasing the probability of an action potential in the postsynaptic neuron. However, the electrical activity that is recorded by the EEG does not comprise of the action potential, rather the summation of the postsynaptic transmissions (Kirschstein & Köhling, 2009; Tatum et al., 2006). Although these electric impulses comprise of short bursts of activity, electrodes at the scalp level may pick them up when many neurons fire together at the same time. This increase or decrease in synchrony of the activity of the neurons increases or decreases the amplitude of the signal, and facilitates slower or faster oscillations, which are indicative of resting or active cortical phases, referred to as event-related synchronization (ERS) or event-related desynchronization (ERD), respectively (Neuper & Pfurtscheller, 2001; Pfurtscheller & Lopes Da Silva, 1999). Typically, global ERS is evident during sleep or quiet states but focal ERS of higher rhythms such as gamma may be indicative of cognitive processing (Ahmed & Cash, 2013). The activity measured at the electrode level is very small and therefore, requires digitization and augmentation of the signals and this process is facilitated by the EEG amplifiers. Further, the electrodes also pick up noise arising from electrical lines/devices, eye blinks or muscular movements, which need to be filtered out before analyzing the data.

Interpretations about the functions of the brain, in response to an event for example, depend on the location of the cortex, generating these EEG signals. However, a major disadvantage of EEG lies in its low spatial resolution and the subsequent inverse problem (Jatoi et al., 2014). In other words, while the EEG signals may denote the activity stemming from a particular cortical area in general (frontal, temporal, central, parietal, occipital), it does necessarily mean that the neurons lying under a specific electrode generate the signals. Hence, one needs to be cautious about extending the EEG findings to specific regions within the general cortical topography, unless such interpretations are supplemented by additional source localization procedures (Jatoi et al., 2014; Michel & He, 2019).

Generally, EEG systems differ in terms of the type of electrodes used, the number of electrodes, the compatibility of different amplifiers and the sampling rate of the signals. In addition, newer mobile EEG systems offer more flexibility and opens up opportunities for incorporating experimental parameters that seem more natural, which is not possible with other methods (Bateson et al., 2017; Lau-Zhu et al., 2019).

2.2 EEG Measures and Oscillatory Analyses

The EEG method has been widely used to examine two distinct measures of neural activity: 1) Event-related potentials (ERPs) and 2) Event-related oscillations (EROs). Both ERPs and EROs are obtained by measuring neural activity derived from the presentation of repeated specific events or stimuli. However, the core difference between the two lies in the process through which this is achieved.

On the one hand, ERPs are assumed to be additive (Bastiaansen et al., 2012). In other words, they are obtained by averaging neural activity generated by repeated specific events or stimuli. This newly generated neural activity is time locked and phase locked (referred to as evoked activity) and is simply superimposed on the ongoing, background activity. The averaging function, therefore, extracts the new activity, while canceling out the dynamic brain activity in the background, which is assumed irrelevant to the cognitive process in question. Therefore, the ERP component, although having excellent temporal resolution, is only an approximate measure of the brain's response (Roach & Mathalon, 2008; Yordanova & Kolev, 2009). Some models suggest that ERPs result from phase resetting of ongoing brain oscillations (Makeig, et al., 2002, 2004). However, attempts to disentangle the processes involved in the additive and phase resetting models have been inconclusive in terms of what the ERPs represent (Sauseng et al., 2007).

On the other hand, neural oscillations, or EROs are considered the 'real brain responses' (Başar et al., 2001). Unlike ERPs, EROs represent changes in the ongoing neural activity, which are triggered by specific stimuli. In other words, exposure to specific events results in the reorganization of the ongoing neural activity, which is time locked but not phase locked (referred to as induced activity). Because these ongoing changes are not phase-locked and therefore not robust, they are cancelled out in an ERP analysis. EROs are typically represented as increasing or decreasing changes in magnitude or power from a particular frequency band. The process involving the decomposition of these neural oscillations with respect to changes in their magnitude and phase at particular frequency bands is called spectral decomposition or time-frequency analysis (Maguire & Abel, 2013; Roach & Mathalon, 2008).

Two methods are commonly used to extract the oscillatory components of the EEG signals: Fourier transform (FT) and wavelet analysis (Csibra et al., 2000; Herrmann et al., 1999; Mørup et al., 2007; Polikar, 1996). Neural oscillations may be captured using the FT procedure, which displays the mean amplitudes of the frequencies that exist without providing any information about the temporal domain. The FT procedure is sufficient when the requirement is only to derive frequency information but not when its relationship with time is also essential. The short time Fourier transform (STFT) was developed to resolve this issue by adding a time window but due to its finite features, the procedure only reduced the frequency resolution (Liu, 2010; Polikar, 1996).

The wavelet transform (WT), specifically the continuous wavelet transform (CWT), resolves the resolution problem of the STFT procedure by varying the width of the time window at different frequencies. In CWT, the transformation function, called the mother wavelet, depends on two parameters – translation and scale. While translation refers to the location of the window, the scale denotes the width, which may either dilate or compress a signal. Once these parameters are decided, the EEG signals are convoluted with the mother wavelet resulting in the transformed signals. Because of the varying parameters at different frequencies, the procedure leads to a trade-off between time and frequency resolution, with higher time but lower frequency resolution for higher frequency ranges, and lower time but higher frequency resolution for lower frequency ranges. Further, CWT comprises of two typically used wavelet transformations – Mexican Hat and Morlet wavelets. The Morlet wavelet is better at detection and localization of scale compared to the Mexican Hat (Herrmann et al., 1999; Mi et al., 2005) and is often reported in EEG studies.

Neural oscillations comprise of the following frequency bands (Chang et al., 2012; Schomer, 2007), with the infant EEG frequency bands much lower when compared to adults (Saby & Marshall, 2012). Specifically, the delta band oscillates at 1-4Hz or 0.5-2.5Hz, the theta band at 4-8Hz or 3-6Hz, the alpha/mu band at 8-13Hz or 6-9Hz, beta band above 13Hz or above 10Hz, and the gamma band above 30Hz or above 20Hz for adults and infants, respectively.

Occipital alpha desynchronization is associated with general attentional processes (Klimesch, 2012). Due to its overlap with the mu frequency range, alpha activity is also analyzed in action understanding studies to rule out the possible confounding effects of attention in the experimental conditions. Although beta desynchronization has been recently linked with execution and planning of motor movements similar to the mu rhythm (Babiloni et al., 2016; Nota et al., 2017; Nyström, 2008; Nyström et al., 2011; Quandt et al., 2012; van Elk et al., 2008), its role has been unclear (Bell, 2002; Engel & Fries, 2010). Mu rhythm activity is the focus of this thesis and the relevant evidence has been reviewed in the previous chapter. However, research with regard to the other frequency bands is irrelevant to the current thesis and thus, will not be elaborated on further.

2.3 The Advantages of EEG in Infancy Research

It is mostly accepted that infants comprehend much more about events around them, despite their limited skills (Baillargeon, 1998). For example, Parise et al. (2010) demonstrated that 5-month-old infants are sensitive to hearing their own names when compared to those of strangers. It is common knowledge that at 5 months, infants cannot pronounce their names. Applying the same logic to actions, they possibly infer meaning from observing others' actions even before they begin to produce them. However, such inferences are implausible to investigate using behavioural studies, where motor or language skills become somewhat necessary. Although the eye tracking method measures online processing of events as they unfold, they are still dependent on anticipatory gaze information, which require infants to disengage their attention from one aspect of the event to another (Southgate, 2013). Therefore, absence of predictive gazes may not always be indicative of infants' lack of goal understanding rather they may simply reflect infants' inability to shift attention. Further, looking time and pupil dilation provide indirect evidence that infants process goals based on their 'surprise' to impossible events but they do not conclusively indicate how they processed possible events.

Hence, investigating mu activity may be advantageous on many grounds, when compared to the behavioural and eye tracking methods. First, it is easy to implement passive observation paradigms, which does not specifically require infants' reactions to different experimental conditions. Second, owing to its excellent time resolution, trials could be made shorter, thereby including more number of trials within a session. Third, as mu desynchronization is evident even before the completion of a grasping action, shorter segments of action execution data may also result in reliable interpretation of the results. In other words, owing to intra- and inter-individual differences among infants in terms of the time taken to grasp objects across trials, it is not possible to include the entire movement duration for all trials and infants for the analysis. Yet, mu activity during the average duration of action execution of the group (from the onset to action completion) may be sufficient. Fourth, despite the high attrition rates in infant EEG studies, carefully planned experimental sessions may increase the chances of retaining more data, as even a small number of artifact-free data is sufficient to analyze mu activity (Bell & Cuevas, 2012; de Klerk et al., 2015). Fifth, compared to cumbersome methods such as fMRI, EEG is an excellent alternative to measure the neurophysiological correlates of infant cognition and development (Bell & Wolfe, 2007; de Haan, 2013).

While these advantages render EEG a promising method to measure action understanding, experimental procedures need to be carefully planned in order to encourage the infant to participate in the session, and reduce artifacts and attrition rates to the extent possible. In the following section, I provide a brief summary of the typical challenges encountered when conducting infant EEG studies.

2.4 Conducting Infant EEG Studies

Over the past couple of decades, infant EEG has grown to be quite a popular and reliable method to investigate the neurophysiological correlates of cognitive capacities or their development in infants. When compared to other noninvasive measures such as fMRI or TMS, which are problematic, EEG appears to be more suitable for the infant population due to its quick and relatively easy procedures, which are vital owing to infants' very limited attention span and willingness to cooperate. Recording EEG with infants, however, needs careful consideration of the various challenges during the session (Bell & Cuevas, 2012; Hoehl & Wahl, 2012).

Prior to the testing session, infants may need longer time to warm up when compared to older children. When recording data from infants, it may also be beneficial to include a second experimenter, who is introduced early on during the warm up phase. During the preparation phase, the role of the second experimenter is that of a distractor or entertainer, who attempts to divert infants' attention to exciting toys or books, thereby reducing their resistance to the EEG cap and the necessary procedures to improve electrical conductance that influences the quality of the data. The experimenters also need to be flexible in their use of strategies during this phase when the planned procedures do not work. For example, while some infants do not resist when made to sit on a high chair, other infants prefer to sit on their parent's lap and yet others may like to play by themselves on a mat during the preparation phase. Sometimes feeding a snack or allowing the infant to take a sip water may work as effective distractors. Whatever the case, keeping an infant happy during the preparation phase is the first step before the subsequent recording of data.

One of the biggest concerns with testing infants using EEG is that they neither remain still during the session nor can they be instructed to do so, as a result, contributing more noise to the data through frequent movements. In addition, when implementing visual stimuli, it is imperative that infants watch the trials, whether conducted live or by means of pre-recorded videos. Trials that infants do not watch are the first to be rejected from further analysis. Therefore, experimental paradigms need to be short, lasting a couple of seconds and need to incorporate various auditory or visual cues that help attract and/or maintain infants' attention. For example, interspersing stimuli blocks with attention getters or planned breaks in between may serve this purpose. Other artifacts are generated by infants' own movements, which render the data unusable. This is especially critical for action understanding paradigms where infants' own movements during the action observation phase may lead to additional confounding variables. Further, infants also tend to eat/drink, fidget with toys, or use a pacifier during the recording. These behaviours could be allowed as last resort solutions to motivate an unwilling, uncooperative infant to continue his or her participation, even though such data with additional movements or other behaviours are unusable and discarded from further analysis. Typically, infants watch the experimental trials as long as they are willing and when no strategies seem to work, the testing is stopped. Therefore, EEG researchers should implement the necessary steps such as providing breaks or including attention getters, to increase the chances of using data from as many infants as possible. Nevertheless, in anticipation of these problems, it is common to collect data from double the required sample of infants for EEG studies (Hoehl & Wahl, 2012).

After eliminating data with different artifacts, only the clean, noise-free segments are analyzed further. Typically, the inclusion criterion is recommended to be set at a minimum of 10-artifact free trials (Hoehl & Wahl, 2012; Stets et al., 2013). However, for action understanding studies, the minimum requirement is much lower and varies across studies, for example, even two or three artifact-free trials may be sufficient (de Klerk et al., 2015; Marshall et al., 2011). According to a recent meta-analysis (Stets et al., 2012), the mean attrition rate for infant EEG data is 47.3%, ranging from 0 to 83.8%, although between 50-75% is generally accepted (DeBoer et al., 2013).

All these factors put together suggest that while working with the infant population, EEG researchers also need to think of ways to create attractive stimuli, suitable for infants and thereby, minimize losing data (for a recent report on challenges with infant EEG and their solutions, see Noreika et al., 2020).

2.5 Methodological Variations in Infant Mu Research

Over the past decade, research on infant mu activity has published findings across different age groups, in different cortical regions, and implemented different experimental paradigms, EEG systems and analysis protocols, therefore contributing to some inconsistencies in the field. In section 1.7.2, I have elaborated on the various experimental paradigms and the corresponding evidence and in this section, I place emphasis on the different methodological procedures.

Figure 3 displays a typical layout for a 32-channel low-density[11] EEG cap, which was used for the studies in the current thesis. Irrespective of whether investigators implement low-density or high-density EEG systems, there are variations in the specific analysis parameters. First, there is a difference in the channels and channel combinations that have been considered to represent the sensorimotor region. For example, in studies using low-density recording systems, Langeloh et al. (2018), Marshall et al. (2013b, 2013a), Paulus et al. (2013), Ruysschaert et al. (2013) either analyzed mu activity from channels C3 and C4 separately or considered the average activity from both the channels combined. Other authors have extended the channel pools to include nearby channels such as Cz (Marshall et al., 2011; Meyer et al., 2016) or included a range of fronto-central, centro-parietal channels such as FC1, FC2, CP1, CP2 etc. to form a larger cluster (Stapel et al., 2010) or also included some lateral channels (Saby et al., 2012).

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[11] Typically, a low-density EEG system includes recording data from 3 to 32 electrodes, while in a high-density system, the number of electrodes range from above 32 up to 256 (DeBoer et al., 2013). The high-density EEG systems used in the studies cited in this section comprised of more than 60 electrodes.

Similarly there are differences in the number and combination of channels pooled using high-density EEG caps (for instance in Cannon et al., 2016; Debnath et al., 2019; Filippi et al., 2016; Montirosso et al., 2019; Rayson et al., 2016; Southgate et al., 2009, 2010; St. John et al., 2016; Yoo et al., 2016). Further, while some studies report activity from the frontal, parietal and occipital regions for both action execution and action observation phases, others do not provide a complete pattern of cortical activity during both action execution and action observation as elaborated in section 1.7.2.

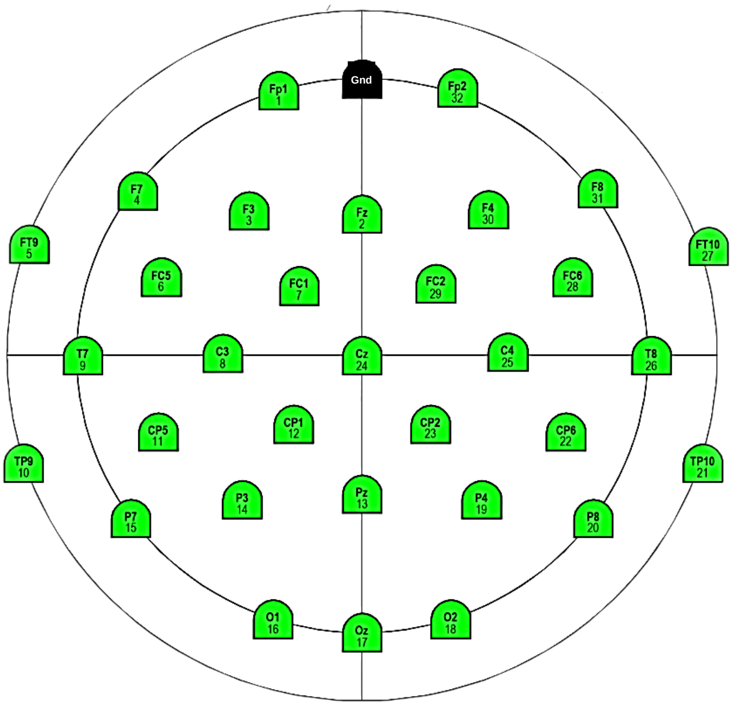

Figure 3: Layout of a 32-channel EEG cap

Courtesy of Brain Products, GmbH

Second, the analysis procedures differ in terms of whether an individual mu frequency range is analyzed for each infant (Ruysschaert et al., 2013; Southgate et al., 2009, 2010; Warreyn et al., 2013) or the established mu frequency range of 6-9Hz for infants is examined (Cuevas et al., 2014; Marshall et al., 2002; Marshall & Meltzoff, 2011). Yet other studies analyze a subset of the established mu frequency band such as 7-9Hz or 6-8Hz (Langeloh et al., 2018; van Elk et al., 2008).

Third, studies differ in their selection of segments of data depicting action execution and action observation. Specifically, while some studies segment data based on the time point when the hand touches the object (For example, Cannon et al., 2016; Marshall et al., 2011; Saby et al., 2012), other studies segment data based on the time point of action onset, i.e., when the action begins (For example, Southgate et al., 2009, 2010).

Therefore, the analysis of the current studies comprised of regions that closely matched the regions reported thus far and the same regions were consistently analyzed across the studies in the thesis and are further elaborated in chapter 4. The regions included all cortical sites including the occipital region in line with the recommendation to analyze mu activity across the scalp regions (Cuevas et al., 2014; Marshall & Meltzoff, 2011). Further, the established mu frequency range of 6-9Hz was analyzed to enable easy comparisons between the current studies and with previous research. Finally, the onset of actions was considered for the segmentation of the data as the actions incorporated in the current studies were not shown to touch the goal objects (specific details are provided in chapters 4, 5 & 6).

Despite the inconsistencies in previous research, the EEG method continues to be widely used to investigate infant action understanding. Methodological advances such as source localization and functional connectivity have also been proven to be insightful in the analysis of infant data (for example, Debnath et al., 2019; Thorpe et al., 2016), which only augments the advantages of EEG as a neurophysiological method for infancy research compared to the other noninvasive techniques.

3 Aim and Outline of the Thesis

In keeping with the relevance of mu activity for action understanding and the variation in infants' motor development and comprehension skills, three main questions guided the EEG investigations included in this thesis.

- Does action experience precede action understanding? (studies 1 & 2)

Considering the complexity of human behaviour including infants, it remains relevant to investigate whether and to what extent previous experience with actions modulates action understanding, specifically mu rhythm desynchronization. In other words, could action understanding be explained by the direct-matching mechanism alone (Rizzolatti et al., 2001)? To answer this question, the back-of-hand action was incorporated in the observation paradigms with a group of adults, who are familiar with the action, and groups of 9-month-old infants, who do not generally produce the action at this age.

- Do communicative actions also modulate the mu rhythm? (studies 1 & 3)

The current investigation comprised of communicative actions, specifically the back-of-hand and pointing, observed within the context of varying social settings, with the objective of investigating whether the elicitation of mu desynchronization is limited to instrumental actions, as Csibra (2003) postulated.

- Does action understanding entail a flexible system that encodes goals of unfulfilled actions and in the absence of object touch? (studies 1, 2 & 3)

The outcome of the observed actions in the current studies was not shown i.e., the goals remained unfulfilled. Nevertheless, the contextual cues suggested that the goals were embedded or distant and therefore, goal attribution may still be possible.

The predominant theme that guided the current studies was associated with factors, both contextual and social, that modulate action understanding. Observing actions under varying situations may alter the meaningfulness of the same action. Therefore, the action by itself does not facilitate action understanding but is modulated by cues that provide a congruent representation of the goal. Table 1 provides an overview of the studies conducted in the current thesis.

Table 1: Overview of the studies in this thesis
AE – action execution; AO – action observation

	Study 1 (Chapter 4)	**Study 2 (Chapter 5)**	**Study 3 (Chapter 6)**
Age Group	Adults 9 months	9 months	12 months
AE	Infants grasped objects	Infants grasped objects	Not conducted
Target Action for AO	Back-of-hand	Back-of-hand Reach	Pointing
AO Conditions	Social Nonsocial Object-absent	Congruent Reach Incongruent Back-of-hand Incongruent Reach Congruent Back-of-hand	Distal Proximal
AO Design	Within-subject (adults) Between-subject (infants)	Mixed design	Between-subject
AO Comparisons	Experiment 1 (adults): social vs nonsocial Experiment 2 (infants): social vs nonsocial Experiment 3 (infants): social (of experiment 2) vs object-absent	Mixed comparisons	Distal vs. Proximal

In the first study (chapter 4) comprising a series of three experiments, the back-of-hand action (palm-up hand configuration), an action that typically does not generate goal attribution when observed (for example, Southgate et al., 2010), was incorporated in social, nonsocial and object-absent settings. A group of adults and three groups of 9-month-old infants participated in this study. I demonstrated that observing the back-of-hand action in the social condition, where a recipient and a goal object were present, elicited significant mu desynchronization in the central and parietal regions for adults, and in the right centro-parietal region for infants. However, observing the same action in the absence of a recipient (nonsocial) and in the absence of a goal object (object-absent) did not elicit mu desynchronization. Infant data from the action execution phase, where infants reached for and grasped objects, revealed a global pattern of mu desynchronization.

In the second study (chapter 5), both the reaching and back-of-hand actions were incorporated in a 2x2 design, where the position of the object defined the congruency of the actions. Using the reaching action (palm-down hand configuration) for an object at an accessible height is congruent with the goal of attaining the object when compared to approaching the object with the back-of-hand action. Similarly, approaching an object that appeared to fall off from an inaccessible height with the back-of-hand action is congruent with the goal of attaining the object but not when using the reaching action in this circumstance. The findings revealed significant mu desynchronization in the right-centro parietal region only for the incongruent-reach condition but not for the congruent-reach and congruent-backofhand conditions. In this study, the evidence suggested that observing unfulfilled reaching and back-of-hand actions does not lead to goal attribution in the absence of additional contextual factors that further validate the observed actions and their lack of goal fulfillment. In the action execution phase, infants reached for and grasped objects. Similar to study 1, the action execution data in study 2 also revealed a global pattern of mu desynchronization.

In the third study (chapter 6), the pointing gesture, which was previously shown to not elicit mu desynchronization (For example, Pomiechowska & Csibra, 2017), was incorporated in social settings. Specifically, 12-month-old infants watched videos of an agent producing the pointing gesture in a distal or a proximal setting, defined by whether the goal object was located further away from the pointing agent but close to the recipient or close to the pointing agent but further away from the recipient, respectively. I demonstrated that observing pointing in both the distal and proximal conditions elicited significant mu desynchronization in the right centro-parietal region along with occipital alpha desynchronization. Observing pointing in the proximal condition resulted in significant desynchronization in the right fronto-central region but not in the distal condition.

Overall, the findings from the action observation data provided further support to the notion that action understanding is not entirely facilitated by action experience or limited to instrumental actions. Social and contextual factors facilitate action understanding, even when goals are embedded and this aspect provided evidence for the overall flexibility of the action understanding system.

4 Mu Desynchronization during the Observation of the ‘Back-of-hand’ Gesture in Socially-congruent Settings

Research highlights:

- *Groups of adults and 9-month-old infants watched videos of agents executing the back-of-hand action in the social, nonsocial and object-absent conditions.*
- *Significant mu desynchronization was elicited only for the social condition in the central and parietal region for adults and in the right centro-parietal region for infants.*
- *The findings suggest that action understanding is not limited to the available motor repertoire or only to instrumental actions but extends to communicative actions as well.*

Keywords: mu rhythm, action understanding, back-of-hand, social context, communicative action, third-party observations

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4.1 Abstract

Infant EEG studies on action understanding have hitherto focused on object-directed, instrumental actions such as reaching and grasping, showing mu desynchronization around the central region for self-executed and observed actions. In comparison, the ‘back-of-hand’ action (which is a mere rotation of the hand such that the palm faces upwards, is typically used as the control; for example, Southgate et al., 2010), does not elicit goal attribution and mu desynchronization. However, within an appropriate social context, the back-of-hand action may be interpreted as a request and thus, meaningful. To investigate this possibility, three conditions – social, nonsocial and object-absent – were incorporated, where an agent produced the back-of-hand action in the presence of a goal object and a recipient, in the presence of a goal object but not a recipient, and in the presence of a recipient but not a goal object, respectively. A group of adults and three groups of 9-month-old infants participated in the study, where the adults watched the social and nonsocial conditions following a within-subject design, and the infants watched the three conditions following a between-subject design. However, only two groups of infants, who watched the social and nonsocial conditions, performed the action execution task, where they reached for and grasped colourful objects. For action observation, observing the back-of-hand action in the social condition elicited significant mu desynchronization in the central and parietal regions for adults (8-13Hz) and in the right centro-parietal region for infants (6-9Hz). Further, infant action execution data revealed a significant global pattern of mu desynchronization. Overall, the findings suggested that within an appropriate context, both adults and infants perceived the back-of-hand action as meaningful. Further, we provided evidence that action understanding is not limited to instrumental actions but also extend to communicative goals, even when the action is not yet part of the motor repertoire and the goal object is not touched.

4.2 Introduction

Using EEG, mu rhythm desynchronization over the sensorimotor cortex has been established as the signature of mirror system activity (Fox et al., 2016; Pineda, 2005, 2008), which is evident during both the execution and observation of goal-directed actions. In recent years, infant EEG research has provided sufficient evidence that the action reconstruction account (Csibra, 2008) offers a more plausible explanation for action understanding when compared to direct-matching (Rizzolatti et al., 2001). While direct-matching suggests that action experience precedes action understanding, action reconstruction proposes that goal prediction and action emulation facilitate action understanding. For example, at 9 months, infants displayed significant mu desynchronization when the goal of a grasping action was implied behind an occluder (Southgate et al., 2010); irrespective of whether they watched a hand or a claw reach for the object or the object move in a self-propelled manner (Southgate & Begus, 2013); at 6 months, when they anticipated an agent to reach inside a box due to a false belief that a ball was present (Southgate & Vernetti, 2014). Further, one-year-old infants displayed stronger mu desynchronization while observing unusual actions such as placing the drinking cup to the ear (Stapel et al., 2010) or when turning on a lamp or a sound box with one's head or foot even when the person's hands were free to carry out the action (Langeloh et al., 2018; Marshall et al., 2013a; Saby et al., 2013).

If infants in these studies relied on their motor experience, mu desynchronization for the unusual and self-propelled actions or the false belief setting would be unlikely. Furthermore, the kinematics of the actions alone did not modulate action understanding, instead contextual factors played a fundamental role. Nevertheless, most of the evidence comes from studies focusing on instrumental actions (such as grasping). If contextual factors facilitated instrumental goal understanding, they could possibly also extend to communicative actions. One such action, which is typically used as a control condition is the back-of-hand action. Specifically, observing an agent touching the object using the back-of-hand configuration, which is a mere rotation of the hand such that the palm faces upwards, is meaningless. Behavioural studies have provided evidence that the back-of-hand action is not construed as goal-directed, when compared to grasping because it does not result in goal attainment (Hamlin et al., 2008; Krogh-Jespersen & Woodward, 2014; Thoermer et al., 2013; Woodward, 1999). Further, Southgate et al. (2010) did not find mu desynchronization when 9-month-old infants observed the back-of-hand action disappear behind an occluder, when compared to grasping. These findings seem to suggest that the back-of-hand action is a meaningless gesture. However, this is far from true because the back-of-hand action has been interpreted to subsume different roles. For example, Darwin (1872) suggested that using the back-of-hand along with shrugging one's shoulders denotes a sign of helplessness. Adult studies have reported that the back-of-hand functions as a co-expressive modality during speech or discourses (Cooperrider et al., 2018; Ferré, 2012; McNeill, 2013) or to request favours, to take turns while speaking, and to share opinions (Givens, 2016), suggesting that such interpretations necessitate contextual cues.

However, only a handful of studies have considered contextual cues when investigating how preverbal infants infer the meaning of the observed back-of-hand action. For example, Thorgrimsson et al. (2014) provided evidence that 14-month-old infants anticipated a recipient to respond to the partner's back-of-hand action for an object from a third-party perspective. 9-month-old infants showed 'surprise' (increased pupil dilation) to the recipient's inappropriate response to the agent's back-of-hand action, when she placed the requested object on the agent's head instead of placing it on the palm (Juvrud et al., 2019). Further, 12-month-old infants produced faster gaze shifts when they watched objects being transferred from a giving hand to the back-of-hand shape of a receiving hand when compared to objects being transferred to a grasping shape of the hand (Elsner et al., 2014). 12- and 14-month-old infants also responded by providing the goal object when the experimenter approached them with a back-of-hand gesture (Hobbs & Spelke, 2015; Liszkowski, 2014). Further, older infants at 21 months offered the distant object instead of the nearby object to a requestive back-of-hand gesture of the experimenter when her hands were free but offered the nearby object more often when her hands were occupied (Grosse et al., 2010). To the best of our knowledge, only one EEG study incorporated the back-of-hand as the target gesture, although not in the context of the mu rhythm. In this study, Bakker et al. (2015) presented static images of the back-of-hand and a non-communicative shape of the hand to 9-month-old infants, while recording EEG. The results showed a significantly higher amplitude of the ERP P400 component, previously reported as an index of (social) gesture understanding (Bakker et al., 2014; Gredebäck et al., 2010), for images of the back-of-hand when compared to the control. These studies suggest that the lack of action understanding for the observed back-of-hand action reported in the previous studies could be attributed to the missing contextual factors.

Research on the age of emergence of the back-of-hand action does not yet exist. However, infants appear to use this gesture to request at around 22 months (Özçalişkan & Goldin-Meadow, 2005b, 2005a). There is evidence that between the ages of 8 and 18 months, infants use the reaching gesture communicatively or use pointing to request for out-of-reach objects (Carpenter et al., 1983; Crais et al., 2004; Franco & Butterworth, 1996; Liszkowski, 2014; Ramenzoni & Liszkowski, 2016; Veena & Bellur, 2015). Hence, previous research seems to suggest that infants do not use the back-of-hand action until the end of their second year. However, during the first year, infants use alternative actions to convey a requestive intention.

For the present study, we conducted three EEG experiments incorporating the back-of-hand as the target action. The action observation phase comprised of three conditions - social, nonsocial and object-absent - where an agent produced the back-of-hand action in the presence of a goal object and a recipient (social), in the presence of a goal object but not a recipient (nonsocial), and in the presence of a recipient but not a goal object (object-absent). The first experiment was conducted with a group of adults, who watched videos of both the social and nonsocial conditions. As a similar paradigm had not been conducted previously, the objectives of the first experiment were to check the effectiveness of the stimuli, to check whether the social condition would elicit significant mu desynchronization, and whether any differences in mu activity could be explained by the differing contextual factors. In the second experiment, two groups of 9-month-old infants watched either the social or the nonsocial condition in the action observation phase and performed an action execution task, where they grasped various objects. In both experiments 1 and 2, we hypothesized that the social condition would elicit significant mu desynchronization when compared against zero and when compared with the nonsocial condition. Further, we expected to find a topographical overlap of mu desynchronization between the action execution and action observation phases for the infants. The third experiment comprised of only the action observation phase, where a third group of infants watched the object-absent condition. The purpose of the third experiment was to investigate the role of the goal object in the social situation. We predicted that in the absence of a goal object, infants would interpret the observed back-of-hand action as meaningless and therefore, this condition would not elicit significant mu desynchronization.

We selected 9-month-old infants because infants at this age do not execute the back-of-hand action themselves in order to request for objects. Therefore, if the above hypotheses were true, it would provide further evidence against the direct-matching account of action understanding but in support of the action reconstruction account.

A relevant question with regard to action understanding is whether goals are attributed to distant and embedded sequences, where the goal is indirectly attained. Specifically, unlike grasping, producing the back-of-hand action does not result in attaining the object and requires a recipient to reciprocate appropriately to complete the sequence. In the action observation videos implemented in the current study, the agents do not touch the objects and the outcome of the back-of-hand action is not shown. Therefore, understanding the requestive intent in the social condition would suggest that embedded and distant goals, although unfulfilled, are also meaningful.

4.3 Experiment 1: adults (social & nonsocial)

4.3.1 Methods

4.3.1.1 Participants

The final sample of adults consisted of 15 participants (f = 7, mean age = 25.75) and all of them reported to be right-handed, with normal or corrected-to-normal vision. Data from an additional 16 adults were not included in the final analysis due to noisy data (4), experimenter error (2), for being an outlier (1) (more than 1.5 times the interquartile range from the median (Marshall et al., 2011, 2013b; Saby et al., 2012)) and for not providing a minimum of 10 artefact-free trials per condition (9). However, this exclusion rate (51.61%) is not typical of adult EEG studies. The participants received either credit points or monetary compensation (10€ per hour) in return for their participation.

4.3.1.2 Stimuli

Action observation. The videos for the social condition showed an agent, producing the back-of-hand action, and a recipient seated across the table, who did not respond. In the nonsocial condition, an agent produced the back-of-hand action but a cupboard was present at the other end of the table. Both the conditions included an object on the table, located out of reach of the agent producing the back-of-hand action. The videos lasted 3.4 or 3.6 seconds, where the first 1200 or 1400ms comprised of the neutral phase, depicting an array of colourful spirals on a grey background. In the action phase, the social or the nonsocial setting appeared on the screen for 200ms, during which the agent and the recipient established eye contact in the social setting. Then the agent produced the back-of-hand action (at 1400ms or 1600ms), stopping at the final position, 1200ms after action onset (i.e., at 2600ms or 2800ms). The final position was frozen on the screen for 800ms after which the trial ended, as illustrated in Figure 4.

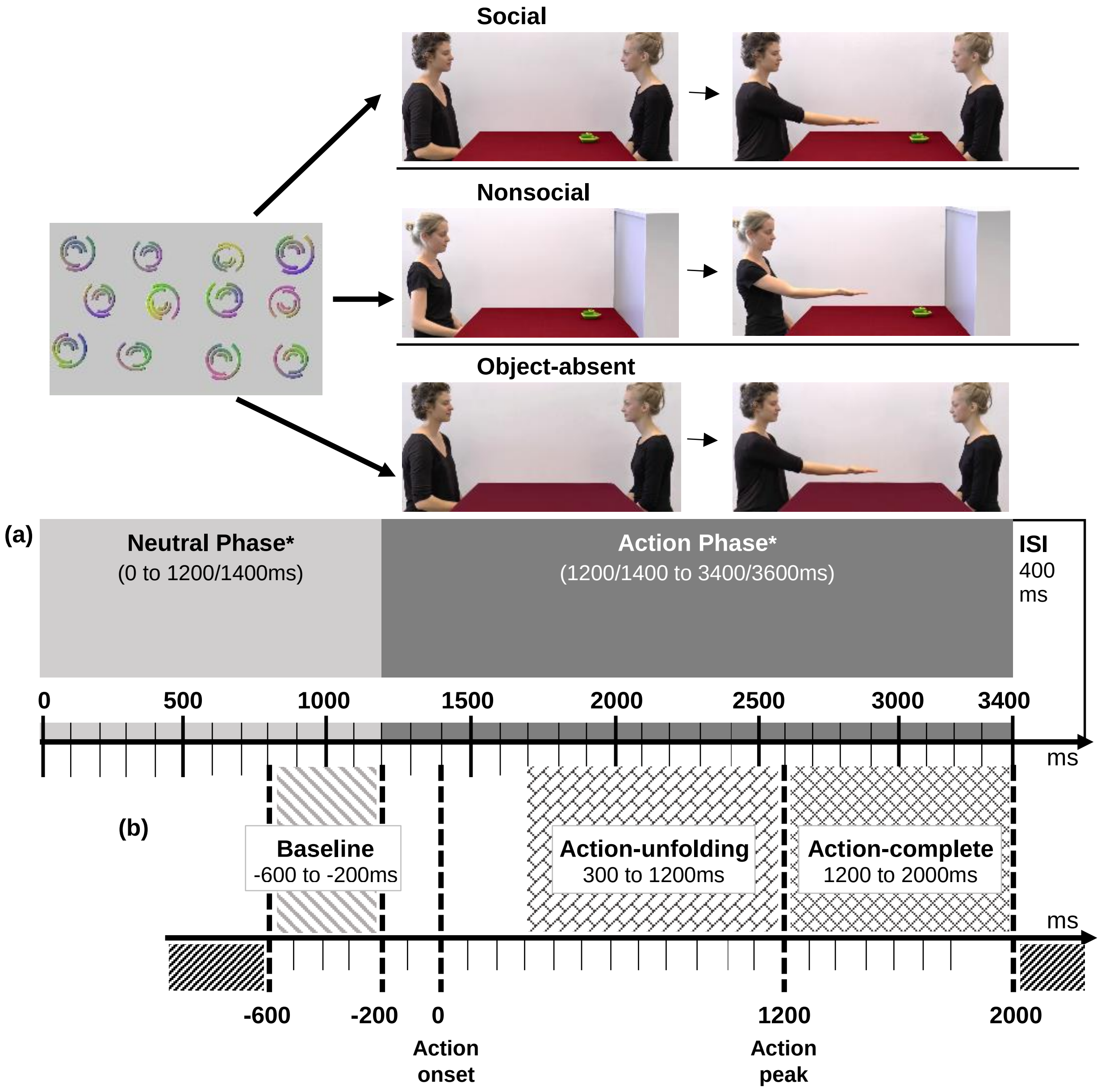

Figure 4: Stimuli presentation and analysis timeline for study 1

**The (a) stimuli videos consisted of varying neutral phases, with half the videos comprising of a 1200ms neutral phase (illustrated in this figure). In the other half of the videos, the duration of the neutral phase lasted 1400ms, therefore the subsequent events were pushed further by 200ms. Specifically, the time at action onset was 1600ms, action peak at 2800ms and end of the action phase at 3600ms, following the longer neutral phase. However, the (b) corresponding time points for the analysis remained the same as the data were segmented based on the action onset; ISI: inter-stimulus interval*

Experiments 1 and 2 included the social and nonsocial conditions, conducted following a within-subject design with adults and a between-subject design with 9-month-old infants. While adults watched either of the two agents producing the back-of-hand action in each condition, videos of both agents were presented to infants in a blocked manner. In experiment 3, a third group of 9-month-old infants watched only the object-absent condition, where videos of both the agents were alternated in blocks.

▨ *- represents the part of the segment chopped from the analysis phase to eliminate the distortion introduced by the wavelet transform.*

The original video was filmed against a plain white wall with two agents seated across a table, using a Panasonic Handycam model number HC-X929. The cupboard (for the nonsocial condition), objects and four different tablecloths (red, blue, brown, and grey) were photographed using a smartphone and then appropriately edited for use in the videos. Forty different objects were included in the videos. The objects belonged to different categories such as animals, vehicles, play objects such as a ball or a rattle, eatables, and household items such as candle or a small pan. The baseline spirals figure was created using Adobe After Effects CS6. All these individual elements were combined and edited further using Adobe After Effects CS6. Finally, the edited videos were flipped in order to balance the side of presentation.

4.3.1.3 Procedure

Informed consent was obtained from the participants before the start of the experiment. During the preparation of the EEG cap, participants filled out forms to provide basic details such as date of birth, age, education and handedness. Discussions regarding the purpose of the study were avoided until after the end of the recording session. We followed a within-subject design, where adults watched videos of both the social and nonsocial conditions in a block manner, displayed on an LCD (liquid crystal display) computer monitor (51.50cm X 32.00cm) at a distance of approximately 80cm. The videos were rendered at a resolution of 1920pixels x 1080pixels and were presented at size 24cm x 40cm. The trials were presented in a pseudo-random order using the Presentation Software (©Neurobehavioural Systems, Inc) in four blocks of 40 trials each, where the first two blocks represented one condition and the last two blocks, the other condition. Each block comprised of trials with varying baseline lengths, however, with no more than two consecutive repetitions of videos with the same baseline length. In addition, adults watched different agents executing the back-of-hand action in the social and nonsocial conditions in order to avoid carryover effects. The order of conditions, blocks and the agents producing the back-of-hand action in the social and nonsocial conditions and the side of presentation were counterbalanced across participants such that there were eight different versions of stimuli presentation. A total of 160 trials were presented, with 80 trials in each condition. Each trial was followed by an inter-stimulus interval (ISI), comprising of a picture of a plain grey background for 400ms. In total, stimulus presentation lasted around 12 minutes. At the end of the session, all participants were requested to explain their understanding of the stimuli and the purpose of the experiment. Finally, participants were briefed about the study.

4.3.1.4 EEG Recording

EEG was recorded using Brain Vision Recorder with actiCAP 32 active ag/agcl electrodes connected to the actiCHamp ampliflier (©Brain Products, GmbH), with the vertex electrode, Cz, used as the reference and at a sampling rate of 500Hz. Channels TP9 and TP10 were detached and replaced by two electrodes to record ocular artifacts. These ocular electrodes were fixed under each eye on the cheekbone. The ground electrode was placed on the forehead between FP1 and FP2, as shown in Figure 3 (chapter 2). The electrode impedances were minimized using conductive gel and impedance levels below 5kΩ were accepted.

4.3.1.5 EEG Analyses

The pre-processing steps of the EEG data were completed using Brain Vision Analyzer (©Brain Products, GmbH). First, the raw data were digitally filtered between 0.1Hz and 100Hz using the infinite impulse response (IIR) filter, implemented as a Butterworth zero-phase shift filter in Brain Vision Analyzer. EEG data were segmented into epochs lasting 3400ms, i.e., 1000ms before and 2400ms after action onset. Artifact rejection was completed using the semi-automatic and manual modes. To elaborate, EEG data from individual channels of each segment were set to be marked as noisy if the amplitudes of the signals were higher than 200μv; 200ms before and after this point were also marked as noisy. Subsequently, the noisy segments were rejected via manual inspection. Noisy channels were removed and the missing data were interpolated from nearby channels, however, restricting this function to not more than three channels, amounting to 10% of the total scalp channels recorded (Gredebäck & Melinder, 2010; Pomiechowska & Csibra, 2017). Datasets with more than three noisy channels were discarded.

The artifact rejection method described is not typical of adult EEG. While methods such as independent component analysis (ICA) would have been more appropriate to remove artifacts, ICA is ineffective and unsuitable with infant EEG data because of the higher amplitude of the EEG signals when compared to the adult data, limited recording time, and unsystematic and abrupt movements that cannot be controlled for (Fujioka et al., 2011). In order to avoid substantial differences in artifact rejection procedures between adults and infants (Cuevas et al., 2014), a combination of semi-automatic and manual methods was implemented for the adult data as well.

The artifact-free segments were exported as .mat files for time-frequency analysis using scripts available from the WTools 2012 toolbox (developed by E. Parise, L. Filippin, & G. Csibra, available upon request) that is compatible with EEGLAB version 13_3_2b and MATLAB 2012a. Using WTools, the data were re-referenced to the average. The baseline comprised of a 400ms duration of the spiral display from the neutral phase. For baseline correction, the average amplitude of the baseline duration was subtracted from the whole segment at each frequency. Finally, time frequency analysis was performed using the Morlet wavelet transform in steps of 1Hz between 5-20Hz. The absolute values of the complex coefficients were calculated (Csibra et al., 2000). Using this method, mu activity represented by negative amplitudes denotes desynchronization whereas positive amplitudes denote synchronization. 400ms on either edge of the segments were chopped off to eliminate the distortion generated by the wavelet transform, therefore reducing the segments further to 600ms before and 2000ms after action onset, as illustrated in Figure 4b. The average mu activity was computed for each dataset across segments and finally the grand average was computed.

The final sample of adults (N = 15) contributed an average of 63.5 trials in total, with 30.86 trials in the social condition (SD = 17.43, Range = 10-70) and 32.73 in the nonsocial condition (SD = 18.43, Range = 10-57) (the difference between the total number of trials contributed in each condition was not significant: $t_{(14)} = -0.515$, $p = 0.614$, two-tailed).

For the analysis of action observation, time periods were selected based on the unfolding of the action on the screen. Action-unfolding comprised of a 900ms duration, starting from 300ms after the onset of action until 1200ms. Action-completion comprised of 800ms, starting from 1200ms after action onset until the end of the trial, as shown in Figure 4b.

4.3.1.6 Frequency & Channel Selection

The average amplitudes during the action-unfolding and action-complete time periods were exported for the adult mu range of 8-13Hz (Hobson & Bishop, 2016, 2017; Fox et al., 2016) from the target regions comprising of central (C3, Cz, C4) and parietal (P3, Pz, P4) regions (Brunsdon et al., 2019, 2020; Hobson & Bishop, 2016; Makhin et al., 2019). In addition, following the recommendations to examine occipital alpha activity (Cuevas et al., 2014; Hobson & Bishop, 2016, 2017), data from the occipital region (O1, Oz, O2) were analyzed separately.

4.3.1.7 Statistical Analyses

The exported mu amplitudes were initially analyzed following the omnibus repeated measures ANOVA by including all the within-subject factors, that is, conditions, action phases and regions. Results from pairwise comparisons were examined to resolve main effects and interactions from the ANOVA, which indicated the factors or the combination of factors that elicited significant differences. However, when reporting findings from follow up t-tests, one-tailed *p* values are reported for the following reasons. When compared against zero, the meaningfulness of the observed conditions was determined by whether they elicited significant mu desynchronization, i.e., negative amplitudes. Given the premise of the current thesis, significant mu synchronization (positive amplitudes) would be theoretically meaningless. Similarly, we expected the social condition to elicit greater mu desynchronization compared to the nonsocial condition but the reverse relationship between these conditions would be meaningless. Consequently, as the current investigations were concerned with unidirectional predictions, one-tailed t-test results are reported (Lombardi & Hurlbert, 2009; Ruxton & Neuhäuser, 2010). Although data from the occipital region were analyzed separately, devoid of specific expectations, one-tailed results are reported to maintain uniformity across the findings.

4.3.2 Results

Based on verbal reports, all 15 participants from the final sample revealed a clear understanding about the purpose of the experimental stimuli. They interpreted the requestive goal of the observed back-of-hand action in the social condition but expressed surprise that the recipient did not respond. However, for the nonsocial condition they admitted to being confused with regard to the purpose of the observed back-of-hand action.

Table 2 provides a summary of the results from experiment 1 and Figure 5 shows the mu activity in the central and parietal regions for both the social and the nonsocial conditions. A repeated measures ANOVA with condition (social, nonsocial), action phase (action-unfolding, action-complete) and region (central, parietal) revealed a significant main effect for condition ($F_{(1,14)} = 7.268$, $p = 0.017$, $\eta_p^2 = 0.342$) and region ($F_{(1,14)} = 6.594$, $p = 0.022$, $\eta_p^2 = 0.320$). Pairwise comparisons revealed greater mu desynchronization for the social condition (Mean = -0.096, SE = 0.025) compared to the nonsocial condition (Mean = -0.042, SE = 0.029) and greater mu desynchronization in the parietal region (Mean = -0.098, SE = 0.032) compared to the central region (Mean = -0.040, SE = 0.022).

Further, we also found a nearly significant two-way interaction between action phase x region ($F_{(1,14)}$ = 4.275, p = 0.058, η_p^2 = 0.234). Pairwise comparisons from the omnibus ANOVA revealed that for the action-unfolding action phase, mu desynchronization in the parietal region (Mean = -0.113, SE = 0.030) was significantly greater than the central region (Mean = -0.040, SE = 0.022, p = 0.010) but for the action-complete phase, the difference was marginally significant ($\text{Mean}_{\text{parietal}}$ = -0.084, SE = 0.035; $\text{Mean}_{\text{central}}$ = -0.040, SE = 0.25, p = 0.076).

In addition, the omnibus ANOVA also revealed a marginally significant three-way interaction among condition x action phase x region ($F_{(1,14)}$ = 4.088, p = 0.063, η_p^2 = 0.266). This three-way interaction was resolved by means of t-tests. For the social condition, one-sample one-tailed t-tests revealed significant mu desynchronization for both the action-unfolding and action-complete phases in the central ($\text{Mean}_{\text{action-unfolding}}$ = -0.054, SE = 0.020, $t_{(14)}$ = -2.686, p = 0.009; $\text{Mean}_{\text{action-complete}}$ = -0.059, SE = 0.027, $t_{(14)}$ = -2.214, p = 0.022) and the parietal ($\text{Mean}_{\text{action-unfolding}}$ = -0.158, SE = 0.033, $t_{(14)}$ = -4.745, p < 0.001; $\text{Mean}_{\text{action-complete}}$ = -0.112, SE = 0.036, $t_{(14)}$ = -3.130, p = 0.003) regions. For the nonsocial condition, we found significant mu desynchronization for the action-unfolding phase in the parietal region (Mean = -0.067, SE = 0.035, $t_{(14)}$ = -1.876, p = 0.041) but not in the action-complete phase (Mean = -0.055, SE = 0.045, $t_{(14)}$ = -1.216, p = 0.122). The nonsocial condition did not elicit significant mu desynchronization in the central region ($\text{Mean}_{\text{action-unfolding}}$ = -0.026, SE = 0.027, $t_{(14)}$ = -0.973, p = 0.173; $\text{Mean}_{\text{action-complete}}$ = -0.019, SE = 0.026, $t_{(14)}$ = -0755, p = 0.231).

Paired samples one-tailed t-tests revealed greater mu desynchronization for the social condition during the action-unfolding phase in the parietal region ($t_{(14)}$ = -2.757, p = 0.015) when compared to the nonsocial condition but not during the action-complete phase ($t_{(14)} = -1.376$, $p = 0.095$). Further, mu desynchronization for the social condition in the central region differed significantly from the nonsocial condition during the action-complete phase ($t_{(14)} = -2.037$, $p = 0.030$) but not during the action-unfolding phase ($t_{(14)} = -1.280$, $p = 0.110$).

Table 2: Results from action observation of experiment 1, study 1

Overview of the (a) ANOVA and (b) t-test results from experiment 1. All results indicate significant mu desynchronization comparisons

(a) Main effect	Interaction
Condition (p=0.017) - Social > nonsocial	**Action-phase x region** (p=0.058) Action-unfolding: parietal>central (p=0.010) Action-complete: parietal>central (p=0.076)
Region (p=0.022) - Parietal > central	**Condition x action-phase x region** (p=0.063)

(b) One-sample t-test$^+$		Paired-samples t-test$^+$
Social:		**Action-unfolding:**
Action-unfolding	**Action-complete**	Parietal: social > nonsocial (p=0.015)
Central (p=0.009)	Central (p=0.022)	
Parietal (p<0.001)	Parietal (p=0.003)	**Action-complete:**
		Central: social > nonsocial (p=0.030)
Nonsocial:		
Action-unfolding		
Parietal (p=0.041)		

$^+$ One-tailed significance
> denotes greater mu desynchronization for the factor on the left of the symbol compared to that on the right of the symbol

One-sample one-tailed t-tests did not reveal significant occipital alpha desynchronization for both the action phases in both conditions (social: $\text{Mean}_{\text{action-unfolding}} = -0.048$, SE = 0.032, $t_{(14)} = -1.515$, $p = 0.076$; $\text{Mean}_{\text{action-complete}} = -0.038$, SE = 0.029, $t_{(14)} = -1.314$, $p = 0.105$; nonsocial: $\text{Mean}_{\text{action-unfolding}} = -0.040$, SE = 0.032, $t_{(14)} = -1.247$, $p = 0.116$; $\text{Mean}_{\text{action-complete}} = -0.018$, SE = 0.041, $t_{(14)} = -0.444$, $p = 0.332$). The spectrographs of the occipital alpha activity elicited from the social and the nonsocial conditions are provided in appendix A.

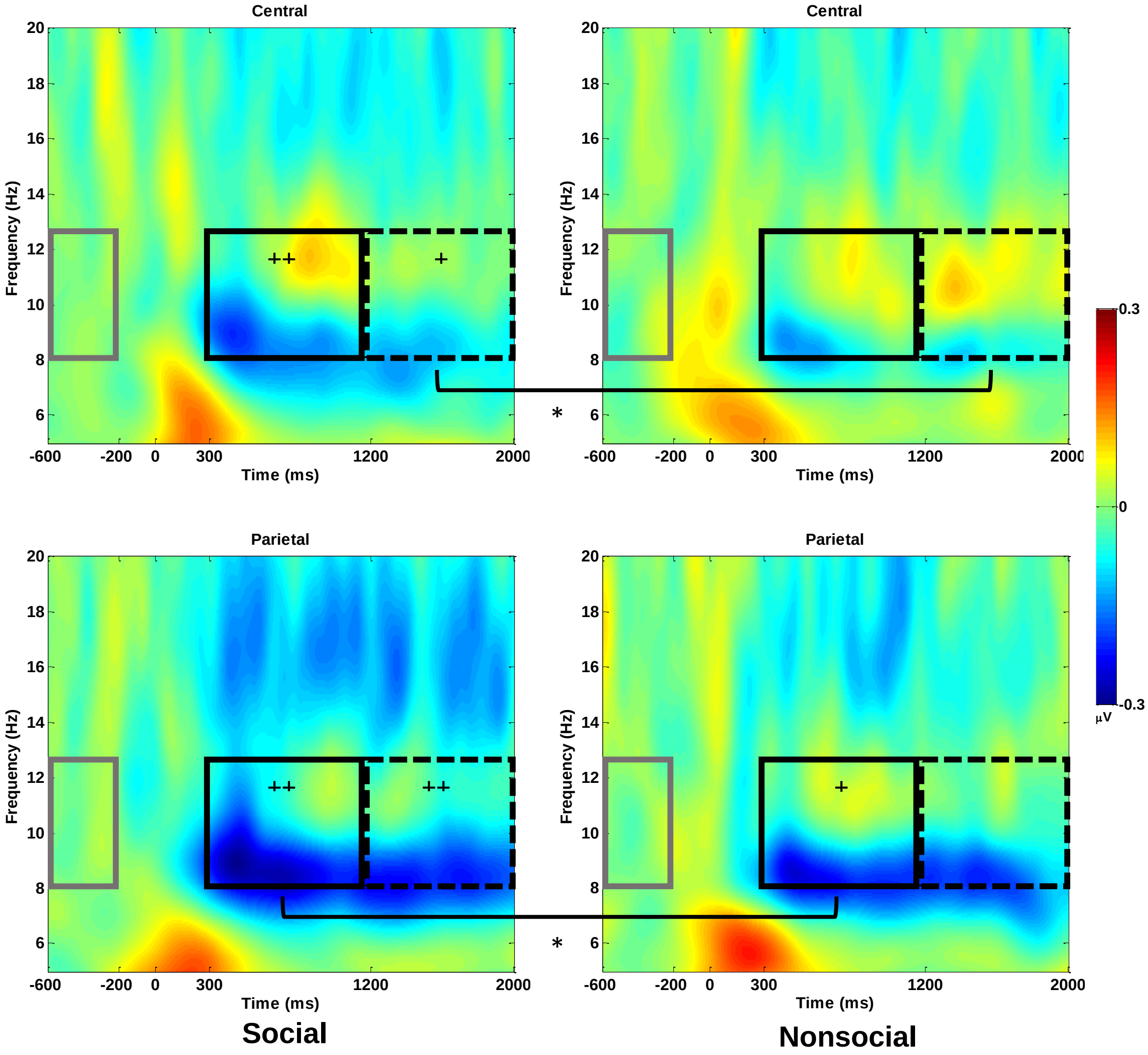

Figure 5: Mu activity during action observation (experiment 1, study 1)

The top panels show mu desynchronization in the central region and the bottom panels show mu desynchronization in the parietal region for both the social and the nonsocial conditions.

The areas marked in grey, solid black and dashed black boxes represent the baseline, action-unfolding and action-completion phases, respectively, in the adult mu frequency band of 8-13Hz.

++ $p < 0.01$; +$p < 0.05$ when compared to 0 (one-sample t-tests)
*$p < 0.05$ when compared between conditions (paired sample t-tests)

4.3.3 Discussion

The experiment with the adult group confirmed that the stimuli served the purpose of the study. The findings revealed significant mu desynchronization in the parietal and central regions for the social condition. Significant parietal mu desynchronization for the action-unfolding phase of the nonsocial condition could be attributed to action familiarity or to the anticipation that the agent will produce the back-of-hand action but it may not be due to their understanding of the communicative goal because the effect did not persist into the action-complete phase like the social condition. This interpretation is reinforced by the participants' own account of the purpose of the two conditions they observed, where they clearly stated that the agent's back-of-hand action in the social condition implied a request but the same action was ambiguous in the nonsocial condition.

The results provide further evidence that social-contextual factors modulated action understanding and mu desynchronization, similar to previous studies (for example, Oberman, Pineda, et al., 2007; Perry et al., 2011; Tikka et al., 2016). Specifically, we were able to show that social-contextual factors could overturn a meaningless action such as the back-of-hand into a meaningful action in a social situation. Moreover, the results suggest that distant goals are encoded, even when the outcome of the action is not presented. However, as adults are familiar with the back-of-hand action, it is difficult to conclude whether the findings from the adult experiment could be better explained by the direct-matching or the action reconstruction account.

An important limitation of this experiment lies in the fact that our attempt to retain procedural similarities between the adults and infants limited the data available for analysis. Specifically, the recording session lasted only around 12 minutes as was planned for the infant sample, whereas presenting multiple blocks and extending the recording session would have been more appropriate. In addition, the method of artifact rejection implemented led to the loss of more data because entire segments containing artifacts were discarded. Future studies incorporating both adult and infant samples need to consider conducting longer sessions and recording more data from adults even though this would be implausible with infants. The presentation scripts also need to be modified by including short pauses between trials and between blocks with instructions to blink and rest during the session. While this procedure could reduce artifacts in general, it could also increase the data available for the final analysis and reduce the attrition rate, which is typically expected to be quite low for adults.

4.4 Experiment 2: infants (social & nonsocial)

4.4.1 Methods

4.4.1.1 Participants

Sixty-seven infants participated in the study, with 33 infants in the social condition and 34 infants in the nonsocial condition. All infants participated in the action execution phase[12].

Action observation. Thirty-six infants (f = 18, mean age = 288 days) were included in the final sample of the action observation phase, with 18 each in the social (f = 8, mean age = 287 days) and the nonsocial (f = 10, mean age = 289 days) conditions. Data from an additional 31 infants were discarded due to unwillingness (1), extreme movements or use of pacifier (3) and for not providing a minimum of five artifact-free trials (27).

Action execution. Twenty-one infants (f = 9, mean age = 288 days) were included in the final sample of the action execution phase, out of which 11 infants watched the social condition (f = 5, mean age = 289 days) and 10 infants watched the nonsocial condition (f = 4, mean age = 286 days) in the action observation phase[13]. Data

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[12] Please note that the data from the action observation and action execution phases were recorded from all infants but were treated separately for the final analysis. In other words, the availability of sufficient data from both phases was not a pre-requisite for inclusion in the final sample of both phases. Such a stringent inclusion criterion would have increased the attrition rate further. Therefore, the final sample does not represent a strict overlap of data obtained from infants providing sufficient artifact-free trials from both phases but also includes data from infants, who provided sufficient artifact-free trials for one phase but not the other.

[13] This does not mean that the infants included for the final analysis of the action execution phase also provided sufficient artifact-free trials for the action observation phase. Nevertheless, this information is relevant for the preliminary analysis of any differential mu activity during action execution.

from an additional 46 infants were discarded due to unwillingness (1), experimenter error (3), extreme movements (13) and for not providing a minimum of 4 artifact-free trials (29).

The attrition rates of 46.26% and 68.65% in the action observation and action execution phases, respectively, falls within the general anticipated rate for infant EEG studies (DeBoer et al., 2013; Hoehl & Wahl, 2012).

4.4.1.2 Stimuli

Action observation. The same social and nonsocial condition videos described in experiment 1 were presented to the infants in this phase (see Figure 4a). During the neutral phase, we included a short tone, played during the first 400ms to attract infants' attention towards the screen. Twenty tones were created using Anvil Studio (© Willow Software), comprising of different types of beats or melodies. In addition to the already existing components, these tones were randomly superimposed for each trial using Adobe After Effects CS6.

Action execution. Figure 6 illustrates the experimental setup for the action execution phase. This phase comprised of a live paradigm, where infants reached for and grasped various objects. A three-sided cabin was created using cardboard, such that it was high enough to occlude the experimenter behind it. The front of the cabin was attached to an enclosed cardboard ramp. Fifteen different, colourful toys were fixed to a small piece of cardboard to enable smooth sliding through the ramp.

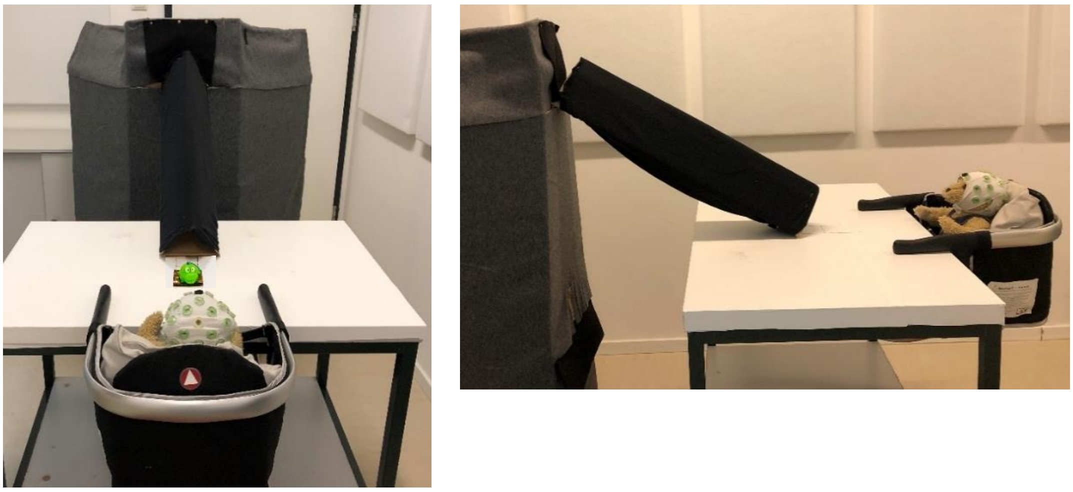

Figure 6: Experimental setup for action execution (experiment 2, study 1)

The figure on the left represents the perspective of the infant and that on the right, the angle recorded from the video camera. The teddy is representative of an infant seated on the baby seat; the parents were seated on a swivel chair immediately behind the infant.

4.4.1.3 Procedure

Two experimenters were always present during the entire session. Infants were given enough time to warm up, during which the parent(s) received information about the procedure to follow. All procedural queries were clarified prior to the start of the preparatory phase. However, questions regarding the purpose of the study were answered only at the end of the session in order to minimize parental influences on infants' behavior during the session. After obtaining written parental consent and the infant was ready, we moved to the EEG room. Most infants sat on the parent's lap during the preparation of the cap. Some infants were allowed to play with toys on a mat due to their restlessness on the parent's lap. Experimenter 1 prepared the EEG cap and experimenter 2 played with the infants to distract them. At the end of the preparation, infants were seated on a baby seat attached to a table (as shown in Figure 6) and the parent was seated closely behind so that they could intervene if necessary. Parents were requested to refrain from reorienting the infant's attention to the task and from talking to the infant unless the infant became restless or unhappy. In addition, parents were told to intervene by holding the infant's hands together if he or she tried to reach for the electrodes or the EEG cap. Further, in case the infants were unhappy and the attention getters did not calm them down, the experiment was paused and they were allowed to play with toys or get a sip of water before resuming the session. When all strategies and distractions failed, and the infants were unwilling to continue, the experiment was stopped. The experiment was conducted in the following manner described below, with the action observation phase always presented first and then followed by the action execution phase[14]. Both the action observation and action execution phases were conducted on the same day.

Action observation. This phase was conducted using a between-subject design. Infants watched short videos of either the social or the nonsocial condition displayed on an LCD computer screen (51.50cm X 32.00cm) at a distance of approximately 80cm. The videos were presented using Presentation (© Neurobehavioural Systems, Inc) in eight blocks of 20 trials, with two attention getters, one presented at the beginning of each block and the other after 10 trials. Within each block, 10 videos were presented with the agent executing the action from the left side of the screen and the next 10 videos from the right or vice versa. Each block also comprised of equal number of trials from both agents producing the action, alternating between the first and second half of the blocks. The presentation scripts also contained codes for the implementation of ‘emergency’ attention getters, when necessary. The side of presentation, the order of the agents producing the back-of-hand action and the order of the blocks were counterbalanced across participants such that there were four different versions of stimuli presentation for both the social and nonsocial conditions. Infants watched for as long as they were willing. If the situation demanded, infants were also given a break to

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[14] Action execution and action observation require different levels of engagement from the infants. While infants participate actively in the former, the latter is passive and monotonous. To minimize the risk of infants’ boredom and fatigue influencing their behavior during action observation, it is preferable to conduct it first. In contrast, due to the interactive nature of action execution and the active participation from infants, the experimenters are able to better motivate the infants to perform. Therefore, it poses lesser risk to conduct action execution as the second phase compared to action observation.

take a sip of water or play briefly with a toy before resuming the presentation of the stimuli.

Action execution. For this phase of the experiment, the seating positions of the infant and the parent were rotated 90° to their right, such that both the infant and the parent sat in a profile position towards the video camera, as illustrated in Figure 6. The cardboard cabin was aligned facing the infant, with the ramp placed along the position marked on the centre of the table. In addition, the ramp itself and its opening were narrow which prevented the objects from swaying to the sides. A piece of white cardboard was placed under the armrest of the baby seat so that the sliding objects stopped at that point and did not fall off the table.

Experimenter 1 always stood behind the mobile booth while presenting the objects. To begin with, the experimenter rang a wireless doorbell to get the infants' attention. Then, she appeared from above the center of the cabin to reveal herself and an object by saying "*Name of the infant, Guck Mal*" (Name, Look here!). After the infant had seen the object, the experimenter hid behind the mobile booth and after three seconds, she slid the same object through the ramp. A mobile camera affixed behind the booth was used for the purpose of keeping track of the infant's behavior after the object was presented. After the infant grasped the object, the experimenter made her way towards the infant to retrieve the object. Two blocks of 15 colourful objects were presented to the infants randomly or until the infants were willing to perform the task.

4.4.1.4 EEG Recording

EEG was recorded using Brain Vision Recorder with actiCAP 30 active ag/agcl electrodes connected to the actiCHamp ampliflier (©Brain Products, GmbH), with the vertex electrode, Cz, used as the reference and at a sampling rate of 500Hz. The ocular electrodes were not used with infants due to the discomfort they caused and infants' low acceptance of these electrodes on their faces. However, the previously detached TP9 and TP10 channels were also not used with the infants. Electrode impedance levels were reduced with the help of preheated (36° C) conductive gel and impedance levels under 30kΩ were accepted for infants due to their limited patience during preparation.

4.4.1.5 EEG Analyses

Action execution. Infants' reaching behaviour for each trial was coded offline using the synchronized EEG and video data using Brain Vision Analyzer (©Brain Products). Codes were set for the onset and the completion of the action and were named 'action begin' and 'action end', respectively. Next, the data were digitally filtered between 0.1Hz and 100Hz using the infinite impulse response (IIR) filter, implemented as a Butterworth zero-phase shift filter in Brain Vision Analyzer. Data from infants that did not grasp at least four objects or those who required additional encouragement to reach for objects were discarded from this initial analysis (N = 4). The average time taken by the remaining infants (N = 63) to grasp objects across trials (i.e., the duration from 'action begin' to 'action end') was about 1200ms. Therefore, EEG data were divided into short segments of 3200ms, i.e., 1600ms before and 1600ms after the onset of reaching. A duration of 200ms, starting from 1200ms before the onset of the reaching action, was considered for baseline correction. All segments, which comprised of movements and head turn away from the mobile booth during the baseline period were discarded. The remaining segments with artifacts were discarded using the semi-automatic and manual modes. To elaborate, EEG data from individual channels for each segment were set to be marked as noisy if the amplitudes of the signals were higher than 200µv; 200ms before and after this point were also marked as noisy. Subsequently, the noisy segments were rejected via manual inspection. Noisy channels were interpolated, however, restricting this function to not more than three channels. Datasets with more than three noisy channels were discarded. In the end, infants (N = 21) who contributed a minimum of four artifact-free trials were included in the final analysis. The artifact-free trials were exported as .mat files for time-frequency analysis using WTools and the same steps elaborated in experiment 1 were followed.

Infants (N = 11) in the social group contributed a mean of 5.18 artifact-free trials (SD = 1.32, Range = 4-8) and in the nonsocial group (N = 10), a mean of 5.60 artifact-free trials (SD = 3.02, Range = 4-14). Combined, infants (N = 21) contributed a mean of 5.38 artifact-free trials (SD = 3.81, Range = 4-14) in the action execution phase. It should be noted that the social and nonsocial group only refers to the stimuli infants watched in the action observation phase but there were no procedural differences during action execution.

Action observation**.** Analyses of infants' looking behaviour and movements were initially performed using the synchronized EEG and video data with Brain Vision Analyzer (©Brain Products). Segments where infants blinked, made arm movements or other general movements, did not look at the monitor, and used a pacifier or placed fingers/toys in the mouth were immediately discarded by means of manual inspection. After this step, the preprocessing of the data and time-frequency analysis were completed following the same procedure as experiment 1.

Infants (N = 18 in each group) contributed a mean of 15.6 trials (SD = 14.78, Range = 5-56) in the social condition and a mean of 10.5 trials (SD = 6.36, Range = 5-25) in the nonsocial condition (the difference between the total number of trials contributed in each condition was not significant: $t_{(23.09)} = 1.347$, $p = 0.191$, two-tailed. As equality of variance could not be assumed in accordance with Levene's test, the corrected values are reported).

4.4.1.6 Frequency & Channel Selection

Previous infant studies have examined the 3Hz individual mu frequency range for each infant during action execution to guide the analyses for the action observation phase (for example, Ruysschaert et al., 2013; Southgate et al., 2009, 2010; Warreyn et al., 2013). However, this method poses a couple of problems. Firstly, it could be possible that infants who provide sufficient artifact-free data for the action execution phase do not provide enough data for the action observation phase. Therefore, this discrepancy would prevent direct comparisons between the two phases due to the missing data. Secondly, owing to the difficulty of obtaining artifact-free data from infants, following such a method would also result in very small sample sizes, thereby effecting the robustness of the results. Therefore, we examined the established mu frequency range of 6-9Hz for infants (Cuevas et al., 2014; Marshall et al., 2002; Marshall & Meltzoff, 2011).

The results from experiment 1 revealed significant mu desynchronization in both the central and parietal regions. However, in the adult experiment, the objective was to confirm whether the social-contextual factors modulated mu activity and not whether an overlap between action execution and action observation would be evident. While early EEG studies with adults have provided evidence that self-executed movements elicited mu desynchronization bilaterally (Derambure et al., 1999; Stancák & Pfurtscheller, 1996), infant EEG findings over the past decade have been inconsistent (as elaborated in section 1.7.2 of this thesis). In line with the findings and procedures from previous infant EEG studies, we decided to separate the regions into left and right hemispheres, while also avoiding the analysis of only individual channels. Therefore, the central channels from the adult experiment were extended to include the left fronto-central (C3, FC1, FC5) and the right fronto-central (C4, FC2, FC6) regions and the parietal channels were extended to include the left centro-parietal (P3, CP1, CP5) and the right centro-parietal (P4, CP2, CP6) regions. In addition, occipital alpha activity (O1, Oz, O2) was analyzed separately, in keeping with the previous recommendations.

4.4.1.7 Statistical Analyses

For action execution, a repeated measures ANOVA was computed to assess between-subject differences of group, if any, followed by within-subject factors including time and region. For action observation, the omnibus repeated measures ANOVA was computed by including both within-subject (region, action phases) and between-subject (condition) factors. Similar to experiment 1, results from pairwise comparisons were examined to resolve interactions, where relevant, and one-tailed results from follow-up t-tests are reported for the same reasons elaborated previously.

4.4.1.8 ERP Nc Component

A key difference between the social and nonsocial conditions was the presence of an additional person in the social setting, which possibly made the videos more interesting for infants because there were more faces to process (Frank et al., 2009; Slater et al., 2010). In order to rule out the possibility that infants may have been more attentive to the social condition due to this reason, we analyzed the infant ERP Nc (Negative central) component, peaking between 400 and 800ms at the frontal and central leads (Fz, Cz) (Courchesne et al., 1981; Richards et al., 2010). If infants' processing of the two conditions could be attributed to differences in attention alone, then we would expect to find a significant difference in the Nc amplitudes between the two groups.

For the ERP analysis, only data from the final sample of infants included in the action observation phase was further analyzed. The data were segmented into shorter epochs lasting 1600ms, i.e., 400ms before and 1200ms after the beginning of the target conditions (from the time the agents were visible on the screen) and did not correspond to the onset of the agent's action. After completing the preprocessing steps as explained previously, the ERP peak detection procedure was implemented based on the function available in Brain Vision Analyzer (©Brain Products). A 400ms duration, starting 600ms before the agent(s) appearance on the screen was chosen for baseline correction. We looked at the maximum negative deflecting peak between 400 and 800ms after stimulus onset. The amplitudes of the Nc peak and the average activity between 400 and 800ms were analyzed from channels Fz and Cz combined.

Infants (N = 18 in each group) contributed a mean of 26.44 segments (SD = 17.55, Range = 10-51) in the social condition and a mean of 23.33 segments (SD = 13.31, Range = 7-48) in the nonsocial condition for the ERP analysis. The difference between the total number of trials contributed in each condition was not significant: $t_{(34)} = 0.599$, $p = 0.533$, two-tailed). For the statistical analyses, the difference between the social and nonsocial conditions in the amplitude of the ERP Nc component and the average activity between 400 and 800ms were computed using t-tests (one-tailed).

4.4.2 Results

4.4.2.1 Mu Rhythm Activity

Action execution. Figure 7 illustrates the mu activity exhibited during action execution across the cortical areas. A 4x2 repeated measures ANOVA with region (left fronto-central, right fronto-central, left centro-parietal and right centro-parietal) as the within-subject factor and group (social, nonsocial) as the between-subject factor did not reveal any main effect of region ($F_{(3,57)} = 1.872$, $p = 0.145$, $\eta_p^2 = 0.090$) or group ($F_{(1,19)} = 0.127$, $p = 0.726$, $\eta_p^2 = 0.007$) or a significant interaction. Therefore, we considered all infants (N=21) as one group.

A follow up 2x4 repeated measures ANOVA with time (baseline, action phase) and region revealed a main effect of time ($F_{(1,20)} = 7.375$, $p = 0.013$, $\eta_p^2 = 0.269$) with significant mu desynchronization during the action phase (Mean = -0.116, SE = 0.043). We did not find a main effect of region ($F_{(3,60)} = 1.966$, $p = 0.129$, $\eta_p^2 = 0.090$) nor a significant interaction between the two factors. This indicated that the action execution phase generated a global pattern of mu desynchronization across all the cortical regions.

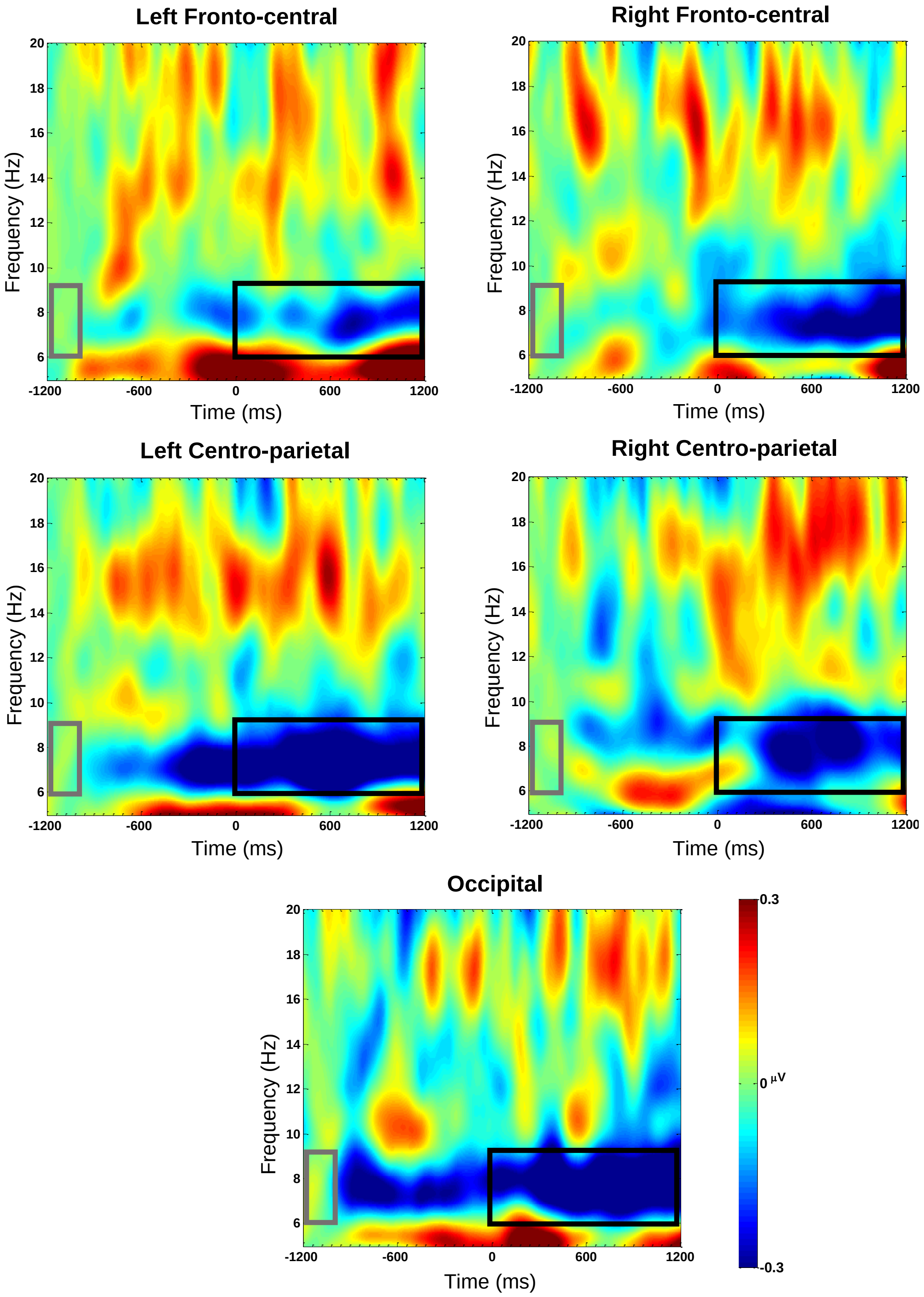

Figure 7: Mu activity during action execution (experiment 2, study 1)

The areas marked in grey and solid black boxes represent the baseline and the action phase, respectively, and the corresponding infant mu frequency range (6-9Hz) in the left fronto-central, right fronto-central, left centro-parietal, right centro-parietal and the occipital regions.

One-sample one-tailed t-test revealed a significant occipital alpha desynchronization ($t_{(20)}$ = 2.011, p = 0.029) during action execution. As revealed by the paired sample t-tests, mu desynchronization in the left fronto-central, right fronto-central, left centro-parietal and right centro-parietal was not significantly greater than the occipital alpha desynchronization (all *p*s > 0.1).

Action observation. Table 3 provides a summary of the mu desynchronization results from experiment 2. A 2x4x2 omnibus repeated measures ANOVA with action phase (action-unfolding, action-complete) and region (left fronto-central, right fronto-central, left centro-parietal, right centro-parietal) as the within-subject factors and condition (social, nonsocial) as the between-subject factor revealed a main effect of region ($F_{(3,102)}$ = 4.831, p = 0.003, η_p^2 = 0.124). Pairwise comparisons from the omnibus ANOVA revealed significant mu desynchronization in the right centro-parietal region (Mean = -0.029, SE = 0.069) when compared to the left fronto-central (Mean = 0.189, SE = 0.058, p = 0.006) and the right fronto-central (Mean = 0.173, SE = 0.058, p = 0.009) regions.

Further, the results of the omnibus ANOVA also revealed a significant interaction between action phase x condition ($F_{(1,34)}$ = 18.095, $p < 0.001$, η_p^2 = 0.347) and a marginal interaction between action phase x region ($F_{(3,102)}$ = 2.355, p = 0.076, η_p^2 = 0.065) and are resolved below.

Action phase x condition. Pairwise comparisons from the omnibus ANOVA revealed significant mu desynchronization in the action-complete action phase of the social condition (Mean = -0.026, SE = 0.070) when compared to the nonsocial condition (Mean = 0.249, SE = 0.070, p = 0.009). Further, this mu desynchronization in the action-complete phase of the social condition was significantly greater than the action-unfolding phase (Mean = 0.074, SE = 0.061, p = 0.049).

Action phase x region. For the action-unfolding phase, pairwise comparisons from the omnibus ANOVA revealed significant mu desynchronization in the right centro-parietal region (Mean = -0.013, SE = 0.075) compared to the right fronto-central region (Mean = 0.151, SE = 0.056, p = 0.040). For the action-complete phase, mu desynchronization elicited in the right centro-parietal region (Mean = -0.044, SE = 0.071) was greater than the left fronto-central (Mean = 0.262, SE = 0.072, p = 0.002) and the right fronto-central (Mean = 0.195, SE = 0.073, p = 0.008) regions.

Overall, pairwise comparisons indicated that significant mu desynchronization was elicited in the social condition and during the action-complete action phase. Further, as evident from the pairwise comparisons results, mu desynchronization in the right centro-parietal region differed significantly when compared to the left and right fronto-central regions. However, comparisons between mu activity in the left centro-parietal region and the other regions did not reveal significant differences. Therefore, for the follow up t-tests, we examined mu activity for each region in both the action phases separately.

One-sample one-tailed t-tests revealed significant mu desynchronization only in the right centro-parietal region for the action-complete phase of the social condition (Mean = -0.205, SE = 0.104, $t_{(17)}$ = -1.977, p = 0.032) but the nonsocial condition did not elicit mu desynchronization (Mean = 0.117, SE = 0.097). While the action-unfolding phase did not elicit mu desynchronization in the right centro-parietal region for the social condition (Mean = 0.032, SE = 0.115), mu desynchronization elicited in the nonsocial condition was negligible (Mean = -0.029, SE = 0.095, $t_{(17)}$ = -0.305, p = 0.382).

Further, independent one-tailed t-test revealed a significant difference between the social and nonsocial conditions in the right centro-parietal region for the action-complete phase ($t_{(34)}$ = -2.266, p = 0.015). The results are spectrographically represented in Figure 9.

The other regions, left fronto-central, right fronto-central and left centro-parietal, did not elicit significant mu desynchronization in both the social and the nonsocial conditions. A spectrographical representation of the mu activity elicited in these regions for both the conditions is provided in appendix A.

Table 3: Results from action observation of experiment 2, study 1

Overview of the (a) ANOVA and (b) t-test results from experiment 2. All results indicate significant mu desynchronization comparisons

(a) Main effect	Interaction
Region ($p=0.003$) • RCP > LFC ($p=0.006$) • RCP > RFC ($p=0.009$)	**Action-phase*condition** ($p<0.001$) • **Action-complete**: social > nonsocial ($p=0.009$) • **Social**: action-complete > action-unfolding ($p=0.049$) **Action-phase*region** ($p=0.076$) • **Action-unfolding**: RCP > RFC ($p=0.040$) • **Action-complete**: RCP > LFC ($p=0.002$) RCP > RFC ($p=0.008$)

(b) One-sample t-test^{+}	Independent t-test^{+}
Social: **Action-complete** **RCP** ($p=0.032$)	**Action-complete:** **RCP**: social > nonsocial ($p=0.015$)

$^{+}$ One-tailed significance
LFC: left fronto-central; RFC: right fronto-central; RCP: right centro-parietal
> denotes greater mu desynchronization for the factor on the left of the symbol compared to that on the right of the symbol

As revealed by the one-sample one-tailed t-test, we did not find significant occipital alpha desynchronization for the action-complete phase in the social condition (Mean = -0.039, SE = 0.094, $t_{(17)} = -0.413$, $p = 0.342$). Occipital alpha desynchronization was not elicited in the nonsocial condition (Mean = 0.236, SE = 0.122) during the action complete phase. The action-unfolding phase did not elicit occipital alpha desynchronization in both conditions. A spectrographical representation of the occipital alpha activity for both the conditions is provided in appendix A.

As evident in the data, mu desynchronization for the social condition was dominant in the right hemisphere. Therefore, we considered additional factors to examine their influence on the results, specifically, the side of presentation and the hand preference. Among the final segments included for the social condition, paired t-test revealed that there was no significant difference in whether infants watched actions unfolded from the left or the right side of the screen more ($\text{Mean}_{\text{Left}}$ = 7.55, SE = 1.93; $\text{Mean}_{\text{Right}}$ = 8.11; SE = 1.72, $t_{(17)}$ = -0.480, p = 0.319, one-tailed).

Further, we examined these infants' hand preference from the action execution data and divided them further into two groups that predominantly preferred using the left (N = 10) or the right hand (N = 8). Independent t-test revealed no significant difference in right centro-parietal mu desynchronization between the left (Mean = -0.174, SE = 0.130) and the right hand (Mean = -0.245, SE = 0.176) preferring infants ($t_{(16)}$ = 0.330, p = 0.373, one-tailed). Therefore, the side of presentation or hand preference cannot explain the right-lateralized results.

4.4.2.2 ERP Nc Component

Figure 8 shows the ERP Nc component elicited from both the social and the nonsocial conditions. One-tailed independent t-tests comparing the averaged ERP Nc component over channels Fz and Cz revealed no significant difference in the amplitude of the Nc peak between the social (Mean = -12.10, SE = 1.45) and the nonsocial conditions (Mean = -13.28, SE = 0.91, $t_{(34)}$ = 0.687, p = 0.248). Further the difference in the overall mean activity between 400 and 800ms was also only marginally significant ($\text{Mean}_{\text{social}}$ = -4.90, SE = 1.56; $\text{Mean}_{\text{nonsocial}}$ = -7.66, SE = 0.94, $t_{(34)}$ = 1.514, p = 0.069, one-tailed).

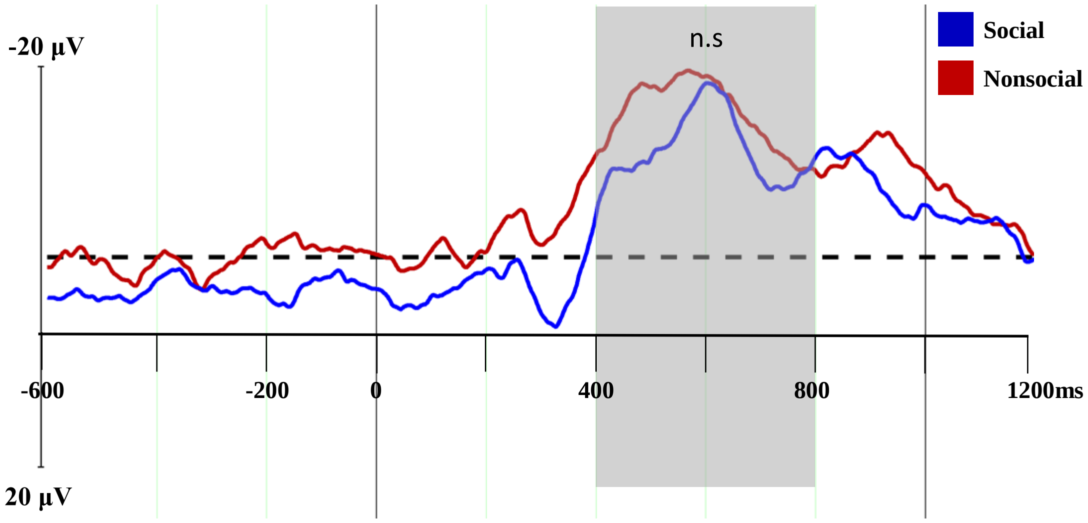

Figure 8: ERP Nc component averaged over channels Fz and Cz (experiment 2, study 1)

The grey area represents the time duration analyzed, i.e., between 400 and 800ms. Note that '0' on the time line represents the start of the video when the agents were visible and not the onset of the action.

4.4.3 Discussion

The findings revealed that 9-month-old infants showed significant mu desynchronization during action execution across cortical regions, indicating the coordination of both action and attentional processes for self-executed movements (Fox et al., 2016). For action observation, we found significant mu desynchronization for the social condition in the right centro-parietal region, although only for the action-complete phase. We did not find significant occipital activity during action observation and the differences in the amplitude or mean activity of the ERP Nc component between the two conditions did not reach significance. All these findings taken together revealed that infants inferred the meaning of the back-of-hand action as meaningful under the social condition. Lower level stimulus features or differences in attention did not by themselves drive the effects. Further, we provided evidence that prior experience does not precede goal attribution and action understanding as postulated by the direct-matching account.

However, unlike the adults, mu desynchronization for the infants was elicited only in the action-complete phase. The reason for the lack of mu desynchronization in the action-unfolding phase could be attributed to infants watching fewer trials intermittently owing to their low attention span, which resulted in lesser probability for anticipating the ensuing action on the screen. Moreover, the form of the palm was unclear during most part of the action-unfolding phase, i.e., up to 800ms after action onset, which may have delayed goal attribution or it may be possible that infants were generally slower in processing the observed action when compared to the swiftness and advanced inferential ability of the adults.

Both experiments 1 and 2 successfully showed that under appropriate circumstances, both adults and infants attribute goals to the observed back-of-hand action. However, when considering real-life complex interactions, a goal object may not always be present. In a typical social setting, a third-party observer or a third person who joined the other pair of people at a later time does not have complete access to the communication that transpired earlier between the two people. Therefore, in a social situation, where one person unfolds the back-of-hand action in the presence of a social partner intransitively, the observer does not find it unusual but probably assumes that the person is requesting for something and that the referent object still exists, albeit under the table or inside a bag or a pocket. However, 9-month-old infants may find such a situation complex and without appropriate cues and background information, may find it difficult to infer any meaning. In keeping with the contextual factors, a visible object may play an important role for infants. To investigate, a third experiment was conducted, where a group of 9-month-old infants watched videos from the social condition without the object present on the table (object-absent condition). We predicted that this condition would not elicit mu desynchronization because in the absence of an object, infants would not be able to detect the intention of the observed back-of-hand action.

4.5 Experiment 3: infants (object-absent)

4.5.1 Methods

4.5.1.1 Participants

Sixteen infants (f = 7, mean age = 291 days) were included in the final sample. Data from an additional 25 infants could not be included due to experimenter error (4), noisy data (2) and for not providing a minimum of 5 artifact-free trials (19). The attrition rate for this sample was 60.97%.

4.5.1.2 Stimuli

Action observation. The same videos presented in the social condition of experiments 1 and 2 were modified to exclude objects on the table (see Figure 4). No other elements were modified.

4.5.1.3 Procedure & Analyses

The procedures for conducting the action observation phase, recording EEG, analysis of data (preprocessing and time-frequency analysis) were identical to experiment 2. The analysis of the ERP Nc component was not required due to the social setting of the object-absent condition, where a recipient was always present unlike the nonsocial condition of experiment 2.

Based on the results of experiment 2, mu activity in the right centro-parietal region during the action-complete phase was relevant for the analysis. Therefore, the average mu activity (6-9Hz) in the right centro-parietal region (P4, CP2, CP6) was further analyzed.

Statistical analysis comprised of only t-tests, due to the focus on a specific region and one-tailed results were examined. Occipital (O1, Oz, O2) alpha activity was analyzed separately.

Infants (N = 16) contributed a mean of 15.12 trials (SD = 9.39, Range = 10-33) in the object-absent condition (and did not differ significantly from the number of trials in the social condition of experiment 2: $t_{(32)} = 0.113$, $p = 0.911$, two-tailed).

4.5.2 Results

Figure 9 shows mu activity in the right centro-parietal region for the social, nonsocial and object-absent conditions. The action-complete phase of the object-absent condition did not elicit mu desynchronization in the right centro-parietal region (Mean = 0.027, SE = 0.090).

One-tailed independent t-test comparing mu activity in the right centro-parietal region between the social and object-absent conditions revealed a near significant difference ($t_{(32)} = -1.669$, $p = 0.052$) between the two conditions.

The object-absent condition did not elicit occipital alpha desynchronization (Mean = 0.190, SE = 0.189). An overview of the mu activity elicited in the remaining regions for the object-absent condition is provided in appendix A.

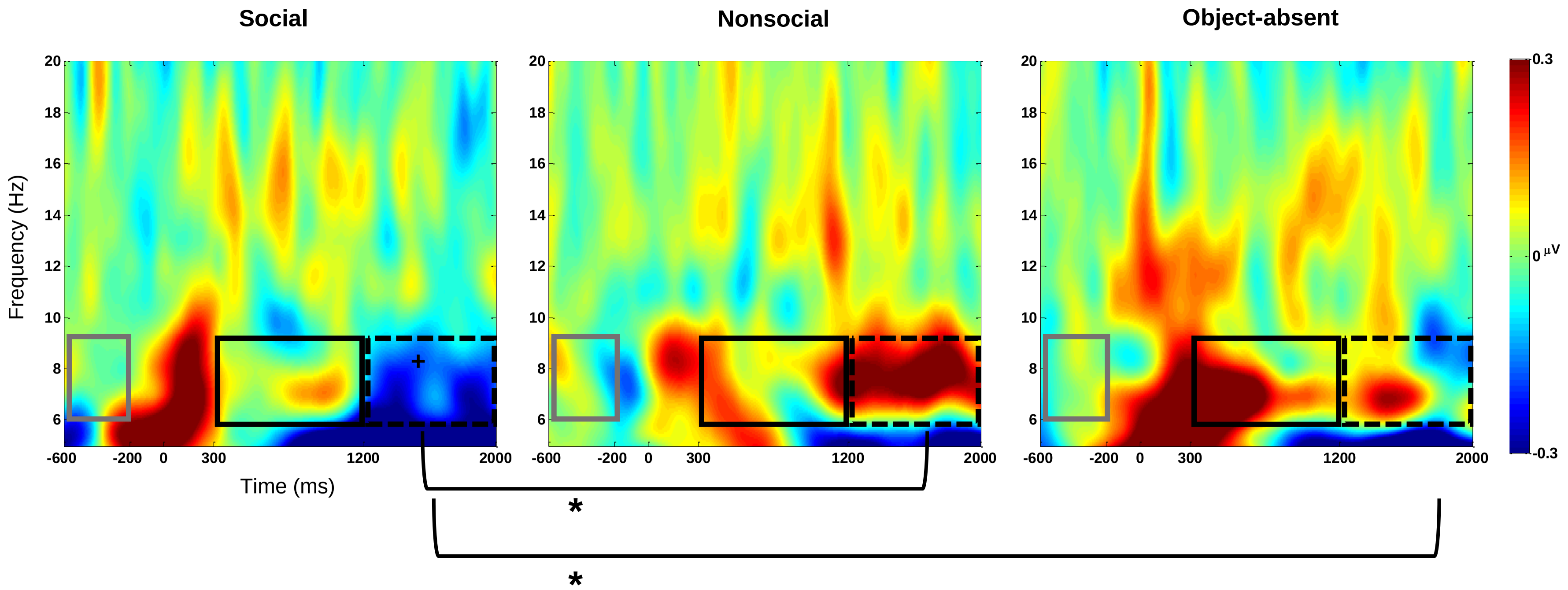

Figure 9: Mu activity during action observation (experiments 2 & 3, study 1)

This figure illustrates the mu activity elicited in the right centro-parietal region for the social, nonsocial and object-absent conditions.

The areas marked in grey, solid black and dashed red boxes represent the baseline, action-unfolding and action-completion phases, respectively, in the infant mu frequency band of 6-9Hz.

+$p < 0.05$ significant mu desynchronization when compared to 0 (one-sample t-tests)

**$p < 0.06$ significant mu desynchronization when compared between conditions (Independent t-tests)*

4.5.3 Discussion

As hypothesized, we did not find significant mu desynchronization in the object-absent condition, suggesting that 9-month-old infants did not attribute a goal to the observed back-of-hand action in the absence of an object. There is evidence from behavioural studies that 12-month-old infants comprehend and point to the location of absent objects if they were previously exposed to the items in the same location (Bohn et al., 2015, 2018; Liszkowski et al., 2009) but not if they were hidden or inaccessible (Osina et al., 2017). Older infants were able to process requests for absent objects, if there was a previous verbal reference to such objects (Ganea & Saylor, 2007) or if the object belonged to a category (Osina et al., 2018). Thus, it is possible that 9-month-old infants in this experiment did not comprehend the back-of-hand action as goal-directed because they perhaps required a clear goal object to make sense of the communicative purpose of the action. Further, these infants were also too young to comprehend absent references, as it seems from existing literature that such a comprehension emerges around the first birthday. It is more likely that younger infants associate communicative actions with visible object goals. Our findings further emphasize on contextual factors, which play a pivotal role on goal attribution and action understanding.

4.6 General Discussion

The purpose of the study was to investigate the role of social-contextual factors on the perception of the goal-directedness of the back-of-hand action. Groups of adults and 9-month-old infants watched videos of an agent producing the back-of-hand action in the social, nonsocial and object-absent conditions. Infants also performed an action execution phase, where they grasped several objects.

For action observation, our main finding was that observing the back-of-hand action in the social condition elicited significant mu desynchronization in the central and parietal regions for adults, and in the right centro-parietal region for infants when compared to the nonsocial condition. The third condition, where infants observed the object-absent condition, did not elicit mu desynchronization. For action execution, we found a global pattern of mu desynchronization across the cortical areas.

Similar to the recent infant EEG studies (Cannon et al., 2016; Debnath et al., 2019; Filippi et al., 2016; Marshall et al., 2013b; Meyer et al., 2016; Montirosso et al., 2019; Yoo et al., 2016), we also found mu desynchronization in the occipital region for the action execution phase. Occipital alpha desynchronization has been associated with selective and focused attention (Klimesch, 2012). Undoubtedly, the action execution phase necessitated constant attention from infants from the time their attention was directed with reference to the object up until they reached for it. The fact that infants had seen the object but had to wait a few seconds before it arrived through the ramp may have created a sense of anticipation for the unfolding trial and for the succeeding trials and therefore, resulted in increased attention. Further, this global pattern of mu desynchronization suggested coordinated action and attention processes during action execution (Fox et al., 2016).

The action observation findings, especially from experiment 2, provided evidence that a direct match between the observed and executed action was not necessary to comprehend action goals, thereby providing evidence against the direct-matching account of action understanding (Rizzolatti et al., 2001). 9-month-old infants in the experiment perceived the back-of-hand action as goal-directed irrespective of the fact that they do not produce this gesture to request for objects at this age. In light of the evidence that infants reach for distant objects communicatively in the presence of another person (for example, Ramenzoni & Liszkowski, 2016), it is possible that infants in this experiment were able to emulate the same situation from a third person perspective, a process postulated by the action reconstruction account (Csibra, 2008). However, the findings clearly suggest that action understanding is not limited to instrumental actions. Rather, it encompasses a more complex yet flexible system, integrating various social-contextual and communicative aspects as well. Further, instrumental and communicative actions may be interlaced early in development as opposed to being independent systems as Csibra (2003) postulated, and hence, emulative processes may be applicable to both these types of actions.

While the findings from the adult experiment reciprocally supported the adults' verbal reports of their perception of the stimuli, the interpretation of the infant results may lead to an important question within the context of their motor development. Specifically, the data do not conclusively specify whether mu desynchronization in the social condition suggested that infants perceived the intention of the back-of-hand action or whether they anticipated the social partner to grasp the object due to the spatial proximity of the objects. Given that by 9 months, infants possess an increasing ability to predict reaching and grasping actions (Hespos et al., 2009), and in the light of the current evidence that the object-absent condition did not elicit mu desynchronization, this ambiguity increases further. However, one needs to consider three important points before conclusions are drawn. Firstly, it should be noted that there were no familiarization trials in the study. This means that infants neither watched objects being grasped nor did they see the social response to the back-of-hand action. Secondly, the action execution phase was always conducted after action observation. Therefore, infants could by no means (temporally within the recording duration) associate their own reaching/grasping actions to that of the recipient in the video. Finally, if infants simply anticipated the grasping action of the social partner, mu desynchronization should have been elicited even before the completion of the back-of-hand action on the screen. However, significant mu desynchronization was evident during the action-complete phase when the back-of-hand configuration of the hand was apparent. Therefore, while the fact that infants anticipated a grasping response cannot be ruled out entirely given the data available, this anticipation cannot be arbitrary. It is more likely that if infants anticipated the social partner to respond (i.e., grasp the object or handover the object), it may be only because they understood that the back-of-hand action in the social condition affords a response. In other words, mu desynchronization in the social condition could be the result of a combined process, where understanding the goal and anticipating the response are inter-dependent.

Further, while we found significant mu desynchronization in the central and parietal regions for the adults in the social condition of the action observation phase, mu desynchronization was localized to the right centro-parietal region in the infants, which was not influenced by the side of presentation infants watched or their hand preference. This right-lateralized activity is consistent with studies suggesting that the right hemisphere plays a specialized role in processing social interactions and emotions (Krall et al., 2015; Semrud-Clikeman et al., 2011). Further, our evidence is also in line with recent infant findings that provided evidence for the association between social factors and mu desynchronization (Rayson et al., 2016; Reid et al., 2011).

To the best of our knowledge, we provide the first EEG evidence that contextual cues enable the attribution of embedded and distant goals of transitive actions that do not involve touching the object or fulfilling the goal. In contrast, the extant evidence from adult EEG research is based on intransitive actions such as finger movements (Babiloni et al., 2002; Llanos et al., 2013), pantomimes (Quandt et al., 2012), or dance sequences (Nota et al., 2017) that are not object-directed. Infant EEG studies incorporating social and/or communicative situations that embed distant goals to investigate action understanding are rare. Therefore, future infant EEG studies need to look into this aspect to gain a better understanding of infants’ action perception mechanisms under naturally-occurring circumstances.

5 Is the Back-of-hand an Efficient Instrumental Action?

Research highlights:

- *9-month-old infants watched videos of unfulfilled reaching and back-of-hand actions in varying object location and action congruency conditions based on the position of the object (bottom or top). They also reached for and grasped various objects.*
- *While the action execution phase elicited a global pattern of mu desynchronization, observing the congruent-reach and congruent-backofhand actions did not elicit mu desynchronization.*
- *However, the incongruent-reach condition elicited significant mu desynchronization in the right centro-parietal region.*
- *The results suggest that contextual cues beyond the implication of action fulfillment are necessary to infer goals.*

Keywords: infants, mu rhythm, action understanding, back-of-hand, reach, context

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5.1 Abstract

In typical action understanding studies, the back-of-hand action is incorporated as the control condition and compared with reaching and grasping actions. However, some situations may justify the use of the back-of-hand action to attain instrumental goals, such as when approaching a falling object (in order to obtain it). Similarly, goals for an observed reaching action may also be attributed even before the action is completed. To examine the question of whether action understanding entails encoding distant goals, two groups of 9-month-old infants watched unfulfilled grasping and back-of-hand actions that represented either action and object location congruence or incongruence in relation to the position of the goal objects. The objects were placed on a tube-like structure, either close to the tabletop or far above from it. While reaching for objects placed close to the tabletop fulfills action-object congruency, approaching the same objects with the back-of-hand action is incongruent. Similarly, approaching an object placed far above the tabletop with the back-of-hand action may be congruent (because the object may fall off) but approaching the same objects with a reaching action is incongruent. However, neither of these actions were shown to fulfill the goal of obtaining the object. The infants also participated in an action execution phase, where they grasped various objects that were presented with a mechanical claw from either the top or bottom positions corresponding to the conditions they watched in the action observation phase. The results demonstrated a global mu desynchronization during action execution. For action observation, the findings were contrary to the hypothesis. Observing the congruent-reach and congruent-backofhand actions did not elicit significant mu desynchronization. Significant mu desynchronization was exhibited only for the incongruent-reach condition in the right centro-parietal region. These findings suggest that distant instrumental goals are not attributed unless the context incorporates a suitable rationale for its lack of goal fulfillment.

5.2 Introduction

Imagine that the goal is to obtain an apple hanging from a branch of a tree, which is unreachable but is about to break away and fall down. This is an example of a situation that renders the conventional reaching and grasping actions useless and may warrant the use of the back-of-hand shape, with the palm facing upwards to obtain the apple. In other words, observing a person with his arm stretched out in a back-of-hand configuration within this context would result in goal attribution even though the goal is yet to be attained but observing the grasping shape of the palm in the same situation would be meaningless.

In previous behavioural studies with infants, the objects were positioned firmly, usually on a table or a box, at a reachable height, and therefore, this context warranted the use of the grasping action (but not the back-of-hand) as the most efficient means to obtain the object (Hamlin et al., 2008; Krogh-Jespersen & Woodward, 2014; Thoermer et al., 2013; Woodward, 1999). Using EEG with 9-month-old infants, Southgate et al. (2010) provided evidence that observing grasping behind an occluder (similar to Umiltà et al., 2001) elicited significant mu desynchronization when compared to observing the back-of-hand action. In addition, both the actions in a mimed condition[15] did not elicit similar effects, suggesting additionally that the presence or the implication of a goal object is essential for instrumental actions.

With regard to using the back-of-hand instrumentally, only two studies provided evidence that infants perceived this action as goal-directed when associated with salient effects. For example, when the observed back-of-hand action resulted in not only touching objects but also extending the action by pushing them to a new location (Király et al., 2003) or picking up objects using sticky mittens after active training (Biro et al., 2014), 12-month-old infants construed the action as goal-directed. Although the goals

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[15] In the mimed condition, both the grasping and back-of-hand actions were directed towards an empty space on the table with no object present (Southgate et al., 2010).

represented in these studies were typically better suitable for the grasping action, evidence that the back-of-hand action also produces similar salient effects enabled infants to attribute goals to this seemingly meaningless action in an instrumental manner.

Overall, it is not the action alone but the contextual situation that renders one action more efficient than the other does. Therefore, infants were unable to attribute a goal to the back-of-hand when used as a control condition in previous studies more likely because of the restricted context in which the action was used. In other words, both grasping and the back-of-hand actions may serve instrumental purposes within an appropriate context.

In the present study, the factors of context and efficiency were modified in videos of reaching and back-of-hand actions to investigate whether they modulated mu activity in 9-month-old infants. A 2x2 design incorporating different positions of the object (bottom, top) and different hand actions (reach, back-of-hand) presented the opportunity to not only investigate the conventional comparisons between the two hand actions as reported in the extant literature but also to examine the reversal of goal attribution by modifying the context. The first objective was to investigate whether infants would attribute an instrumental goal to the back-of-hand action within an appropriate setting. To examine this question, reaching and back-of-hand actions were placed within the context of varying object positions. Specifically, the objects were placed either close to the tabletop (referred to as bottom) or far above the tabletop (referred to as top), where the former was easily accessible but the latter was placed at a height. In both these positions, the familiarization trials showed that the objects appeared from one end of a tube-like structure and then moved towards the edge in a self-propelled manner. However, in the subsequent test conditions, the last frame depicting the position of the objects at the edge of the tube were presented along with the actions (see Figure 10 and Figure 11).

The more efficient action to obtain objects located at the bottom would be to reach for and grasp them (congruent-reach). However, when an object is located on top and appears to fall off, approaching it with the back-of-hand configuration would be optimal in preventing it from falling down and with the result of obtaining it (congruent-backofhand). However, the reverse combinations of object position and actions would not enable attainment of the object. Specifically, approaching an object located at the bottom with the back-of-hand action (incongruent-backofhand) and approaching an object located on top with the reaching action (incongruent-reach) would be meaningless.

The second objective was to investigate whether the goal of instrumental actions is attributed, even when they seem embedded and distant, and when the objects are not touched. To investigate this question, the goals in the study were shown to be unfulfilled. In other words, neither by means of reaching nor the back-of-hand actions were the objects obtained. Similar to the previous study elaborated in chapter 4, infants were not shown the outcome of the actions and therefore, their understanding of the congruent and incongruent conditions were dependent on their inference from the cues provided by the context. Therefore, if contextual cues are sufficient to attribute goals, then not touching the object should not alter infants' perception.

The specific hypotheses for the study comprised of the following: we hypothesized to find significant mu desynchronization for the congruent-reach condition but not for the incongruent-backofhand, when the objects were placed at the bottom. In addition, we expected to find significant mu desynchronization for the congruent-backofhand condition but not for the incongruent-reach condition, when the objects were placed on top. Further, we expected that mu desynchronization in the congruent-reach condition would be significant when compared to incongruent-reach, and congruent-backofhand would elicit greater mu desynchronization when compared to the incongruent-backofhand condition.

For the present study, 9-month-old infants were recruited because they do not produce the back-of-hand gesture at this age. Although there is no extant literature on the age of emergence of the back-of-hand gesture, infants do not seem to use it until around 22 months (Özçalişkan & Goldin-Meadow, 2005b, 2005b). Therefore, if 9-month-old infants perceived the back-of-hand as an efficient action in the congruent condition, it would also provide further evidence against the direct-matching theory (Rizzolatti et al., 2001), which postulates that action experience precedes action understanding. In addition, if our hypotheses were true, it would support the idea that goal attribution of instrumental actions might not always depend on action completion, as the goal driving a particular action remains valid despite the lack of its fulfillment.

5.3 Methods

5.3.1 Participants

Two groups of 9-month-old infants participated in the study. Data were collected from 91 infants, out of which 46 infants belonged to the bottom group and 45 infants belonged to the top group. All infants participated in the action execution phase.

Action observation. 26 infants (f = 12, mean age = 286 days) were included in the final sample of the action observation phase, with 12 infants (f = 4, mean age = 288 days) in the bottom group and 14 infants (f = 8, mean age = 284 days) in the top group. Data from 65 infants were discarded due to unwillingness (2), technical errors (3) extreme movements or use of pacifier (35) and for not providing a minimum of 5 artifact-free trials (33) for each of the reach and back-of-hand conditions.

Action execution. 34 infants (f = 24; mean age = 288 days) were included in the final sample of the action execution phase, with 19 infants in the bottom group (f = 13, mean age = 289 days) and 15 infants in the top group (f = 11, mean age = 287 days). Data from 57 infants were discarded due to unwillingness or requirement of additional motivation (5), extreme movements and noisy baseline (13) and for not providing a minimum of 4 artifact-free trials (39).

The attrition rates of 72.63% and 64.21% in the action observation and execution phases, respectively is typical of infant EEG and falls within the general anticipated rate (DeBoer al., 2013; Hoehl & Wahl, 2012).

5.3.2 Stimuli

***Action observation*.** This phase comprised of familiarization and test trials, presented using short videos. In the familiarization videos, objects were shown to move in a self-propelled manner from one end of the tube to its edge but they never toppled off the tube for both the bottom and top settings, as depicted in Figure 10. The terms bottom and top indicated the position of the objects placed on a tube-like structure. The bottom position was located close by, about 5cm from the tabletop and the top position was located about 30cm above the tabletop. The familiarization videos also comprised of the corresponding sounds matching the objects shown in the video. For example, a rattle with small bells inside was accompanied by a bell sound in the video; similarly, a chugging sound was included for the video with a toy train. The table was filmed separately and the other elements such as the tube and the objects were superimposed using Adobe After Effects CS6. Six different familiarization videos were created for the bottom and top settings each and the videos were flipped to represent both the left and right sides of the presentation. Each familiarization video lasted 3 seconds.

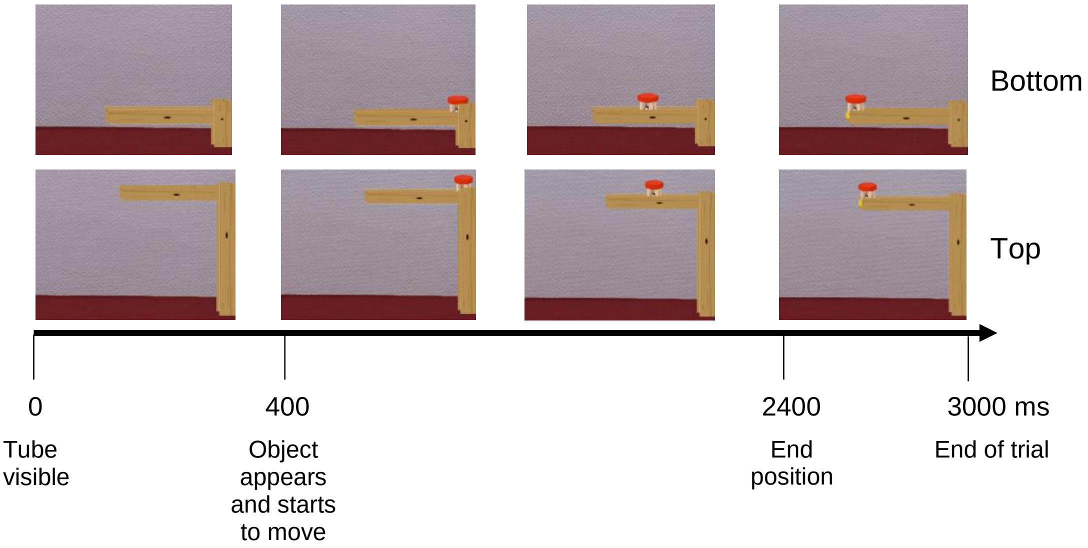

Figure 10: Timeline of the familiarization trials of study 2

Videos depicting reaching and the back-of-hand actions comprised of the test trials in the action observation phase. The agent's face was not visible, instead only the hand movements were shown. The videos lasted 3 or 3.2 seconds, where the first 1000 or 1200ms comprised of a neutral phase depicting a cross on a grey background with a melody (the melody was played only for 400ms in the beginning to attract infants' attention). This was followed by the object phase, where the objects were shown at the edge of the tube, lasting 600ms. In the subsequent action phase, the unfolding of the reach and back-of-hand actions lasted around 600ms from the onset to the final position. The final position was frozen on the screen for the next 900ms. Neither did the hand touch the objects nor did the objects move or fall off during the test trials. The outcome of the observed actions was never shown to the infants. The test trials comprised of four conditions: congruent-reach, incongruent-backofhand, incongruent-reach and congruent-backofhand based on the different combinations of object position and action congruency, as shown in Figure 11.

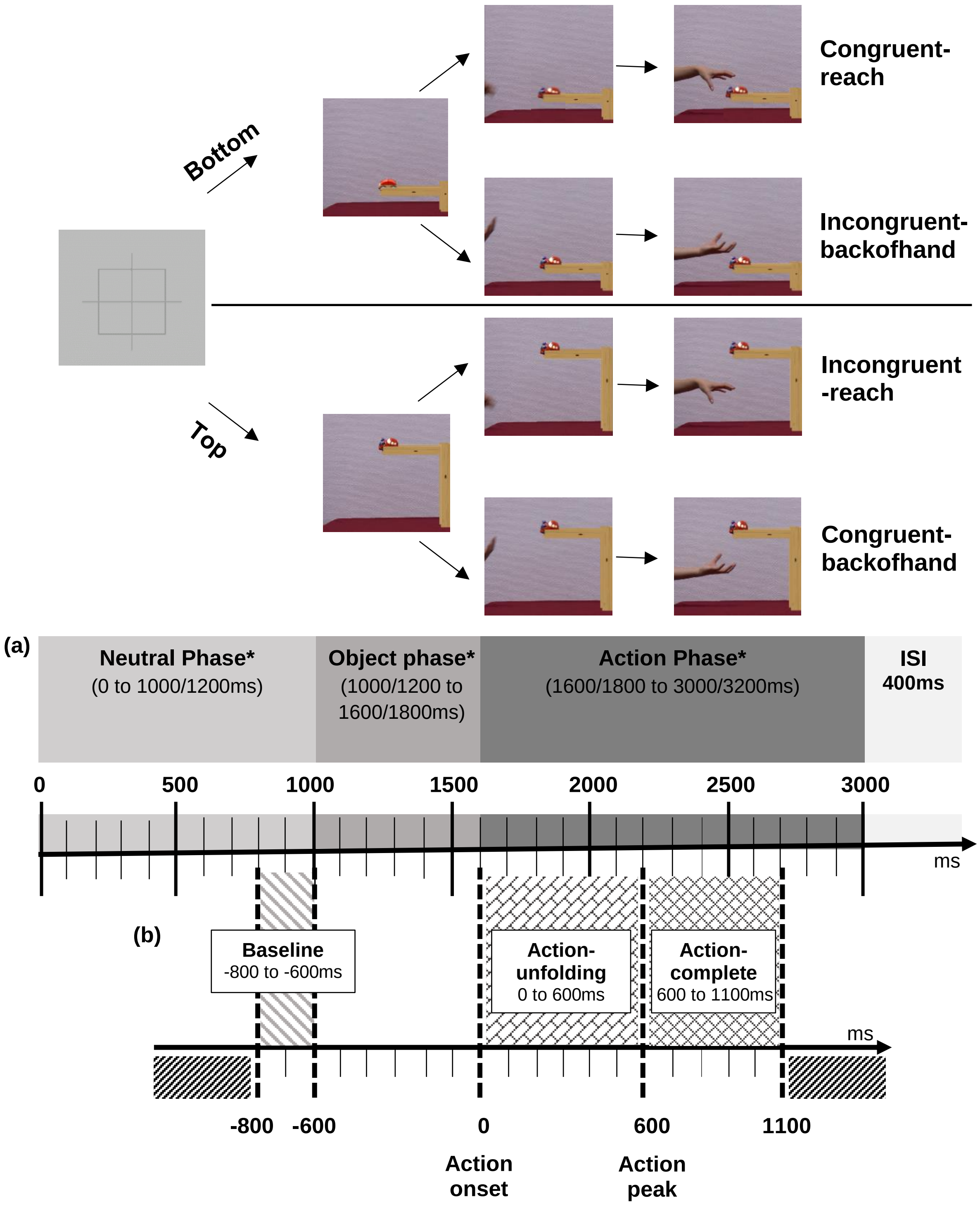

Figure 11: Stimuli presentation and analysis timeline for study 2

**The (a) stimuli videos consisted of varying neutral phases, with half the videos comprising of 1000ms neutral phase (illustrated in this figure). In the other half of the videos, the duration of the neutral phase lasted 1200ms and the subsequent events were pushed further by 200ms. Specifically, the time at action onset was 1800ms, action peak at 2400ms and the end of the action phase at 3200ms. However, the (b) corresponding time points for the analysis remained the same as illustrated in the figure as the data were segmented based on action onset; ISI: inter-stimulus interval.*

▨ - *represents the part of the segment chopped from the analysis phase to eliminate the distortion introduced by the wavelet transform.*

The reach and back-of-hand actions were filmed against a plain white wall using a Panasonic Handycam model number HC-X929. The melodies created for the previous study (chapter 4) were used in the neutral phase. The objects were photographed using a smartphone and then suitably edited for use in the videos. The wooden frames depicting the tube-like structure were created using Adobe Photoshop CS6 and the baseline figure using Microsoft Word 2016. All these individual elements were combined and edited further using Adobe After Effects CS6. Finally, the edited videos were flipped in order to balance the side of presentation during testing.

With regard to the actions, one master video each for both the actions was selected and the objects were superimposed for every trial, thereby controlling the duration of the trials to a millisecond precision. The objects belonged to different categories such as animals, vehicles, play objects such as a ball or a rattle, eatables, and household items such as candle or a small pan. Moreover, different set of objects were used for the familiarization trials and the test trials.

***Action execution*.** This phase comprised of a live paradigm, where infants reached for and grasped various objects. Similar to Southgate et al. (2010), a mechanical claw was used to present the objects to the infants. However, in order to match the position of the objects in the test trials of the action observation phase, a three-sided cabin was created using cardboard with two small cutouts, ‘bottom’ and ‘top’, covered by black curtains, through which the objects were presented to the infants, as shown in Figure 12. The objects comprised of 20 different attractive, colourful, and graspable toys.

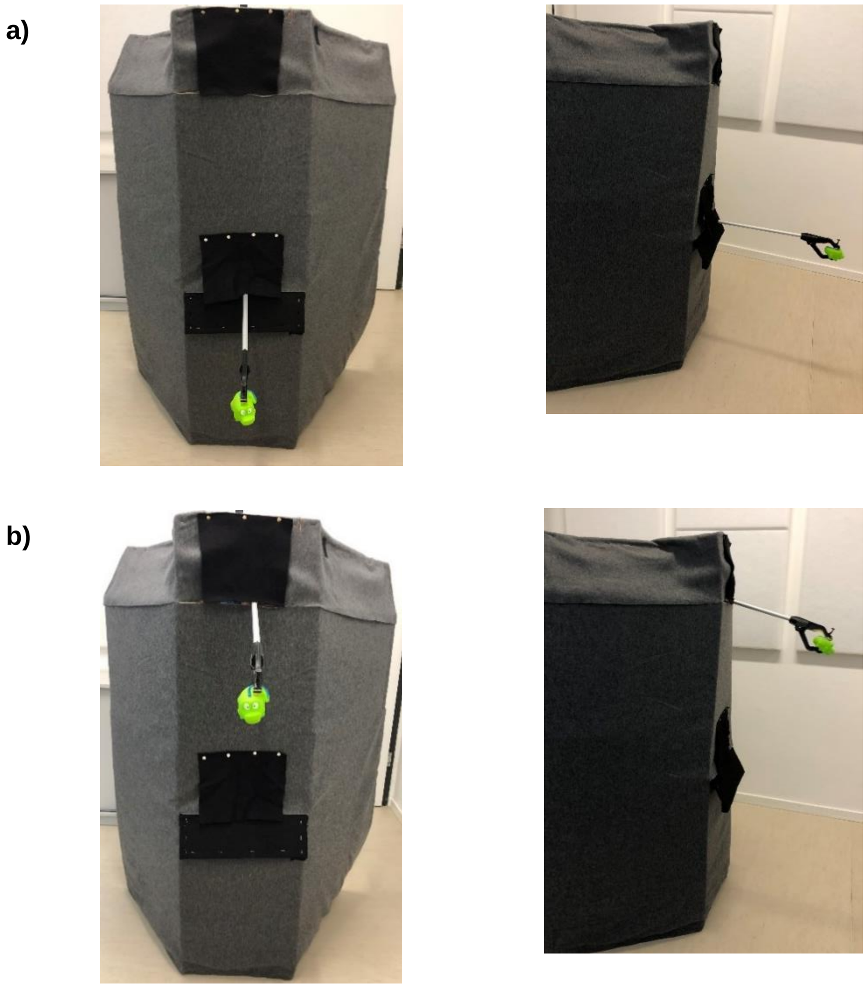

Figure 12: Experimental setup for action execution in study 2

Three-sided cabin with two small cutouts and covering curtains were built for the action execution phase. The experimenter presented the objects using a mechanical claw either from the cutout at the (a) bottom or from the (b) top corresponding to the conditions infants watched in the observation phase. The pictures on the left represent the perspective of the infants and those on the right depict the perspective of the video recording available for analysis.

5.3.3 Procedure

The general procedure prior to the start of the experimental session, ways to motivate infants during the session, and termination of recording was similar to study 1 (chapter 4).

Action observation. This phase was conducted following a 2x2 mixed-model design. The within-subject factor comprised of the hand actions, reach and back-of-hand, and the between-subject factor comprised of the position of the objects, bottom or top.

Infants watched short videos of both the reach and back-of-hand actions in either the bottom or top setting displayed on an LCD computer screen (51.50cm X 32.00cm) at a distance of approximately 80cm. The videos were rendered at a resolution of 1920pixels x 1080pixels and were presented at size of 29cm x 30cm on the screen. Infants' EEG recordings were synchronized with the videos of their behaviour during the session. The Presentation (©Neurobehavioural Systems, Inc) scripts comprised of 16 blocks of 14 test trials each, with an attention getter interspersed after every seven trials, presented in a pseudo-random order. The first two blocks began with three familiarization trials but all the blocks thereafter began with only one familiarization trial. Each block comprised of a combination of reach and back-of-hand actions with no more than two consecutive repetitions of the same action. In addition, each block comprised of trials with varying baseline length with no more than two consecutive repetitions of the same baseline length. Every familiarization and test trial was followed by a 400ms inter-stimulus interval (ISI), which comprised of a plain grey background. The order of trials and blocks, and the side of presentation were counterbalanced across infants such that there were four different versions of stimuli presentation for both the bottom and the top settings. Infants could watch a maximum of 224 test trials comprising of 112 trials for each action. The experiment comprised of 20 familiarization trials in total and 16 scripted attention getters.

Action execution. For this phase of the experiment, the seating position of the infant and the parent was moved 90° to their right, such that both the infant and the parent sat in a profile position towards the video camera. The three-sided cardboard cabin was aligned such that the small cutouts faced the infant. Experimenter 1 always stood behind the cabin while presenting the objects and experimenter 2 sat beside the infant. To begin with, experimenter 1 produced some nonsense sounds spontaneously in an infant-direct tone such has '*kuhuu'* to gain the infants' attention. When the infants looked up toward the source of sound generation, that is the cabin, experimenter 2 signaled the start of the trial by saying '*jetzt'* in German (translation: now). Upon receiving this signal, experimenter 1 obtained an object with the mechanical claw and pushed it through either the bottom or the top opening corresponding to the bottom or top videos infants watched in the action observation phase. Experimenter 1 held on to each object for as long as the infants required to complete their grasp. At the point of grasp completion, experimenter 2 provided a cue by saying *'ja'* in German (translation: yeah) and experimenter 1 released the grasp of the claw and pulled it back in to the cabin. The infants were allowed to play with the objects for a little while before experimenter 2 secured it away and the next trial began. If infants were hesitant to grasp objects or did not react initially, experimenter 2 motivated the infant to obtain it by saying "*Guck mal, da gibt's einen Spielzeug*" (Look! There is a toy). If the infants continued to be hesitant, experimenter 2 obtained the object and showed it to the infant or requested the parent to demonstrate in a similar manner. During the action execution phase, infants did not interact with experimenter 1 after she disappeared behind the cabin unless additional intervention was required, for example, in case of a crying infant. Infants could complete 20 grasping actions during this phase.

5.3.4 EEG Recording & Analyses

The procedure followed for EEG recording and analyses was similar to the previous study (chapter 4). Therefore, in the following, only the specific details relevant for this study are elaborated.

Action execution. After completing the initial preprocessing steps, data from infants that did not grasp at least four objects or those who required additional encouragement to reach for objects were discarded from this initial analysis (N = 5). The average time taken by the remaining infants (N = 86) to grasp objects, from both the bottom and top groups combined, was about 1600ms. Therefore, EEG data was divided into short segments of 3800ms, i.e., 1800ms before and 2000ms after the onset of reaching. A duration of 400ms, starting from 1400ms before onset of reach, was considered for baseline correction. Steps for artifact rejection and time-frequency analysis were identical to the previous study (chapter 4).

Infants (N = 19) in the bottom group contributed a mean of 9.21 artifact-free trials (SD = 4.31, Range = 4-19) and in the top group (N = 15), a mean of 6 artifact-free trials (SD = 2.03, Range = 4-10). Combined, infants (N = 34) contributed a mean of 7.79 artifact-free trials (SD = 3.81, Range = 4-19) in the action execution phase.

Action observation. The artifact-free EEG data comprised of segments lasting 2700ms, i.e., 1200ms before and 1500ms after action onset. 400ms on either edge of the segments were chopped off to eliminate the distortion generated by the wavelet transform, therefore further reducing the segment to 800ms before action onset and 1100ms after action onset, as illustrated in Figure 11b. A 200ms duration, which comprised of a dark grey cross on a light grey background, was chosen for baseline correction. Similar to the previous study, two target periods based on the events in the trial, referred to as ‘action-unfolding’ (0 to 600ms after action onset) and ‘action-complete’ (600 to 1100ms after action onset) were selected.

Infants in the bottom group (N = 12) contributed a mean of 10.91 trials (SD = 7.76, Range = 5-28) for the congruent-reach and a mean of 11.91 trials (SD = 7.67, Range = 5-27) for the incongruent-backofhand conditions (the difference between the total number of trials contributed in each condition was not significant: $t_{(11)} = -1.058$, $p = 0.313$, two-tailed). Infants in the top group (N = 14) contributed a mean of 7.14 trials (SD = 3.24, Range = 5-15) for the incongruent-reach and a mean of 7.78 trials (SD = 4.78, Range = 5-19) for the congruent-backofhand conditions (the difference between the total number of trials contributed in each condition was not significant: $t_{(13)} = -0.720$, $p = 0.484$, two-tailed). Similarly, the number of final trials contributed for each action was not significant between the two groups (Between-subject$_{\text{reach}}$ $t_{(24)} = 1.700$, $p = 0.102$, Between-subject$_{\text{back-of-hand}}$ $t_{(24)} = 1.684$, $p = 0.105$, two-tailed).

Similar to the previous study (chapter 4), the target channels comprised of left fronto-central (C3, FC1, FC5), right-fronto central (C4, FC2, FC6), left centro-parietal

(CP1, CP5, P3), and right centro-parietal (CP2, CP6, P4) regions. Occipital (O1, Oz, O2) alpha activity was analyzed separately. The averaged mu activity in the 6-9Hz range across the artifact-free segments was exported for each infant as absolute values for each of the four conditions. The procedure for statistical analysis was similar to the previous study (chapter 4).

5.4 Results

Action execution. During the action execution phase, infants tended to use the grasping hand configuration despite the position from which the objects were presented (bottom or top). No infant used the back-of-hand shape of the palm to obtain objects.

Figure 13 shows the mu activity elicited during action execution. A 4x2 repeated measures ANOVA with region (left fronto-central, right fronto-central, left centro-parietal, right centro-parietal) as the within subject factor and group (bottom, top) as the between subject factor did not reveal significant main effects of region ($F_{(3,96)}$ = 1.172, p = 0.324, η_p^2 = 0.035) or group ($F_{(1,32)}$ = 0.310, p = 0.582, η_p^2 = 0.010). The results also did not reveal an interaction between the two factors. Therefore, all infants (N = 34) were treated as one group for the analysis of the action execution data.

A 2x4 repeated measures ANOVA with time (baseline, action phase) and region (left fronto-central, right fronto-central, left centro-parietal, right centro-parietal) revealed a significant main effect of time ($F_{(1,33)}$ = 13.185, p = 0.001, η_p^2 = 0.285) with significant mu desynchronization during the action phase (Mean = -0.172, SE = 0.047). We did not find a significant main effect of region ($F_{(3,99)}$ = 1.439, p = 0.236, η_p^2 = 0.042) or an interaction, indicating a global pattern of mu desynchronization.

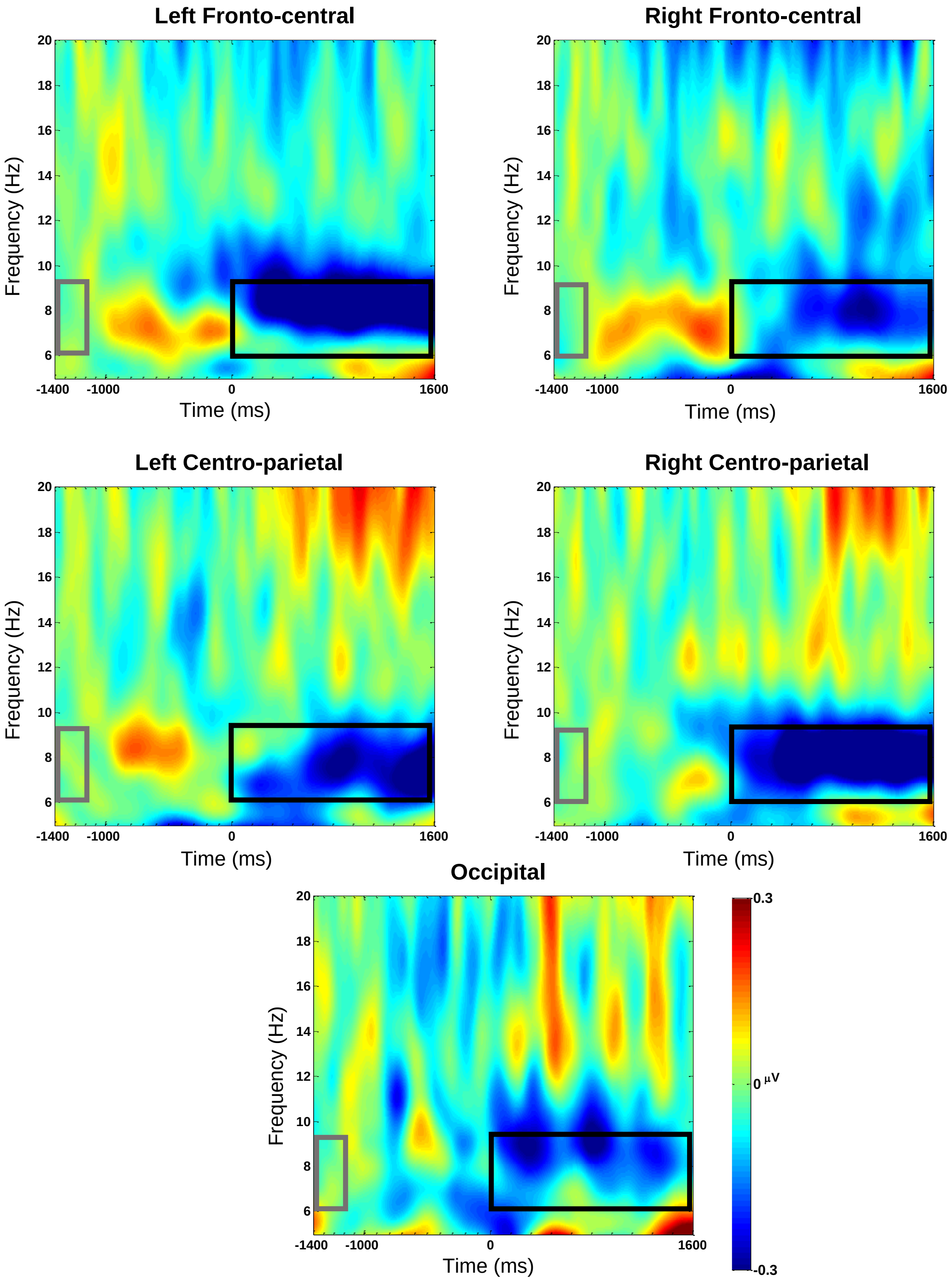

Figure 13: Mu activity during action execution of study 2

The areas marked in grey and solid black boxes represent the baseline and the action phase, respectively, and the corresponding infant mu frequency range (6-9Hz) in the left fronto-central, right fronto-central, left centro-parietal, right centro-parietal and the occipital regions.

Further, one-sampled t-tests revealed significant occipital alpha desynchronization ($t_{(33)} = -1.774$, $p = 0.042$, one-tailed) during the action phase. Paired t-tests revealed that mu desynchronization in the left fronto-central, right fronto-central, left centro-parietal and right centro-parietal was not significantly greater than occipital alpha desynchronization (all *p*s > 0.1).

Action observation. Table 4 provides a summary of the results obtained from the action observation phase. A 2x2x4x2 omnibus repeated measures ANOVA[16] with action (reach, back-of-hand), action phase (action-unfolding, action-complete), and region (left fronto-central, right fronto-central, left centro-parietal, right centro-parietal) as the within subject factors and object-position (bottom, top) as the between subject factor revealed a significant main effect of region ($F_{(1.94,46.75)} = 3.602$, $p = 0.036$, $\eta_p^2 = 0.131$). Pairwise comparisons from the omnibus ANOVA revealed significant difference between the right centro-parietal (Mean = -0.08, SE = 0.087) and the left fronto-central regions (Mean = 0.110, SE = 0.049, $p = 0.013$) and between the right centro-parietal and the right fronto-central (Mean = 0.081, SE = 0.046, $p = 0.040$) regions. The significant interactions between region x object-position ($F_{(3,72)} = 3.423$, $p = 0.022$, $\eta_p^2 = 0.125$), region x action ($F_{(3,72)} = 3.034$, $p = 0.035$, $\eta_p^2 = 0.112$), and action x action phase x object-position ($F_{(1,24)} = 12.226$, $p = 0.002$, $\eta_p^2 = 0.337$) are resolved below.

Region x object-position. Pairwise comparisons from the omnibus ANOVA revealed marginally greater mu desynchronization in the right centro-parietal region for the top object-position (Mean = -0.248, SE = 0.119) when compared to the bottom object-position (Mean = 0.088, SE = 0.128, p = 0.067). Further, in the top object-position, mu desynchronization was significantly greater in the right centro-parietal region than the left fronto-central (Mean = 0.056, SE = 0.067, $p = 0.004$), the right fronto-central (Mean =

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[16] In cases where the sphericity assumption was violated (based on Mauchly's test of Sphericity), corrected results following the Greenhouse-Geisser method are reported.

0.112, SE = 0.062, *p* = 0.002) and the left centro-parietal (Mean = -0.002, SE = 0.067, *p* = 0.038) regions.

Region x action. Pairwise comparisons from the omibus ANOVA revealed greater mu desynchronization in the left centro-parietal region for the back-of-hand action (Mean = -0.054, SE = 0.065) when compared to reach (Mean = 0.163, SE = 0.073, *p* = 0.035). Further, for the reach action, mu desynchronization in the right centro-parietal region (Mean = -0.105, SE = 0.114) was significantly greater than left centro-parietal region (Mean = 0.163, SE = 0.073, *p* = 0.023) and marginally greater than the left fronto-central region (Mean = 0.089, SE = 0.069, *p* = 0.078). Finally, for the back-of-hand action, mu desynchronization in the left centro-parietal region (Mean = -0.054, SE = 0.065) was significantly greater than the left fronto-central (Mean = 0.130, SE = 0.072, *p* = 0.030) and right fronto-central regions (Mean = 0.155, SE = 0.056, *p* = 0.001). In addition, mu desynchronization in the right centro-parietal (Mean = -0.054, SE = 0.098) was marginally greater than the left fronto-central (*p* = 0.060) and right fronto-central (*p* = 0.066) regions.

Action x action-phase x object-position. For the action-complete action phase, pairwise comparisons from the omnibus ANOVA revealed greater mu desynchronization for the incongruent-reach (Mean = -0.115, SE = 0.093) than congruent-reach (Mean = 0.201, SE = 0.100, *p* = 0.029). Further, mu desynchronization for the incongruent-reach during the action-complete action phase was nearly significant when compared to the action-unfolding action phase (Mean = 0.012, SE = 0.090, *p* = 0.055).

Overall, the results from the pairwise comparisons indicated that the significant mu desynchronization effects appeared to be restricted to the left and right centro-parietal regions but not to the left and right fronto-central regions. Therefore, in the follow up t-tests, mu desynchronization only in the left and right centro-parietal regions were considered.

Table 4: Results from action observation of study 2

Overview of the (a) ANOVA, pairwise comparisons and (b) t-test results for action observation. All results indicate significant mu desynchronization comparisons

(a) Main effect	Interaction
Region (*p*=0.036) • RCP > LFC (*p*=0.013) • RCP > RFC (*p*=0.040)	**Region*object-position** (*p*=0.022) • **RCP**: top > bottom (*p*=0.067) • **Top**: RCP > LFC (*p*=0.004) RCP > RFC (*p*=0.002) RCP > LCP (*p*=0.038)
	Region*action (*p*=0.035) • **LCP**: backofhand > reach (*p*=0.035) • **Reach**: RCP > LCP (*p*=0.023) RCP > LFC (*p*=0.078) • **Backofhand**: LCP > LFC (*p*=0.030) LCP > RFC (*p*=0.001 RCP > LFC (*p*=0.060) RCP > RFC (*p*=0.066)
	Action*actionphase*object-position (*p*=0.002) • **Action-complete**: incongruent-reach > congruent-reach (*p*=0.029) • **Incongruent-reach**: action-complete > action-unfolding (*p*=0.055)

(b) One-sample t-test^{+}	Independent t-test^{+}
Incongruent-reach: **Action-complete** RCP (*p*=0.021)	**Action-complete:** **RCP**: Incongruent-reach > congruent-reach (*p*=0.013)

$^{+}$ One-tailed significance

LFC: left fronto-central; RFC: right fronto-central; LCP: left centro-parietal; RCP: right centro-parietal

> denotes greater mu desynchronization for the factor on the left of the symbol compared to that on the right of the symbol

One-sample one-tailed t-test revealed significant mu desynchronization only in the right centro-parietal region for the incongruent-reach condition (Mean = -0.424, SE = 0.186, $t_{(13)}$ = -2.260, p = 0.021) during the action-complete phase but not in the action-unfolding phase (Mean = -0.210, SE = 0.162, $t_{(13)}$ = -1.292, p = 0.109). In the right centro-parietal region, the congruent-reach and incongruent back-of-hand conditions did not elicit mu desynchronization (Congruent-reach: $\text{Mean}_{\text{action-unfolding}}$ = 0.001, SE = 0.116; $\text{Mean}_{\text{action-complete}}$ = 0.210, SE = 0.192; Incongruent-backofhand: $\text{Mean}_{\text{action-unfolding}}$ = 0.073, SE = 0.161; $\text{Mean}_{\text{action-complete}}$ = 0.065, SE = 0.156). Further, the congruent-backofhand condition did not exhibit significant mu desynchronization in this region (Mean$_{\text{action-unfolding}}$ = -0.187, SE = 0.141, $t_{(13)}$ = -1.327, p = 0.103; Mean$_{\text{action-complete}}$ = -0.169, SE = 0.139, $t_{(13)}$ = -1.214, p = 0.123). Figure 14 illustrates the mu activity elicited in the right centro-parietal region for the four conditions.

None of the four conditions elicited significant mu desynchronization in the left centro-parietal region. While congruent-reach and incongruent-reach conditions did not elicit mu desynchronization, mu desynchronization elicited in the congruent-backofhand and incongruent-backofhand conditions did not reach significance. (Congruent-reach: Mean$_{\text{action-unfolding}}$ = 0.246, SE = 0.082; Mean$_{\text{action-complete}}$ = 0.348, SE = 0.127; Incongruent-backofhand: Mean$_{\text{action-unfolding}}$ = -0.061, SE = 0.086, $t_{(11)}$ = -0.714, p = 0.245; Mean$_{\text{action-complete}}$ = -0.089, SE = 0.104, $t_{(11)}$ = -0.860, p = 0.204; Incongruent-reach: Mean$_{\text{action-unfolding}}$ = 0.051, SE = 0.100; Mean$_{\text{action-complete}}$ = 0.005, SE = 0.118; Congruent-backofhand: Mean$_{\text{action-unfolding}}$ = -0.068, SE = 0.096, $t_{(13)}$ = -0.710, p = 0.245; Mean$_{\text{action-complete}}$ = 0.005, SE = 0.110). A spectrographical representation of the mu activity in the remaining regions is provided in appendix B.

As revealed by one-tailed independent and paired t-tests respectively, mu desynchronization elicited in the action-complete phase of the incongruent-reach in the right centro-parietal region was significantly greater than the congruent-reach condition ($t_{(24)}$ = 2.353, p = 0.013) but not greater than the congruent-backofhand condition ($t_{(13)}$ = -1.341, p = 0.101).

One-sample one-tailed t-tests did not reveal significant occipital alpha desynchronization for the incongruent-reach condition (Mean$_{\text{action-unfolding}}$ = -0.021, SE = 0.160, $t_{(13)}$ = -0.135, p = 0.447; Mean$_{\text{action-complete}}$ = -0.318, SE = 0.218, $t_{(13)}$ = -1.457, p = 0.084). The other conditions also did not elicit significant alpha desynchronization. Congruent-reach: Mean$_{\text{action-unfolding}}$ = -0.023, SE = 0.106, $t_{(11)}$ = -0.224, p = 0.413; Mean$_{\text{action-complete}}$ = -0.095, SE = 0.210, $t_{(11)}$ = -0.455, p = 0.329. Incongruent-backofhand: Mean$_{\text{action-unfolding}}$ = -0.055, SE = 0.214, $t_{(11)}$ = -0.259, p = 0.499; Mean$_{\text{action-complete}}$ = -0.111, SE = 0.239, $t_{(11)}$ = -0.463, p = 0.326. Congruent-backofhand: Mean$_{\text{action-unfolding}}$ = 0.251, SE = 0.097; *t*-test not applicable because of synchronization; $\text{Mean}_{\text{action-complete}}$ = -0.010, SE = 0.164, $t_{(13)}$ = -0.064, *p* = 0.475).

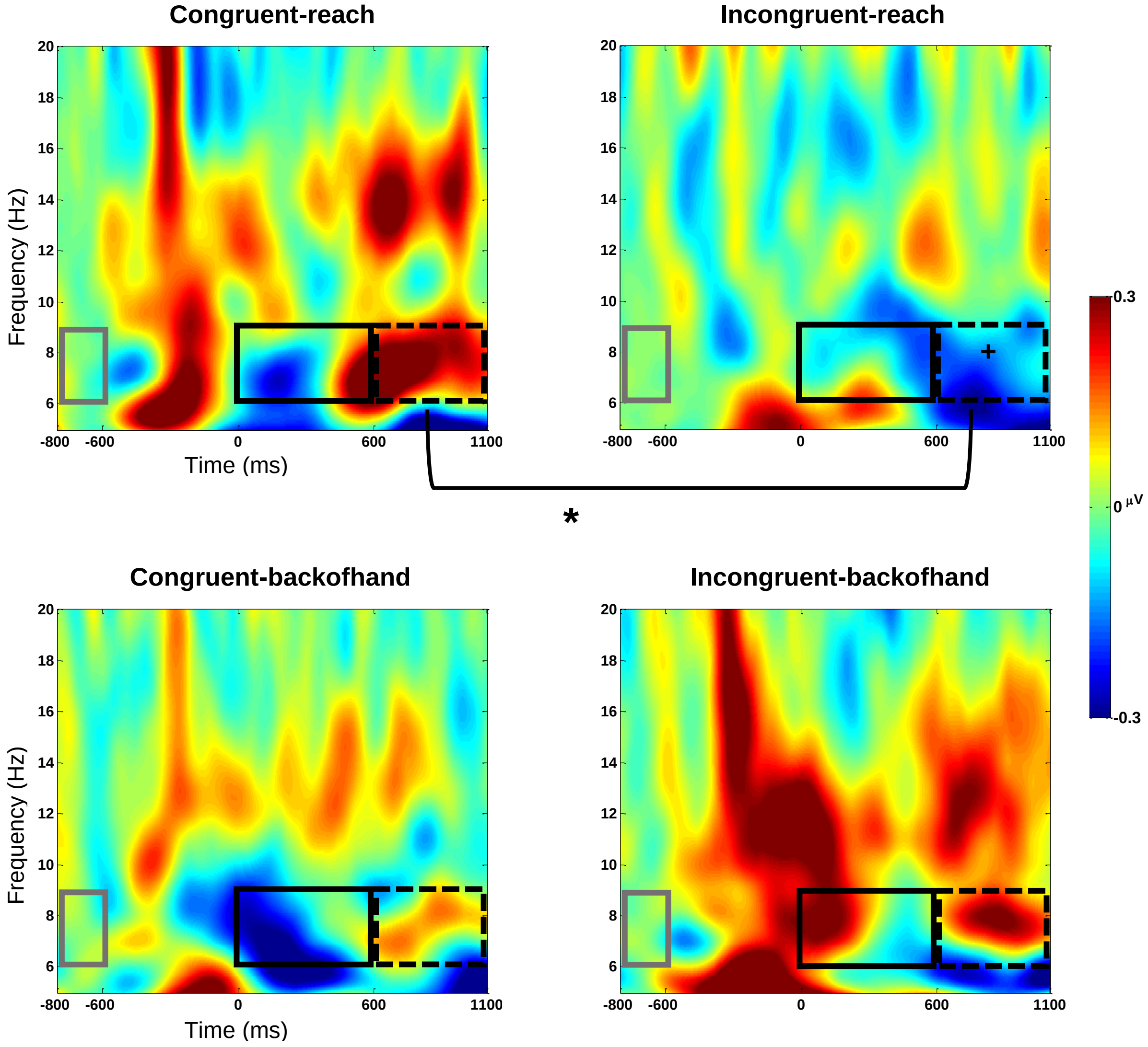

Figure 14: Mu activity during the action observation phase of study 2

This figure illustrates mu activity elicited in the right centro-parietal region for the congruent-reach, incongruent-reach, congruent-backofhand and incongruent-backofhand conditions.

The areas marked in grey, solid and dashed black boxes represent the baseline, action-unfolding and action-completion phases, respectively, in the infant mu frequency band of 6-9Hz.

+p < 0.05 significant mu desynchronization when compared to 0 (one-sample t-tests)

**p < 0.05 significant mu desynchronization when compared between conditions (Independent t-test)*

5.5 Discussion

The purpose of this study was to incorporate factors of context and efficiency to investigate the influence of observing congruent and incongruent action-context contingencies on action understanding, specifically mu desynchronization. Following a mixed design, two groups of 9-month-old infants watched the following experimental conditions as part of this study - congruent-reach and incongruent-backofhand conditions, incongruent-reach and congruent-backofhand conditions - categorized based on the position of the objects (bottom or top). Further, infants also grasped various objects presented using a mechanical claw through the bottom or top opening of a cardboard cabin.

For action execution, we found significant mu desynchronization across all target regions. Further, infants resorted to approaching the objects using the grasping hand configuration irrespective of the position of the object. Similar to other published studies (Cannon et al., 2016; Marshall et al., 2013b; Montirosso et al., 2019; Ruysschaert et al., 2013) and the previous study in this thesis (chapter 4), mu desynchronization elicited during action execution was not region specific, suggesting that both action and attentional mechanisms may be working in close coordination (Fox et al., 2016). In an interactive paradigm such as the one conducted in the present study, this may not be surprising, as infants are possibly attending to factors such as the cabin, mechanical claw, or the colourful objects besides planning and executing their actions.

The results of the action observation phase revealed significant mu desynchronization in the right centro-parietal region only for the incongruent-reach condition but not for the congruent-reach or the congruent-backofhand conditions, which is in contrast to the hypotheses. The incongruent-backofhand condition did not elicit significant mu desynchronization, which was consistent with our expectations.

One fundamental difference between the occlusion-grasping condition from Southgate et al. (2010) and the congruent-reach condition in this study lies in the fact that the former implied completion of the goal, achieved by the movement of the hand behind the occluder. In the current study, the goal is clearly incomplete or unfulfilled because the grasping hand does not touch the object. However, the incompleteness of the goal does not justify infants' lack of goal attribution. In the previous study (chapter 4), we provided evidence that 9-month-old infants attributed meaning to embedded goals, when observing an agent produce the back-of-hand action in the social condition, where the outcome was not shown. Further, there is evidence from eye tracking studies that 10- and 11-month-old infants anticipated the goals of observed reaching and grasping actions for both successful and failed attempts over a barrier (Brandone et al., 2014; Jarto & Liszkowski, in prep.). Further, both 9- and 18-month-old infants anticipated a neutral agent to help another agent if attempts to reach were unsuccessful due to the visible hindrances as opposed to helping an agent that could fulfill goals easily (Köster et al., 2016). Evidence from behavioural studies showed that infants, 6 months (Marsh et al., 2010) and older (9-18 months, (Behne et al., 2005)) displayed impatience and gaze aversions when an adult failed to provide infants with a toy due to unwillingness compared to when the goal was obstructed, such as by accidentally dropping the toy.

In keeping with the above evidence, it is possible that the infants in the current study failed to attribute goals to the observed congruent-reach condition due to the apparent absence of any obstacle. The grasping hand stopped rather abruptly over the objects without touching them. Only the hand was visible throughout and the infants were not provided with any additional cues such as the distance from the object or other factors preventing the completion of the grasp. In such a scenario, it was probably not clear why the goal was not reached. It is also possible that the presence of a goal itself was being reevaluated. Similar paradigms, which depicted a hand suddenly withdrawing from grasping or stopping short of an object, did not elicit significant mu desynchronization in both the infant and adult groups (Nyström, 2008; Pomiechowska & Csibra, 2017) and also did not result in referential expectation in a recent eye tracking study (Jarto & Liszkowski, submitted). Similarly, infants in the current study were unable to attribute a goal when observing the congruent-reach condition as the context rendered it meaningless and observing this condition did not elicit significant mu desynchronization.

Observing the congruent-backofhand condition did not elicit significant mu desynchronization, indicating that infants were unable to attribute an instrumental goal to the back-of-hand action and it possibly serves a communicative purpose as evident in the previous study of this thesis (chapter 4). However, it could also mean that while the goal seemed embedded, this was not made clear to the infants in the familiarization videos. Specifically, infants watched objects stopping at edge of the tube but they did not see the objects topple down. Other cues, which may have suggested the imminent fall, such as objects wobbling or being pushed from behind, were absent. Therefore, an object positioned at the edge of the tube may still be obtained using the more efficient grasping action and there was no clear reason to use the back-of-hand action instead. Using the back-of-hand action in this case, was counterintuitive, especially when the objects were never shown to fall down. This probably explains why infants failed to understand the ‘congruency’ of this condition. In addition, irrespective of whether the objects were presented from the bottom or top opening of the cabin during the action execution phase of the current study, infants did not produce the back-of-hand action to obtain the objects. This reinforces the notion that a stationary object may be obtained using the conventional reach and grasp action unless additional events alter the efficiency of this action for the same purpose.

An unexpected but interesting finding of this study was the significant mu desynchronization for the incongruent reach condition in the right centro-parietal region. As mentioned previously, it is possible that infants never expected the objects to fall down and anticipated the normal grasping action as the efficient means to achieve the goal. However, the hand never touched the object and going by the result of the congruent-reach condition, this could have been enough reason to reevaluate the goal. The only possibility is that infants identified with grasping as the efficient action and judged the angle of the action as a miscalculation. Nonetheless, this interpretation is only speculative given the data at hand and there is not clear reason why this condition elicited significant mu desynchronization.

Although the hypotheses for the study could not be confirmed, it is not possible to draw firm conclusions on the instrumental role of the back-of-hand action. Instead, we believe that the portrayal of context and efficiency in this study was rather ineffective in representing the physical constraints necessitating the use of the corresponding congruent actions. Therefore, the study needs to be repeated after correcting for the irregularities in the experimental conditions. Specifically, the familiarization videos should incorporate a clear representation of the goal. If the objects were meant to fall down, then this needs to be shown. Additional conditions involving obstacles and/or occlusion in similar settings may be employed for further comparisons. The study may also be conducted with older infants or toddlers because the overarching question of the instrumental role of the back-of-hand does not pertain to the age of the infants per se, although we tested 9-month-old infants for comparative purposes. Finally, within-subject experimental conditions need to be avoided with special population like infants to reduce attrition rates to the extent possible.

6 Observing Distal and Proximal Pointing Elicits Mu and Alpha Desynchronization in 12-month-old Infants

Research highlights:

- *12-month-old infants watched videos of an agent pointing in a social situation with objects positioned either distally or proximally.*
- *We found significant desynchronization for the observation of both distal and proximal pointing in the right centro-parietal and occipital regions but in the right fronto-central region only for proximal pointing.*
- *The findings provide further evidence that action understanding extends to communicative actions and is not simply the result of anticipating an instrumental response from the social partner.*

Keywords: pointing, infants, EEG, mu rhythm, action understanding, imperative, declarative, distal, proximal, third-party observations

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6.1 Abstract

In study 1 of this thesis (chapter 4), we were able to show that infants attribute communicative goals to the observed unfulfilled actions within an appropriate context, which was inconsistent with extant literature that observing communicative actions do not elicit significant mu desynchronization (Pomiechowska & Csibra, 2017). However, while the back-of-hand action is appropriate in distal situations, pointing may be construed as meaningful even when objects are located nearby. Specifically, pointing may be used to request for objects similar to the back-of-hand action, and it may also be used to direct attention or share information, therefore not necessarily prompting an instrumental response from the social partner. Therefore, the aim of this EEG study was to investigate whether 12-month-old infants attributed communicative goals when observing the pointing gesture in social settings. In the distal pointing condition, an agent pointed to an object, that was unreachable and in the proximal pointing condition, an agent pointed to an object within her reach, with a social partner present in both conditions. Due to the position of the object, an instrumental response from the social partner may be anticipated only for distal pointing but not for the proximal pointing condition. The findings revealed significant desynchronization for both the conditions in the right centro-parietal and occipital regions with no significant difference between the conditions. Additionally, mu desynchronization in the right fronto-central region was greater in the proximal condition than in the distal condition. These results provide further evidence that mu desynchronization was not simply obtained due to the infants' anticipation of an instrumental response and further reinforce that action understanding entails communicative goals and is not restricted to only instrumental actions.

6.2 Introduction

Observing an agent produce the back-of-hand action in the social condition elicited mu desynchronization in a group of 9-month-old infants, when compared to the nonsocial and the object-absent conditions (chapter 4). While the social condition included both an object and a recipient, the nonsocial condition was devoid of a recipient but included an object; the object-absent condition involved a recipient but not an object. Therefore, we raised the probability of whether infants' anticipation of the recipient's instrumental response in the social condition influenced the findings. There is now sufficient evidence that approaching an object with the back-of-hand action does not result in instrumental goal attribution (Hamlin et al., 2008; Krogh-Jespersen & Woodward, 2014; Thoermer et al., 2013; Woodward, 1999; chapter 5 of the current thesis) unless it produced salient effects (Biro et al., 2014; Király et al., 2003). Therefore, examining a social condition, where an agent produces the back-of-hand action for nearby, reachable objects would be meaningless.

One gesture that is used universally across cultures (Liszkowski et al., 2012) and forms the basis of social interactions in infancy and language development is the conventional pointing gesture. Broadly speaking, pointing serves two purposes, imperative or declarative (Bates et al., 1975). Imperative pointing leads to obtaining objects or information from another and declarative pointing aims at directing attention to an object or sharing information (see also Tomasello et al., 2007; but see also Southgate et al., 2007). In both cases, pointing occurs within a socially appropriate setting, where the former prompts an instrumental response (especially in the event of requesting for objects) but the latter does not. In the case of declarative pointing, the location of objects becomes irrelevant and pointing to nearby objects may still be meaningful. Therefore, in the current study, we incorporated the pointing gesture distally and proximally to examine the role of different contextual factors influencing goal attribution in communicative settings.

Research over the past two decades has shown that infants point communicatively to not only achieve individualistic goals (for example, Begus & Southgate, 2012; Camaioni et al., 2004; Kovács et al., 2014; Liszkowski, 2005; Liszkowski et al., 2007b; Southgate et al., 2007) but do so also in a prosocial manner (Liszkowski et al., 2007a, 2008; Tomasello et al., 2007). There is now sufficient evidence that by the end of their first year, infants comprehend and produce the pointing gesture (see Rohlfing et al., 2017 for a review) and they are able to distinguish among different social intentions of observed pointing acts and respond appropriately (Esteve-Gibert et al., 2017). A recent investigation showed that 12-month-old infants responded to an experimenter’s sudden and out-of-context requestive reach and back-of-hand and pointing actions by offering the objects, however, preferring to handover distant objects more often when compared to those that were closer to the experimenter (Liszkowski, 2014). This differential response indicated that pointing in the distal situation was construed as a request but the same action was interpreted as an intent to share attention to the object in proximity. However, around this age, infants’ comprehension of the pointing gesture and social preferences are not limited to second-person interactions but are also extended to third-party observations as evident in behavioural and eye tracking studies (For example, Fawcett & Liszkowski, 2012; Gräfenhain et al., 2009; Krehm et al., 2014; Thorgrimsson et al., 2014).

Considering the evidence thus far, we selected 12-month-old infants for the current EEG study for the following reasons. Firstly, the main question of the current investigation was not to test whether mu desynchronization would be elicited from non-pointers. Secondly, the results obtained would be more comparable with previous infant pointing studies. Finally, this study would be the first point of reference in order to accommodate modifications in future EEG studies of pointing and their modulation on the mu activity in infants belonging to earlier or more advanced stages of pointing. To our best knowledge, infant EEG studies investigating the influence of social context on the interpretation of the observed pointing action do not yet exist.

So far, only one adult EEG study has directly investigated mu activity during the observation of the pointing gesture along with two other actions, i.e., grasping and reaching (Pomiechowska & Csibra, 2017). In this study, two groups of adults watched grasping, unfulfilled reaching, and pointing actions that were blocked either by action and sound or only by sound, where the onset of the actions were preceded by pure tones or speech (such as ‘Look’). All the observed actions were object-directed and only the arm movement was visible. The findings revealed that observing the grasping action preceded by pure tones elicited significant mu desynchronization in the central region but the effect disappeared when the action was preceded by speech. Observing unfulfilled reaching and pointing actions did not elicit significant mu desynchronization both when preceded by pure tones or speech. Based on the findings of the study, the authors concluded that only actions that could be interpreted as instrumental but not referential engaged the sensorimotor cortex. However, it should be noted that the pointing and unfulfilled reaching actions were presented in unrealistic circumstances in this study. For example, the unfulfilled reaching action stopped abruptly before touching the object, and therefore observing this action could have been interpreted as ambiguous, similar to the 9-month-old infants in our previous study (chapter 5). Further, a real communicative context for the pointing action was missing, similar to when the back-of-hand action was used as a control condition in previous research. The conclusion drawn by these authors also speaks against the recent evidence that observing communicative actions elicited mirror system activation in a similar manner as instrumental actions (elaborated in section 1.5 of this thesis). Therefore, we expected that similar to the back-of-hand action, observing pointing within appropriate social-contextual situations may be construed as meaningful and may elicit significant mu desynchronization.

To investigate, we created two social conditions using the pointing gesture. In the distal pointing condition, an agent pointed at an object that was located far away and unreachable. In the proximal pointing condition, she pointed at an object, located within her reach. In both the conditions, a social partner watched the agent unfold the pointing action but did not respond. In the distal condition, the object was located close to the recipient and in the proximal condition the object was located away from the recipient. While observing distal pointing may prompt an instrumental response from the social partner, observing proximal pointing simply directs attention. Without additional cues in the proximal condition, it may be difficult to predict what happens next. Nevertheless, pointing in both conditions is driven by a social, communicative goal and represents typical, conventional, real-life situations. Therefore, we hypothesized that observing the pointing gesture in both the distal and proximal conditions would elicit significant mu desynchronization, thereby indicating that the activity was not elicited simply due to infants' anticipation of a social (instrumental) response. Moreover, this would provide further support to our previous evidence (chapter 4) that attributing communicative goals also elicits mu desynchronization, with emphasis on the role of contextual factors.

We did not conduct the action execution phase in this study. The results from the previous studies (chapters 4 & 5) showed a global mu desynchronization pattern as opposed to topographical specificity and we were unable to determine a specific overlap of activity between the action execution and action observation phases. Under the assumption that the action execution phase may result in similar outcomes, we decided to exclude this phase from the current study.

6.3 Methods

6.3.1 Participants

Eighty-four 12-month-old infants participated in the study, with 42 infants in each of the distal and proximal conditions. Thirty-eight infants (f = 19, mean age = 382 days) were included in the final sample, with 19 each in the distal (f = 8, mean age = 384 days) and proximal (f = 11, mean age = 381 days) conditions. Data from an additional 46 infants were discarded due to extreme movements or use of pacifier (16) and for not providing a minimum of 5 artifact-free trials (30). The attrition rate of 54.76% falls within the general anticipated rate (DeBoer et al., 2013; Hoehl & Wahl, 2012).

6.3.2 Stimuli

Action observation. The stimuli presented for this study is illustrated in Figure 15. The videos of distal and proximal pointing showed an agent performing the pointing action in a social setting. In both the conditions, two agents sat at either end of the table. In the distal condition, an object was positioned far away from the pointing agent but in the proximal condition, an object was positioned close to her. The social partner only followed the pointing action but did not respond in both the conditions.

The videos lasted 3.4 or 3.6 seconds, where the first 1200 or 1400ms comprised of the neutral phase depicting a plain grey background. The melodies created for study 1 (chapter 4) were also superimposed during the initial 400ms of the neutral phase. This was followed by the appearance of the distal or proximal setting on the screen for 200ms, during which the agent and the recipient established eye contact. Next, the agent started to unfold the pointing action, stopping at the final position, 1000ms after onset. The final position was frozen on the screen for the next 1000ms. In case of the longer baseline, the corresponding events were shifted by 200ms.

Similar to the other two studies elaborated in this thesis (chapters 4 & 5), the original videos were filmed against a plain white wall, with two agents seated across a table, using a Panasonic Handycam model number HC-X929. The objects and four different tablecloths (red, blue, brown, and grey) were photographed using a smartphone and then appropriately edited for use in the videos. The baseline grey background figure was created using Adobe After Effects CS6. All these individual elements were combined and edited further using Adobe After Effects CS6. Finally, the edited videos were flipped in order to balance the side of presentation during testing.

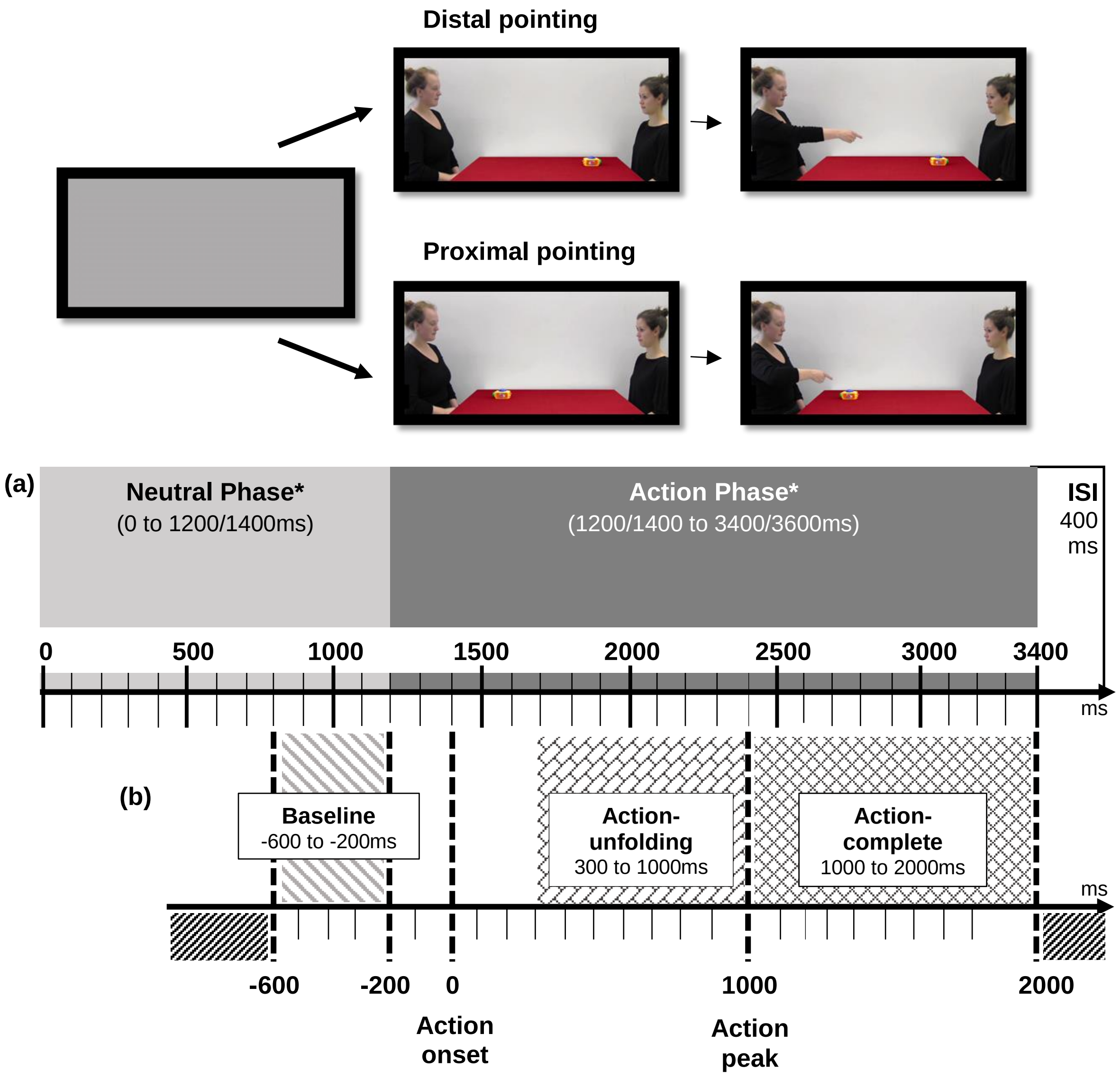

Figure 15: Stimuli presentation and analysis timeline for study 3

**The (a) stimuli videos consisted of varying neutral phases, with half the videos comprising of a 1200ms neutral phase (illustrated in this figure). In the other half of the videos, the duration of the neutral phase lasted 1400ms, therefore the subsequent events were pushed further by 200ms. Specifically, the time at action onset was at 1600ms, action peak at 2600ms and the end of the action phase at 3600ms. However, the (b) corresponding time points for the analysis remained the same as data were segmented based on the action onset; ISI: inter-stimulus interval*

▨ *- represents the part of the segment chopped from the analysis phase to eliminate the distortion introduced by the wavelet transform.*

6.3.3 Procedure

This study was conducted using a between-subject design, where two groups of 12-month-old infants watched either the distal pointing or the proximal pointing condition. The general procedure, stimuli presentation, number of trials presented, use of attention getters were similar to experiment 2 of study 1 (chapter 4). The size of the videos presented on the screen was 21cm x 40cm.

6.3.4 EEG Recording & Analyses

The recording procedure was the same as mentioned in chapters 4 and 5. All preprocessing steps and time-frequency analysis were performed as elaborated previously.

The artifact-free EEG data comprised of segments lasting 3400ms, i.e., 1000ms before and 2400ms after action onset. A 400ms duration before the onset of the action, which comprised of the plain grey background, was chosen for baseline correction. Similar to previous studies, the action-unfolding (300-1000ms) and action-complete (1000-2000ms) phases were analyzed as shown in Figure 15b.

Infants (N = 19 in each group) contributed a mean of 11.5 trials (SD = 7.39, Range = 5-26) in the distal condition and a mean of 8.2 trials (SD = 2.91, Range = 5-15) in the proximal condition (the difference between the total number of trials contributed in each condition was marginally significant: $t_{(23.46)} = 1.347$, $p = 0.077$, two-tailed. As equality of variance could not be assumed in accordance with Levene's test, the corrected values are reported).

We analyzed the mu activity (6-9Hz) in the same target regions mentioned previously. Occipital alpha activity was analyzed separately. Statistical analyses were similar to the previous studies.

6.4 Results

Table 5 provides a summary of the mu desynchronization results and Figure 16 depicts the findings of the current study spectrographically. A 2x4x2 omnibus repeated measures ANOVA with action phase (action-unfolding, action-complete) and region (left fronto-central, right fronto-central, left centro-parietal, right centro-parietal) as the within-subject factors and condition (distal, proximal) as the between-subject factor revealed a significant main effect of region ($F_{(3,108)} = 7.508$, $p < 0.001$, $\eta_p^2 = 0.173$). Pairwise comparisons from the omnibus ANOVA revealed significant mu desynchronization in the left centro-parietal region (Mean = -0.081, SE = 0.052) when compared to the left fronto-central region (Mean = 0.060, SE = 0.052, $p = 0.043$). Further mu desynchronization in the right centro-parietal region (Mean = -0.238, SE = 0.058) was greater than the left fronto-central ($p < 0.001$), the right fronto-central (Mean = 0.028, SE = 0.057, $p = 0.001$) and the left centro-parietal ($p = 0.035$) regions. The results also revealed a marginal effect for condition ($F_{(1,36)} = 3.325$, $p = 0.077$, $\eta_p^2 = 0.085$), with greater mu desynchronization for the proximal pointing (Mean = -0.121, SE = 0.049) than the distal pointing condition (Mean = 0.005, SE = 0.049).

Although the ANOVA results did not reveal a main effect of action phase ($F_{(1,36)} = 1.130$, $p = 0.295$, $\eta_p^2 = 0.030$) or any interaction, we decided to treat the two action phases (action-unfolding, action-complete) separately to facilitate easy comparisons of the results with the previous studies in the thesis. As the ANOVA results indicated greater mu desynchronization in the left and right centro-parietal regions, we initially focused only on these regions for the follow up t-tests.

One-tailed one sample t-tests revealed significant mu desynchronization in the right centro-parietal region for both the distal ($\text{Mean}_{\text{action-unfolding}} = -0.234$, SE = 0.111, $t_{(18)} = -2.101$, $p = 0.025$; $\text{Mean}_{\text{action-complete}} = -0.137$, SE = 0.079, $t_{(18)} = -1.733$, $p = 0.050$) and the proximal conditions ($\text{Mean}_{\text{action-unfolding}} = -0.307$, SE = 0.103, $t_{(18)} = -2.984$, $p = 0.004$;

$\text{Mean}_{\text{action-complete}}$ = -0.273, SE = 0.089, $t_{(18)}$ = -3.058, p = 0.003). Mu desynchronization in the left centro-parietal region did not reach significance in either the distal ($\text{Mean}_{\text{action-unfolding}}$ = -0.084, SE = 0.074, $t_{(18)}$ = -1.134, p = 0.136; $\text{Mean}_{\text{action-complete}}$ = -0.132, SE = 0.072, $t_{(18)}$ = 0.181, p = 0.428) or the proximal condition ($\text{Mean}_{\text{action-unfolding}}$ = -0.109, SE = 0.086, $t_{(18)}$ = -1.268, p = 0.110; $\text{Mean}_{\text{action-complete}}$ = -0.143, SE = 0.102, $t_{(18)}$ = -1.402, p = 0.089).

One-tailed independent t-tests did not reveal significant differences between the conditions in both the left centro-parietal (action-unfolding: $t_{(36)}$ = 0.217, p = 0.414; action-complete: $t_{(36)}$ = 1.247, p = 0.110) and the right centro-parietal regions (action-unfolding: $t_{(36)}$ = 487, p = 0.314; action-complete: $t_{(36)}$ = 1.145, p = 0.130).

Considering the marginal significance of condition from the repeated measures ANOVA results and the pairwise comparisons with region, we assumed this could be due to marginal differences in mu desynchronization between the conditions in either the left or right centro-parietal regions but the findings from the independent t-tests revealed the contrary, as reported above. As a result, we computed t-tests for the left and right fronto-central regions.

One-tailed independent t-tests revealed a significant difference between distal and proximal pointing in the right fronto-central region (action-unfolding: $t_{(36)}$ = 1.946, p = 0.030; action-complete: $t_{(36)}$ = 1.662, p = 0.052). Follow-up one-sample one-tailed t-test confirmed significant mu desynchronization in the right fronto-central region only for the action-unfolding phase of proximal pointing ($\text{Mean}_{\text{action-unfolding}}$ = -0.1494, SE = 0.059, $t_{(18)}$ = -2.509, p = 0.011; $\text{Mean}_{\text{action-complete}}$ = -0.017, SE = 0.083, $t_{(18)}$ = -0.206, p = 0.419). However, the distal condition did not elicit mu desynchronization in the right fronto-central region ($\text{Mean}_{\text{action-unfolding}}$ = 0.080, SE = 0.101; $\text{Mean}_{\text{action-complete}}$ = 0.198, SE = 0.099).

Table 5: Results from action observation of study 3

Overview of the (a) ANOVA and (b) t-test results from study 3. All results indicate significant mu desynchronization comparisons

(a)	Main effect	Interaction
	Region ($p<0.001$) • LCP > LFC ($p=0.043$) • RCP > LFC ($p<0.001$) • RCP > RFC ($p=0.001$) • RCP > LCP ($p=0.035$) **Condition** ($p=0.077$) • Proximal > Distal	**None**

(b)	One-sample t-test$^+$		Independent t-test$^+$
	Distal:		**Action-unfolding:**
	Action-unfolding	**Action-complete**	**RFC**: proximal > distal ($p=0.030$)
	RCP ($p=0.025$)	RCP ($p=0.050$)	
	OCC ($p<0.001$)	OCC ($p=0.001$)	**Action-complete:**
			RFC: proximal > distal ($p=0.052$)
	Proximal:		
	Action-unfolding	**Action-complete**	
	RCP ($p=0.004$)	RCP ($p=0.003$)	
	OCC ($p<0.001$)	OCC ($p=0.001$)	
	RFC ($p=0.011$)		

$^+$ one-tailed significance
LFC: left fronto-central; RFC: right fronto-central; LCP: left centro-parietal; RCP: right centro-parietal; OCC: occipital

> denotes greater mu desynchronization for the factor on the left of the symbol compared to that on the right of the symbol

One-sample one-tailed t-tests revealed significant occipital alpha desynchronization for both the conditions (distal: Mean$_{\text{action-unfolding}}$ = -0.779, SE = 0.196, $t_{(18)}$ = -3.968, p < 0.001; Mean$_{\text{action-complete}}$ = -0.708, SE = 0.194, $t_{(18)}$ = -3.635, p = 0.001; proximal: Mean$_{\text{action-unfolding}}$ = -0.507, SE = 0.1264, $t_{(18)}$ = -4.001, p < 0.001; Mean$_{\text{action-complete}}$ = -0.5692, SE = 0.162, $t_{(18)}$ = -3.508, p = 0.001). However, one-tailed independent t-tests did not reveal a significant difference between occipital activity in the distal and proximal pointing conditions (action-unfolding: $t_{(36)}$ = -1.165, p = 0.126; action-complete: $t_{(36)}$ = -0.550, p = 0.293). Further, one-tailed paired t-tests revealed that occipital alpha desynchronization elicited for the distal condition was significantly greater than mu desynchronization in the right centro-parietal region (action-unfolding: $t_{(18)}$ = 2.432, p =

0.013; action-complete: $t_{(18)} = 3.035$, $p = 0.003$) but only marginally greater than the action-complete phase in the proximal condition (action-unfolding: $t_{(18)} = 1.289$, $p = 0.107$; action-complete: $t_{(18)} = 1.484$, $p = 0.077$). Finally, occipital alpha desynchronization elicited for the action-unfolding phase of the proximal condition was also significantly greater than mu desynchronization in the right fronto-central region ($t_{(18)} = 3.369$, $p = 0.001$). A spectrographical representation of mu activity elicited from left fronto-central and left centro-parietal regions for both the conditions is provided in appendix C.

Similar to the previous studies in this thesis, mu desynchronization was found to be right-lateralized in the present study. However, the side of presentation on the screen could not explain this right-lateralized activity. Specifically, additional paired t-tests revealed no significant difference between the number of segments watched from the left or the right side of presentation in either the distal ($\text{Mean}_{\text{left}} = 6.15$, SD = 4.51; $\text{Mean}_{\text{right}} = 5.42$, SD = 3.70, $t_{(18)} = 0.877$, $p = 0.196$, one-tailed) or the proximal pointing conditions ($\text{Mean}_{\text{left}} = 4.52$, SD = 2.01; $\text{Mean}_{\text{right}} = 3.68$, SD = 2.45, $t_{(18)} = 1.078$, $p = 0.1472$, one-tailed).

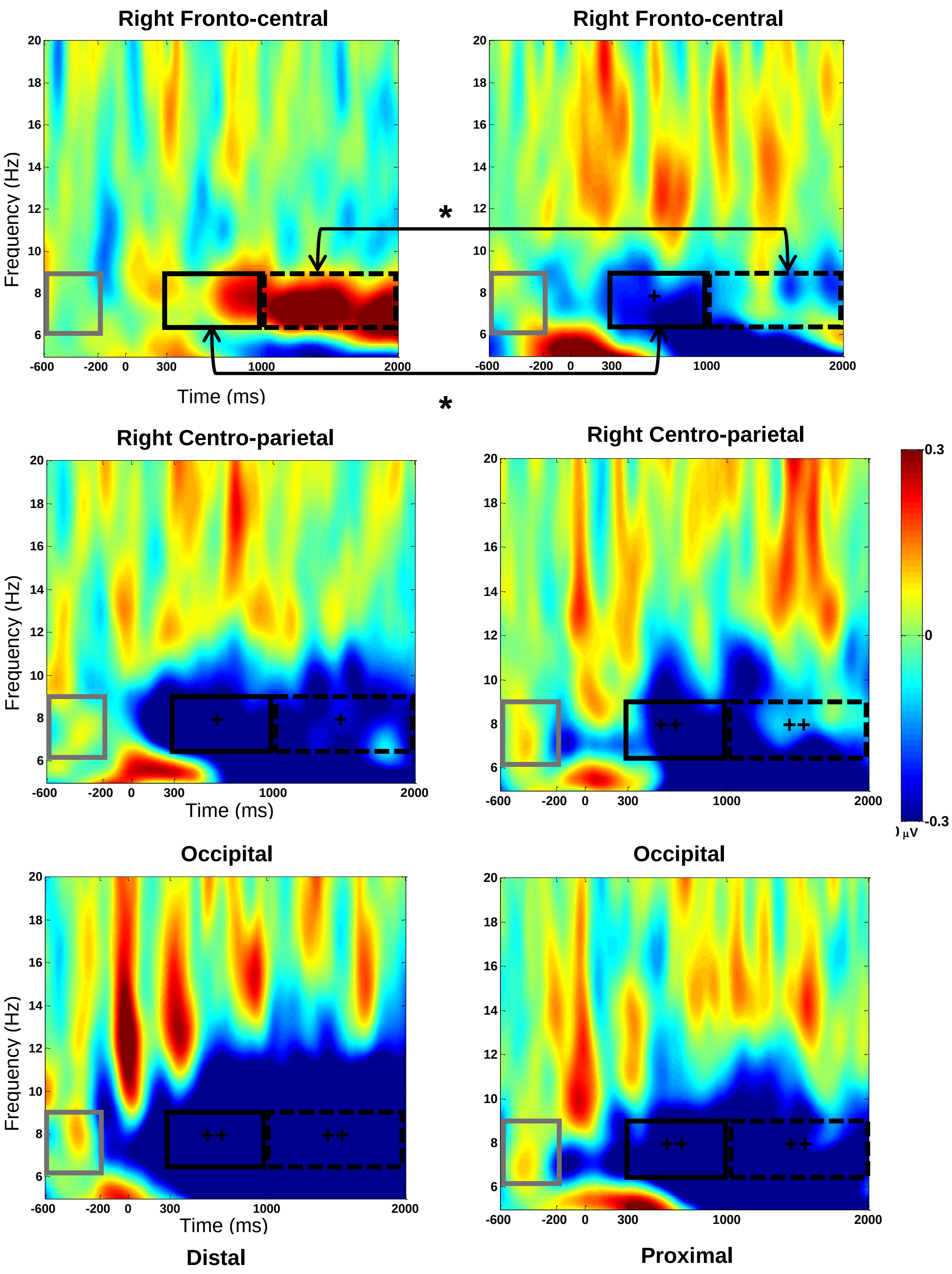

Figure 16: Mu activity during action observation of study 3

This figure illustrates mu activity elicited in the right fronto-central, right centro-parietal and occipital regions for the distal and proximal pointing conditions. The areas marked in grey, solid and dashed black boxes represent the baseline, action-unfolding and action-completion phases, respectively, in the infant mu frequency band of 6-9Hz.

+$p < 0.05$ significant mu desynchronization when compared to 0 (one-sample t-tests)

**$p < 0.06$ significant mu desynchronization when compared between conditions (Independent t-tests)*

6.5 Discussion

The first purpose of the study was to disambiguate infants' understanding of communicative actions in social situations. In other words, we wanted to investigate whether the mu desynchronization elicited reflects infants' understanding of the communicative intention or their anticipation of an instrumental response from a social partner. As the back-of-hand action was unsuitable for this purpose, we incorporated the pointing gesture. The second purpose of the study was to determine whether observing conventional communicative actions within appropriate situations also elicited mu desynchronization. 12-month-old infants watched an agent produce a pointing gesture towards objects either located away from her (distal) or within her reach (proximal). Our findings revealed significant mu desynchronization for both the distal and proximal pointing conditions during both the action-unfolding and action-complete phases in the right centro-parietal and occipital regions, however, with no significant differences between the conditions in these regions. In addition, we found significant mu desynchronization in the right fronto-central region for the action-unfolding phase of the proximal condition, which was also significantly greater than the distal pointing condition.

As evident in this study, the results were not elicited simply due to infants' anticipation of an instrumental response. If this were the case, observing pointing in the proximal condition would not elicit mu desynchronization. Therefore, the results obtained reflected an understanding of the communicative purpose afforded by the social setting. In other words, the presence of a goal object and a social partner were necessary cues that provided meaning to the agent's communicative action, similar to the findings from study 1 of this thesis (chapter 4). Significant mu desynchronization in the proximal condition confirms further that attributing communicative intentions also elicits mu desynchronization within appropriate social situations. This is in contrast to the findings by Pomiechowska & Csibra (2017), who concluded that observing communicative actions generate referential expectations and do not elicit mu desynchronization.

A surprising finding of the current study was the significant alpha desynchronization for both distal and proximal pointing, which we did not expect considering the results from the action observation paradigms of the previous studies in this thesis. Occipital alpha desynchronization has been implicated in imitation and turn taking paradigms, with alternating action observation and action execution sequences (Cannon et al., 2016; Debnath et al., 2019; Warreyn et al., 2013) and for observational learning (Makhin et al., 2019; van der Helden et al., 2010). Other studies have ascribed occipital alpha desynchronization to additional processes such as selective attention and visual processing (Filippi et al., 2016; Meyer et al., 2016) during action observation. According to Pineda (2005), entrainment/gating mechanism translates visual or auditory information from ‘seeing’ or ‘hearing’ in to ‘doing’ and multiple alpha generators become coupled when they are coherently engaged in action perception. The occipital alpha findings in the current study most likely resonates with the idea that additional factors beyond action perception were simultaneously employed during action observation. Bearing in mind that by 12 months, infants comprehend and produce pointing gestures (Rohlfing et al., 2017), it is probable that their ability to recognize the action as part of their motor repertoire and the social setting of the stimuli enhanced their attention further.

Although one could argue that the findings in the right centro-parietal region may represent dispersed activity from the occipital region, this may not be the case given the results from the previous study (chapter 4). In addition, the same pattern of results was obtained from two different groups of infants that watched either the distal and proximal pointing condition in the current study. Therefore, the results could reflect simultaneous action perception and attentional processes. However, additional studies and analyses parameters such as functional connectivity or coherence analyses (For example, Barzegaran & Knyazeva, 2017; Imperatori et al., 2019) are required to further examine cortical connections, which are beyond the scope of this study and thesis.

The results also revealed a significant difference between the distal and proximal conditions in the right fronto-central region, with greater mu desynchronization for the latter. This finding may provide some support to the recent studies that have investigated the neural correlates of imperative and declarative pointing. For example, Brunetti et al. (2014) provided evidence that both production and comprehension of declarative pointing elicited greater beta activity in the dorsal anterior cingulate cortex within the medial frontal cortex in a group of adults when compared to imperative pointing. Further, an adult PET study revealed that producing the pointing gesture with an intention to show an object activated the right hemisphere, particularly the posterior STS at the temporo-parietal junction and the pre-SMA (supplementary motor area) in the medial frontal cortex (Cleret de Langavant et al., 2011). Henderson et al. (2002) provided evidence from a study with 14-month-old infants that frontal power between 6-9Hz correlated with the frequency of pointing for joint attention (declarative pointing) when they were 18 months old but not with pointing for behaviour regulation (imperative pointing). In the light of these findings, it appears that the difference in the fronto-central mu activity in the current study may be attributed to a difference in how the goals were processed. Although pointing in both the distal and proximal situations entails communicative actions, the former caters to an individualistic, (quasi) instrumental goal of the pointing agent but the latter represents a shared, interpersonal one simply because it is inefficient for an agent to request for an object that she can obtain herself.

One limitation of this study was the absence of an action execution phase, even though we initially assumed that this would not be necessary. Considering the findings from the action observation phase, incorporating parameters to encourage infants to point imperatively or declaratively may have helped us confirm whether mu desynchronization in the fronto-central region differentiates between the goals of the communicative intentions during action execution as well. Future studies may examine this idea and may consider recruiting older children or adults by providing explicit instructions to adhere to their use of gestures unaccompanied by speech or other cues in conveying their intention.

7 General Discussion

The focus of this thesis was to investigate the influences of social and contextual factors on action understanding by means of three studies, during the course of which, I sought to answer the following questions.

- Does action experience precede action understanding?
- Do communicative actions also facilitate mu rhythm desynchronization?
- Does action understanding entail a flexible system that encodes goals of unfulfilled actions and in the absence of object touch?

I have used the EEG method to measure mu rhythm from a group of adults and several groups of infants under different contextual conditions. In the ensuing sections, I will provide a brief summary of the findings, followed by a comprehensive discussion of the key findings and their implications and contributions to the field of action understanding.

7.1 Summary of the Findings

Study 1 (chapter 4) investigated the contextual factors, influencing the meaning of the back-of-hand action. A group of adults watched an agent produce the back-of-hand action in the social and nonsocial conditions and three different groups of 9-month-old infants watched the social, nonsocial and object-absent conditions. Further, the infants in the social and nonsocial action observation group also participated in the action execution phase, where they reached for and grasped several objects. The results revealed a global pattern of mu desynchronization for action execution. In the action observation phase, both adults and infants exhibited significant mu desynchronization for the social condition in the central and parietal regions, and in the right centro-parietal region, respectively but not for the nonsocial and object-absent conditions.

In study 2 (chapter 5), the spatial location of the object was altered, by placing it either close to the tabletop or far above the tabletop, to investigate whether two groups of 9-month-old infants interpreted the goal-directedness of the reach and back-of-hand actions interchangeably in the congruent and incongruent conditions. The infants also reached for and grasped various objects in the action execution phase. The results revealed a global pattern of mu desynchronization for action execution. However, in the action observation phase, the results displayed significant mu desynchronization in the right centro-parietal region only for the incongruent-reach condition but not for the congruent-reach and congruent-backofhand conditions.

Finally, study 3 (chapter 6) examined the prospect that mu desynchronization demonstrated in study 1 reflected infants' anticipation of an instrumental response as opposed to an understanding of the communicative intention. Two groups of 12-month-old infants watched an agent produce a pointing gesture towards an object far away from her (distal) or close to her (proximal) in the presence of a social partner. The findings revealed significant mu desynchronization for both the conditions in the right centro-parietal and the occipital regions. In addition, mu desynchronization in the right fronto-central region was significantly greater for the proximal than for the distal condition.

7.2 Significance of the Findings

The current findings provide further support to recent infant studies (Rayson et al., 2016; Reid et al., 2011; St. John et al., 2016) and adult studies (Aragón et al., 2014; Brown et al., 2013; Oberman, Pineda, et al., 2007; Perry et al., 2011; Streltsova et al., 2010; Tikka et al., 2016) that revealed that mu rhythm activity is modulated by social factors. In addition, the evidence also shows that observing communicative actions within a communicative context as opposed to an individualistic context overturns a meaningless action into something meaningful. When compared to research over the past decade, the current studies provide robust EEG evidence of infants' ability to attribute goals for social, communicative settings as passive third-person observers, providing further support for an early onset of social action understanding from a third-person perspective (Elsner et al., 2014; Liszkowski, 2014). In the following subsections, I discuss the significance of the current findings in detail by incorporating evidence from the extant literature.

7.2.1 Right Hemisphere and Social Information Processing

Mu desynchronization across the current infant studies exhibited significant right-lateralized activation. It should be noted that three of the four conditions (social, distal and proximal) that elicited significant mu desynchronization comprised of third-party (social) settings, depicting simple, real-life communicative situations, although the outcome was never shown. These findings provide some support to infant studies and dual EEG studies with adults that incorporated social factors. For example, a recent report revealed that 30-month-old infants displayed significant mu desynchronization in the right central region when producing and observing facial emotive expressions (Rayson et al., 2016). Similarly, 14-month-old infants exhibited greater mu desynchronization in the right central region during their participation in dyadic interactive settings when compared to observing non-interactive gross movements (Reid et al., 2011).

Further, evidence from adult dual EEG studies indicated greater mu desynchronization and greater interbrain coupling in the right centro-parietal region during behavioural synchrony encompassing imitation and self-paced finger movements (Dumas et al., 2010; Tognoli et al., 2007). Similar interbrain coupling was also reported between the central region of the pain receiver and right hemisphere of the pain observer (Goldstein et al., 2018).

To the best of my knowledge, only one study incorporated a social interaction task when recording EEG from mother-children dyads (Liao et al., 2015). In a turn-taking ‘bubble popping’ game, both mothers and their 3-year-old children displayed significant mu (and beta) desynchronization in the left and right sensorimotor clusters. Further, infant studies incorporating turn-taking and imitation paradigms (for example, Cannon et al., 2016; Debnath et al., 2019; Ruysschaert et al., 2013) and adults observing social interaction from a third-party perspective demonstrated bilateral cortical activation (for example, Oberman, Pineda, et al., 2007; Streltsova et al., 2010).

It should be noted that the turn-taking and imitation paradigms in infant studies comprised of execution and observation of identical instrumental actions such as grasping or button press and the behaviour of the infants were not contingent upon the experimenter’s actions. In other words, placing an object in front of the infant was sufficient for the infants to grasp them, which did not fulfil any complementary or shared goals. In comparison, the paradigms described in the current thesis portray conventional social settings, where the actions of the social partners possibly elicit complementary responses and represent shared goals, such as when requesting for objects or sharing attention.

Considering that human beings learn from and influence others’ behaviours through shared experiences and activities, already beginning in infancy (Tomasello & Carpenter, 2007), perceiving and producing actions frequently occur within such social environments. These highly stimulating settings are not limited to instrumental goals but are also embedded with communicative exchanges, which serve different purposes, specifically behaviour regulation, engaging in joint attention, and processing social information (Crais et al., 2004).

It has been well documented that processing social and emotional information, and social interactions has predominantly engaged the right hemisphere (Adolphs, 2001; Corballis, 2017; Karolis et al., 2019; Krall et al., 2015; Lemée et al., 2018; Semrud-Clikeman et al., 2011). Within this framework, the consistent results displayed in this thesis provide robust evidence for the dominant right hemisphere activity for processing social information and social goals in infants. Further, this interpretation is applicable to processing social information not only from a third-person perspective, as evident from the current findings but also from a second-person perspective, as revealed by previous studies described above.

7.2.2 Goals and Actions

Early research of the MNS in the monkey cortex indicated that intentions are coded in the posterior parietal regions (Andersen & Buneo, 2002; Fogassi et al., 2005). The role of this posterior region for intention understanding and predictive action processing were confirmed subsequently in research with human participants (for example, Aflalo et al., 2015; Fontana et al., 2012; Hamilton & Grafton, 2006; Pereira et al., 2017; Turella et al., 2020). In keeping with this line of research, the consistent findings of this thesis, specifically significant mu desynchronization in the right centro-parietal region for infants, could be driven by the top-down processing of goals of the observed actions but not essentially by lower level action kinematics (see Hamilton & Grafton, 2007). In addition, this interpretation also supports a context-based, predictive cortical activation rather than a sensory-driven, reactive processing of the actions (Bonini, 2017; Kilner et al., 2007; Southgate, 2013). The present evidence demonstrates that the right centro-parietal region was activated, irrespective of whether the observed action comprised of unfulfilled grasping, back-of-hand or pointing actions. Moreover, ascribing goals for these actions resulted in embedding the observed actions within this predictive framework in order to achieve a coherent action-context representation. Therefore, the current findings also provide the evidence that observing actions with distant, embedded goals as well as actions that do not result in touching the object elicit significant mu desynchronization.

With reference to the present data, significant right fronto-central mu desynchronization was evident only for the observed proximal pointing but not for the observed distal pointing or unfulfilled grasping or back-of-hand actions. There could be some possible explanations for this result. The frontal areas of the parieto-frontal mirror circuit have been associated with motor analysis of the action (Hamilton & Grafton, 2007; Leo et al., 2016; Turella et al., 2020), and probably fulfills a supplementary function to goal attribution. The reciprocal connections between the parietal and frontal areas also allow for monitoring and minimizing errors during action processing (Kilner et al., 2007), Therefore, due to the proximity of the object to the pointing agent, the infants perhaps focused on the lower level features of the palm and fingers to verify the purpose of the action. When observing distal pointing or the social back-of-hand action, the distance of the object perhaps did not require such verification of the initial goal attribution of the action. Another likelihood is that the frontal areas encode imperative and declarative pointing differently as elaborated in chapter 6 (Brunetti et al., 2014; Cleret de Langavant et al., 2011; Henderson et al., 2002) and the current results provide some support to this line of research. A third related possibility could be that observing proximal pointing engaged both the mirroring and the mentalizing systems, which also includes the frontal regions (Hari et al., 2015), considering that infants' ability to perceive and produce declarative pointing indicates early mentalizing skills (Carpenter, 2009), albeit from a third-person perspective. The latter possibility is rather speculative given the current data available and a discussion of the literature on the mentalizing system is beyond the scope of this thesis. Nevertheless, this line of thought offers an interesting prospect for future research.

7.2.3 Occipital Alpha, Visual Processing and Attention

The most common theme underlying EEG studies of action understanding is how well the mu activity generated during action observation or action execution exhibits the processes related to action understanding and is not merely due to differences in attentional demands, typically defined by the alpha activity generated in the occipital region (Cuevas et al., 2014; Fox et al., 2016; Hobson & Bishop, 2017). Due to the similarity of the frequency band of mu and alpha (8-13Hz in adults; 6-9Hz in infants), it has been suggested that significant mu and alpha effects when observing an action could reflect attentional components as opposed to action understanding (Perry & Bentin, 2010).

In this thesis, the action execution task in studies 1 and 2 (chapters 4 & 5) elicited global mu desynchronization, including occipital alpha. The observation of distal and proximal pointing (chapter 6) elicited significant mu and alpha desynchronization in the right centro-parietal and occipital regions, respectively. Moreover, the other conditions that elicited significant mu desynchronization in the right centro-parietal region (chapters 4 & 5), i.e., the social condition and the incongruent-reach condition, also exhibited occipital alpha desynchronization, although not significant.

To conduct successful EEG studies with infants, the investigator needs to consider some variability in the stimuli to enhance interest and attention, and thereby, increase the number of valid trials per infant (Stets et al., 2013). Implementing such procedures for the current studies resulted in incorporating interactive action execution procedures, with a variety of colourful objects and including similar variations in the type of objects used, the colour of the tablecloth, and different melodies for the videos presented during action observation. These varying elements possibly already induce some amount of attention due to their saliency and attention-orienting properties (Amso & Scerif, 2015; Colombo, 2001) and cannot be avoided in infant studies. However, it should be noted that these variations were included in all the conditions presented in the current studies and were identically counterbalanced across trials. Therefore, if the difference in attention was caused by these low-level variations alone, the effect should have been evident in all the conditions, irrespective of the actions observed or the contexts in which the actions were observed.

When infants execute a goal-directed action, there are several aspects that they may pay attention to such as the features of the object, or the distance or their preference for the objects and the like. The last feature, i.e., their preference for the object is particularly interesting because this also leads to some form of decision-making on whether the infant is motivated to grasp the object. For example, an infant from study 1 showed a tendency to grasp colourful objects but not the black-and-white ones. Similar non-motor processes may also influence infant's attention during the action observation phase. Moreover, familiarity with and recognition of the pointing action may have driven 12-month-old infants to pay more attention to the pointing videos. Finally, in order to perceive social cues, infants and even adult participants in the current studies had to construe meaning primarily from visual information, which may have also resulted in allocating some attentional processes. Further, this holds true for most action execution and action observation paradigms, where much of information processing is dependent on the visual system.

Nevertheless, this is not the first time that occipital alpha desynchronization was evident in parallel with mu desynchronization. Recent infant turn-taking and imitation paradigms involving grasping and button press actions have also elicited occipital alpha desynchronization, which has been attributed to visual processing and selective attention (Cannon et al., 2016; Debnath et al., 2019; Filippi et al., 2016; Meyer et al., 2016; Montoirosso et al., 2019; Warreyn et al., 2013; Yoo et al., 2016;). Using functional connectivity analyses, Debnath et al. (2019) were able to demonstrate that central mu and occipital alpha desynchronization reflect distinct but functionally connected processes, and that both attention and motor processes are involved in both action execution and action observation. Further, similar findings from adult EEG studies also implicate processes involved in observational learning and visual and sensorimotor integration during turn-taking and imitation paradigms (Makhin et al., 2019; Quandt et al., 2011; van der Helden et al., 2010).

The above evidence seems to indicate that the visual system not only plays a role in encoding the visual features of the object but it is also involved in generating a visual representation of the actions before converting this information into a motor code (Csibra, 2008). Therefore, the evidence reported in this thesis provides further support to brain activation patterns encompassing coherent task-related processing. The evidence also suggests that visual processing and attention are essential for action understanding and are not merely confounding variables as indicated by Coll et al. (2015, 2017) and Hobson & Bishop (2017).

Indeed, future studies may incorporate functional connectivity analyses procedures to disentangle motor and attentional processes in order to gain a better understanding of how these processes and other coherent aspects of a social setting modulate infants' action understanding during development. In addition, future paradigms may also include an additional control condition that does not depict actions or social cues. Observing such a condition should not lead to the allocation of motor processes, but could still induce attentional components due to the saliency of such cues. These control conditions may help examine the factors that elicit alpha or mu activity alone and those that modulate both alpha and mu rhythms simultaneously.

7.2.4 Revisiting Action Execution

Infant EEG research over the past decade has repeatedly emphasized on the need to incorporate both action execution and observation paradigms to decipher whether the reactivity of the mu frequency band is related to motor and mirroring processes (Cuevas et al., 2014; Marshall & Meltzoff, 2011). Specifically, a topographical overlap between action execution and action observation may be construed as evidence for the aforementioned processes even in the absence of a one-to-one correspondence between the executed and observed actions (Cuevas et al., 2014; Marshall & Meltzoff, 2011). The paradigm included in the studies of this thesis is an example of this lack of correspondence between the actions, where infants executed an action within their motor repertoire (grasping) but observed an action outside their motor repertoire (back-of-hand) (chapters 4 & 5). Further, the infants played the role of the second person in the former but of a third-party observer in the latter. The results from the current studies did not reveal a specific topographical overlap between the action execution and action observation phases.

Considering that other coherent processes may also be involved during action execution, it is surprising that other studies do not find a similar global pattern of mu desynchronization as described in this thesis, although recent investigations have shown this tendency (for example, Cannon et al., 2016; Montirosso et al., 2019; Yoo et al., 2016). A closer look at the action execution paradigms brings to light the rapidly unfolding reciprocal nature of the task, where an experimenter presents an interesting situation for the infant by calling for attention, establishing eye contact and presenting an object. Following the agent's signal, infants typically respond in a contingent manner by turning their head, sharing eye contact and grasping an object. A recent study provided evidence that 9-month-old infants exhibited global desynchronization in the 5-7Hz range when an adult demonstrated novel objects after establishing eye contact but not otherwise (Hoehl et al., 2014). As eye contact marks the first step of social interaction (Holleman et al., 2020; Jarick & Bencic, 2019), this is an important finding and needs to be considered in future studies. Further, executing goal-directed arm movements also require close attention to the distance, size, or shape of the object as well as the form of the palm and fingers and may engage potential action monitoring processes that enable obtaining the objects successfully.

Therefore, when numerous non-motor processes occur simultaneously, a global pattern of activation may be acceptable for action execution and it may be difficult to isolate these concurrent processes. Nevertheless, the absence of topographical specificity does not conclusively indicate that the results were being driven from general attentional or motivational components, despite their relevance for these tasks. Consequently, the objective of finding a specific topographical overlap between action execution and action observation should not be used as the sole criterion to investigate action understanding, as action execution and action observation may entail some overlapping and yet differential allocation of coherent processes. Finally, the current findings provide further support to the importance of analyzing mu activity across cortical regions to gain an insight into the different factors that modulate goal attribution of self-executed actions.

7.3 Theoretical Implications

The pattern of the current findings cannot be explained solely by means of the direct-matching theory (Rizzolatti et al., 2001) or the social responding account (Hamilton, 2016). The action reconstruction account (Csibra, 2008) also falls short, as the postulated emulative process is considered relevant for understanding instrumental actions alone (Pomiechowska & Csibra, 2017). In the following subsections, I discuss the current findings in light of the existing theories, challenge the premise of these theories, and suggest that a composite perspective is more suitable to explain the mechanisms of action understanding.

7.3.1 The Role of Action Experience

One of the questions I have sought to answer in this thesis is whether active experience with an action precedes action understanding. The results from study 1 (chapter 4) indicate that 9-month-old infants, who do not typically produce the back-of-hand gesture to request for objects, perceive this gesture as meaningful when observing it in a social situation and in the presence of the goal object. In addition, the study did not incorporate training sessions or familiarization trials and infants had to rely on their inference to attribute meaning to the actions. Therefore, the results cannot be explained by the direct-matching account that suggests that action experience precedes action understanding (Rizzolatti et al., 2001). Further, the other findings from this study are also crucial, i.e., the nonsocial and the object-absent conditions do not elicit mu desynchronization. These negative results indicate that the infants do not attribute a goal to the back-of-hand action in the absence of a social partner and a goal object.

Considering these results, I challenge previous evidence that suggests that prior action experience facilitates action understanding.

A crucial feature that distinguishes active training from observational learning lies in the greater level of engagement for the former when compared to the latter. Studies in this line of research focus on the difference in mu desynchronization following these two types of training/learning methods (for example, Cannon et al., 2014; Gerson, Bekkering, et al., 2015; Marshall et al., 2009; Paulus et al., 2012, 2013; Quandt & Marshall, 2014). Therefore, it is possible that the difference in subsequent motor activation during action observation could be related to the question of degree or intensity of activation (Cross et al., 2009) and not whether the observed action was interpreted as meaningful or not. In other words, if action observation following active training and observational learning elicits significant mu desynchronization (when compared against a baseline or zero) but differs significantly in intensity, it does not necessarily imply that one group understood the action or attributed the goal more than the other did. Specifically, it does not seem practical to categorize action understanding in terms of low or high understanding, based on the magnitude of mu desynchronization, unless such an interpretation is supported by additional behavioural measures or verbal reports. While most training studies focus on this significant difference between the groups, the fact that both groups elicited mu desynchronization during observation may have been overlooked. The reason for a difference in the magnitude of mu desynchronization could result from a temporal association between active training and action observation, although it is not clear why such an association should elicit greater desynchronization in one group compared to the other.

Evidence from studies investigating the association between motor competency and mu desynchronization (Cannon et al., 2016; Upshaw et al., 2016; Yoo et al., 2016) also overlook similar possibilities as above. In other words, differences in grasp latency or grip strength, for example, do not prevent the infant from obtaining the object, which is the overarching goal of the grasping action. Therefore, for a robust evidence of the influence of action experience on action perception, it does not suffice that mu desynchronization between differently trained or competent groups differs significantly but it is also necessary to examine the results of each group separately.

The findings from infant behavioural and eye tracking studies incorporating training paradigms also seem to elevate the role of active experience in action understanding (See Hunnius & Bekkering, 2014 for a review). However, the effects that are taken as evidence could also be explained by novelty recognition as opposed to goal attribution. For instance, 3-month-old infants that accidentally picked up objects while wearing sticky mittens paid more attention later to the observed grasping action when compared to those that did not receive similar prior training (Sommerville et al., 2005; see also Needham et al., 2017 and Wiesen et al., 2016). In this case, the infants with active experience possibly recognized the novel action-object contingency that they recently discovered but it does not provide conclusive evidence that active experience played a causal role in goal attribution (see also Williams et al., 2015).

Finally, evidence from studies investigating differential motor activation between experts and novices, especially in the case of dancing or sports (see Yang, 2015 for a review) cannot be considered as conclusive evidence that action understanding necessitates experience with an action. Dancing and sports require a specific set of skills and practice with movements that enable the experts to perform at their optimal level and these skills are not commonplace for everyday actions and social interactions, and thus, are possibly considered meaningless by novices. Therefore, it may be justified that the experts but not the novices are able attribute goals to a specific sequence of movements.

However, while the above arguments question the efficacy of the evidence in support of the direct-matching account in qualifying one's action understanding, the current findings do not disregard the influence of action experience entirely. Human beings acquire several different experiences and knowledge systems during development and across their lifespan. Consequently, it is difficult to decouple whether action understanding involved purely experiential influences or only inferential processes. For example, in study 1 of this thesis (chapter 4), the adult participants applied their experience and knowledge regarding the purpose of the observed back-of-hand action to infer a goal, which was confirmed by their verbal reports. Nevertheless, their experience with the action was not a pre-requisite to attribute a goal, as evident from the infant data. Thus, the direct-matching approach, which advocates action experience as causal for action perception is somewhat flawed. The processes that enable goal attribution and action understanding are not dependent entirely on the available motor repertoire, but other flexible, inferential processes also play an influential role and is further elaborated in the following subsections.

7.3.2 The Rationality of Alternative Accounts

The action reconstruction account (Csibra, 2008), according to which action understanding follows a predictive, emulative process or the social responding theory (Hamilton, 2016) that advocates a prospective role in action understanding, seem to offer some flexibility in explaining the current findings, when compared to the direct-matching account.

The fact that 9-month-old infants, who do not typically produce the back-of-hand action to request for objects, displayed significant mu desynchronization while observing the back-of-hand action in the social condition conforms to the action reconstruction account (Csibra, 2008). There is already evidence that young infants either reach communicatively towards or point to distant objects that they cannot reach (Carpenter et al., 1983; Crais et al., 2004; Franco & Butterworth, 1996; Liszkowski, 2014; Ramenzoni & Liszkowski, 2016; Veena & Bellur, 2015) and therefore, infants in the current study possibly emulated a similar means to request during their observation of the back-of-hand action. Importantly, the context of the setting – the presence of a social partner and an object – set the scene for such an inference and not simply the unfolding of the back-of-hand action itself, which also provides further support for action reconstruction.

Communicative situations are replete with opportunities for exchange of information, or collaborative actions. Turn-taking and imitation paradigms are some basic examples of such settings, where such an exchange is possible. Consequently, as social beings, we do not resort to passive observation of such situations but also prepare ourselves to respond appropriately (Dezecache et al., 2013), and in coherence with the previously received input. Therefore, the successful emulative process may not have been passive in a communicative context and it seems natural to anticipate the response of the social partner.

Considering the evidence from studies 1 and 3 (chapters 4 & 6), where infants exhibited significant mu desynchronization for the (social) back-of-hand and distal pointing conditions, it may be relevant to further investigate whether mu desynchronization reflects infants' anticipation of a response from the social partner, even though the results suggested the contrary. Therefore, the current findings seem to provide some support to the social responding theory of action understanding (Hamilton, 2016), according to which social situations are dynamic and demand active involvement.

At the outset, it appears as if the present findings conform to both the accounts as I have explained above because such emulative processes and response predictions govern social interactions in real-life settings. However, these two plausible mechanisms were temporally inseparable with regard to the data available from the current studies, and therefore, presented an interesting dilemma regarding the interpretation of the mu desynchronization. Specifically, it is not possible to differentiate conclusively whether action reconstruction or social responding by itself could explain the findings. In the following, I provide some counter arguments, which question the premise of these two accounts of action understanding with reference to the current findings.

***Reconstructing communicative intentions*.** The teleological stance (Csibra, 2003; Csibra & Gergely, 2013; Gergely & Csibra, 2003) advocates an efficient, non-mentalistic mechanism of action perception that is contingent upon contextual information regarding the goal, situation constraints and the means to attain the goal. However, this system pertains only to instrumental actions that serve to achieve end states but not to communicative or referential actions, which attribute mental states and communicative intentions (Csibra, 2003; Pomiechowska & Csibra, 2017).

Considering the evidence that young infants are able to recognize communicative intentions, when directly addressed using ostensive signals such as eye contact, infant-directed speech or contingent responsivity (Csibra, 2010), it does not seem fit that the emulative processes of action reconstruction do not apply to communicative intentions. Precisely this viewpoint relates directly to the question that I have sought to answer – does observing communicative intentions modulate the mu rhythm?

Drawing on the ‘Relevance Theory’ postulated by Wilson & Sperber (2002), Csibra (2010) suggested that informative intention and communicative intention are procedurally and temporally separate but conceptually related, where the former is embedded within the latter. Once infants recognize a communicative intention of the communicating agent by means of ostensive cues, they try to infer the subsequent content of the informative intention, although the process may not be similar to the more advanced inferences of adults (Csibra, 2010).

In the current studies, the observation settings included both communicative and informative situations, especially in the presence of a social partner. The videos showed a brief eye contact between the two agents, followed by the unfolding of the action. Therefore, the above mechanisms proposed by Csibra (2010) are applicable to these situations as well, albeit from a third-person perspective. In other words, infants were able to recognize the communicative intention due to the brief eye contact between the agents, followed by their inference of the informative intention of the observed action. In settings where the contextual cues were not congruent, they failed to recognize the communicative intention or infer the informative intention or both, as the case may be.

The findings of the current studies may be explained by combining the aforementioned processes – the emulative mechanism of action reconstruction, the concept of efficiency, based on infants' teleological representation of actions (Csibra, 2003) and infants' ability to recognize communicative intentions (Csibra, 2010). Specifically, the experimental setting (social back-of-hand and distal pointing) represented quasi-instrumental goals because the end state of a request action is to obtain the object. I refer to it as quasi-instrumental because the goal could not be directly attained by the agent producing the action but could be indirectly achieved by means of a communicative gesture. However, such a request also generated a referential expectation because the request refers to a specific object, which is also the case in real life object-directed requests. Therefore, considering the situational constraint or context (distance from the object), the most efficient way that the agent could attain the goal (object) was to request for it (action or means – communicative/informative), especially in the presence of a social partner. Conversely, going around the table to obtain the object by herself would have been inefficient and would have required the agent to expend unnecessary effort, especially in the presence of a social partner.

Further, the interpersonal setting of proximal pointing represented a typical communicative scenario devoid of instrumental goals, where the agent established a communicative intention, followed by an informative intention towards the object. In this case, the agent sought to draw the partner's attention to the object (goal) by pointing to it (action) and there were no apparent situational constraints. The process in this case could be emulative as one could use various other means, such as eye gaze towards the object or holdout and show the object, to drawn attention to it. The most efficient means to do so could be achieved in conjunction with establishing a communicative intention.

Importantly, the mechanism to infer both these communicative goals remains non-mentalistic because the infant has little knowledge of the mental states or beliefs of the agent requesting for or pointing to an object or the reason she requested for or shared attention towards it. In other words, infants' interpretation of the back-of-hand and the pointing actions is no different from an observed grasping action, where they possibly associate the agent's reaching and grasping action with obtaining the goal object but nothing beyond this, especially in the absence of additional cues. However, it is possible that these early inferences lead to more complex collaborative or joint attention activities, where there is a gradual shift from a non-mentalistic to a mentalistic representation of subsequent actions (Csibra & Gergely, 1998; Gergely, 2003).

Considering the above arguments, it may be appropriate to suggest that the mechanism of action reconstruction can be applied to both instrumental and communicative actions alike. The goals in both these cases pertain to the immediate task and these basic inferential processes are not contingent upon one's knowledge of prior beliefs or mental states as evident in the present findings.

***Anticipating social responses*.** According to the concept of contingent responsivity (Csibra, 2010), infants participate in communicative exchanges with the caregiver from early on, following a typical turn-taking format, where an initial social behaviour stimulates an appropriate response. This is similar to the prospective account of action understanding, as advocated by the social responding theory (Hamilton, 2016). Within the context of the current studies, observing the agents' communicative actions may result in anticipating a social response, considering the logical sequential progression of such actions. Specifically, a request action may be followed by the partner's hand over response. Sharing attention towards an object could result in playing with it together or learning about the object. This is also similar to the concepts of '*chained motor organization*' (Fogassi et al., 2005, p.665) or logically-related neurons (di

Pellegrino et al., 1992), where actions embedded in a sequence do not merely represent temporal association of such actions.

At the outset, the current evidence could suggest that the significant mu desynchronization could depict infants' anticipation of a social response, such as picking up the object to handover or generating an appropriate reaction following shared attention. However, the social responding account cannot be applied to one's understanding of conventional, individualistic instrumental actions such as grasping objects unless the observer has more information regarding its future relevance at his or her disposal. For example, if an agent grasps a pen and a piece of paper is present nearby, then one could anticipate that the agent may use the pen to write as the next step. Similarly, after grasping the handle of a mug with one hand, one's response anticipation that the individual may grasp the other side of the mug with the other hand (Hamilton, 2013a) requires additional cues that facilitate such a response. Conversely, without the additional information, it is not possible to prepare for what comes next and it may be possible that the actions do not require a response.

Following a similar thread, the anticipation of subsequent responses are contingent upon one's inference of the goal of the initial action and is not arbitrary. To elaborate, it is not possible to anticipate that an agent's goal would be to write if the goal-directedness of the grasping action towards the pen is not initially attributed. Similarly, expecting that the agent would reach for the mug using the other hand is contingent upon the perception of the initial grasp of the handle of the mug.

In the context of the current findings, for example, it is not possible to anticipate that the social partner would handover the object unless the purpose of the initial request is understood. As these processes are quite swift in real-life situations, it is not possible to temporally separate one's inference of the goal and the subsequent response anticipation by means of mu desynchronization, despite their typical ordinal sequence. Specifically, as the two processes are continuous, it may not be possible to decipher what part of the mu desynchronization belongs to goal attribution and what part belongs to response anticipation during the timeline of the events. Further, participants may differ in their processing speed of the actions or at what point they begin to anticipate a response. Unless the investigator eliminates the overlap between these processes, it is difficult to analyze whether goal attribution or response anticipation in isolation would facilitate mu desynchronization in the social settings of the current studies. One possible way to incorporate a clear distinction would be to introduce the recipient after the agent completes her unfolding of the action. Further, the time between the completion of the action and the arrival of the recipient may be varied and these trials may be interspersed with nonsocial events, in order to avoid the anticipation of the sequence of events that may confound the results. While such a paradigm allows for a separate analysis of the mu desynchronization elicited from these processes, goal attribution and response anticipation remain inter-dependent. Therefore, it is appropriate to postulate that understanding or predicting complementary social actions requires a combined mechanism involving both goal attribution and response anticipation, where the latter follows the former and cannot occur in isolation.

7.3.3 Contextual Congruency and Action Understanding

In the previous subsections, I have discussed the current findings within the framework of three prevailing theories of action understanding and provided sufficient reasons for their shortcomings in explaining the current findings. The direct-matching theory (Rizzolatti et al., 2001), as elaborated before, does not offer a justifiable explanation, as infants are able to perceive actions that they do not yet produce. The action reconstruction account (Csibra, 2008) postulates that infants understand goals of instrumental but not of communicative actions (Csibra, 2003; Pomiechowska & Csibra, 2017), which is contradictory to the current findings. Finally, the social responding theory (Hamilton, 2016) is more applicable to situations implying communicative or social exchanges but not every situation necessitates a response. Therefore, it is implausible that only one of these theories provide the most suitable explanation for action understanding under all circumstances, considering the diverse behavioural patterns in humans.

As a result, one's interpretation of actions is contingent upon the **contextual congruency** of the observed actions. By emphasizing on contextual congruency, I propose that action understanding is facilitated by an amalgamation of the several mechanisms that have been proposed thus far – such as knowledge, experience, action kinematics, emulation, inference, or response prediction – however, not necessarily in any particular order. Specifically, goal attribution entails relating the three factors, i.e., action, goal and context (Csibra, 2003) and the congruent relationship among these factors may be facilitated by any of the mechanisms listed above, thereby not operating in a restricted manner. The separation of these possible mechanisms that facilitate action understanding as postulated by the existing theories offers limited scope and flexibility in the interpretation of the observed action-goal-context contingencies.

Importantly, action understanding is not limited to one's motor repertoire, to only instrumental actions or to anticipatory responses. In other words, action understanding is dependent on one's inference of goals and the contingency of the observed action within a given context. The mechanisms that facilitate successful goal attribution, action understanding or efficiency monitoring such as retrieving an exact motor copy of the action, emulating the action, predicting a response or a combination of these processes are rather supplementary to the demands and inferences of the action context. In addition, as these processes are supplementary, the non-availability or non-implementation of one or more mechanisms need not necessarily hinder goal attribution and action understanding. To elaborate, if an action is not part of the motor repertoire, it may still be understood by means of emulation. Even if an observed action does not result in anticipating a response, it does not alter the meaningfulness of the attributed goal. Therefore, the absence of some mechanisms are compensated by the availability and implementation of the others, thereby offering the highest possible flexibility for goal attribution and action understanding. Moreover, contextual congruency may be applicable to both instrumental and communicative actions because it allows for the processing of both instrumental and communicative goals by similar means. The composite perspective of contextual congruency with reference to the existing theories is illustrated in Figure 17.

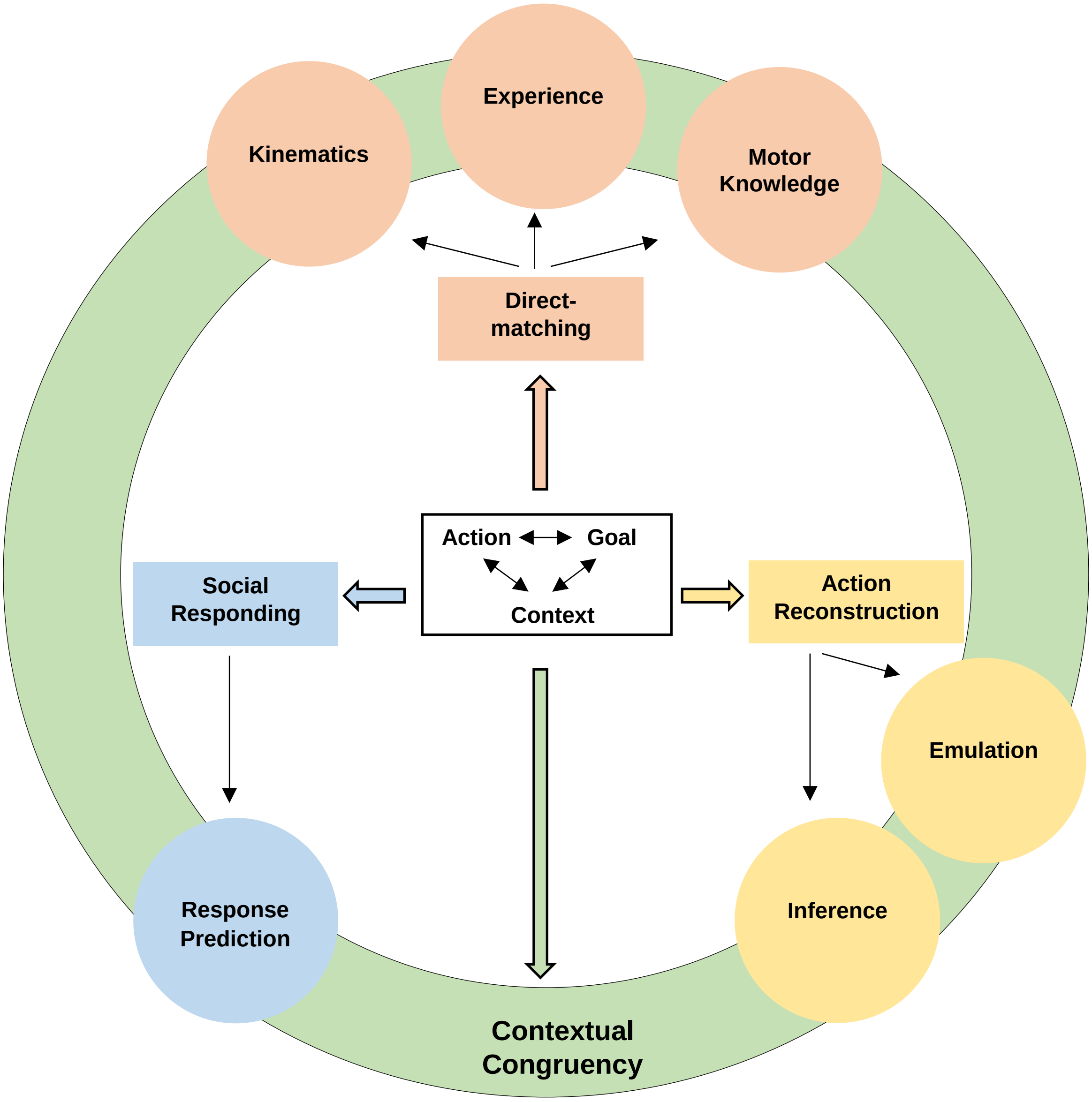

Figure 17: Contextual congruency

The interaction of the three factors, i.e., action, context and goal, facilitates action understanding, however, in a flexible manner by incorporating one or more mechanisms or combinations of mechanisms put forth by the existing theories (direct-matching, action reconstruction and social responding).

Contextual congruency provides the most suitable explanation for the findings of this thesis and may be applicable to most findings from previous literature. For example, the observation of the back-of-hand action did not result in action understanding when implemented as a control condition (Hamlin et al., 2008; Krogh-Jespersen & Woodward, 2014; Southgate et al., 2010; Thoermer et al., 2013; Woodward, 1999). In this case, when the back-of-hand action simply replaced the grasping action, it was perceived as meaningless as grasping was contextually more congruent to obtain the object instead of the back-of-hand action. However, when the back-of-hand action was incorporated within a social context (chapter 4 of this thesis), it was perceived as relevant to the goal as long as the contextual criteria were fulfilled. In other words, the action was not perceived as meaningful in the absence of a social partner or a goal object. Similarly, pointing also requires a social context, as was evident from the findings of the distal and proximal pointing conditions (chapter 6). The lack of mu desynchronization for the observed pointing action reported by Pomiechowska & Csibra (2017) could be due to this missing feature. Further, observing the unfulfilled reach or the unfulfilled back-of-hand actions was not perceived as meaningful (chapter 5) due to the contextual incongruence of the sudden termination of the action and the absence of more relevant cues, respectively. On the contrary, previous studies that incorporated grasping actions exhibited goal attribution because the contextual factors allowed for direct fulfillment of the goals or created an appropriate, realistically plausible situation that did not result in goal attainment (for example, Brandone et al., 2014; Köster et al., 2016). Thus, whether goals are attributed from a second- or third-person perspective, within a social or object-only context or in interactive turn-taking settings, contextual congruency seems relevant and plays an important role, especially when considering the fact that real-life situations are much more complex and even more so during infant development.

Based on the extant evidence, the interpretation of action understanding should be cautiously limited to a lean approach that is restricted to the inference of imminent goals and the congruency of the means to attain them. In other words, the observed actions do not involve attributing complex inferences or additional parameters by means of further reflection of the actions, the goals or the context. Instead, the interpretation is based on the information available to the observer. This could also explain the lack of goal attribution for the object-absent condition in study 1 (chapter 4), where the possibility of a goal object located ‘somewhere’ could not be established and such an inference may have necessitated some amount of reflection regarding the object. Further, on observing a grasping action, one understands that the goal of the action was to obtain an object, followed by a possible related task, such as to write with a pen or to drink from a mug, depending on the inferences drawn from additional cues available. However, this understanding does not entail a rich interpretation that encompasses complex inferences about the mental states, desires, beliefs, motives or the distant plans of the individual executing the action. Therefore, one cannot infer whether the individual drank from a mug to quench his or her immediate thirst or to achieve a distant goal but is limited to the perceptible features of the goal. Therefore, despite the promising evidence and the increasing interest in EEG mu rhythm studies over the years especially with infant samples, caution needs to be exercised before extending its implications to functions beyond the perceptible action goals and action understanding.

7.4 Developmental Implications

As communication and social influences play an enormous role during development (Bourvis et al., 2018; Ramírez et al., 2020; Shin, 2012), the ability to process social and/or communicative cues during infancy possibly prepares for further acquisition and implementation of these skills or the lack thereof in various settings. Therefore, from a developmental perspective, I predict that the present findings may find their implications in two major fields of developmental research: language acquisition and developmental disorders such as autism spectrum disorders (ASD).

***Language acquisition*.** Recent EEG research with adult samples revealed that processing action verbs elicited significant mu desynchronization in the same sensorimotor cortical regions as when observing the corresponding actions themselves (Cuellar & del Toro, 2017; Klepp et al., 2019; Moreno et al., 2013; Niccolai et al., 2014).

To the best of my knowledge, only one study has investigated the relationship between mu activity and hearing action verbs with young toddlers, aged 18 and 24 months (Antognini & Daum, 2019). In this study, simple action verbs (such as cut, draw, build) were presented both in the auditory modality, as a two-word sentence (for example, “I cut”) or in the visual modality, with an agent performing the actions. The results revealed significant mu desynchronization in the left central region for action verbs in the auditory modality and right central region for action observation in the visual modality along with significant occipital alpha desynchronization in both modalities.

If the current experimental paradigms depicting social and/or communicative goals were also presented in the auditory modality, I would expect to find similar results as reported in this thesis due to the implied social significance of the auditory request. However, the verbal presentation of the actions could also elicit left hemisphere activation consistent with the study by Antognini & Daum (2019) and with previous evidence that language and action processing share the same left-lateralized network (Corballis et al., 2012; Hayek et al., 2018; Healey & Braun, 2013; Xu et al., 2009).

The concept of contextual congruency may also be applied to one’s interpretation of infants’ development and understanding of language skills, considering that novel words and their meanings are acquired through contingent social interactions (for example, see Roseberry et al., 2014). Therefore, a consequence of implementing such paradigms would also be to determine infants’ receptive vocabulary skills at different stages and their relationship with later speech production and language acquisition.

Autism spectrum disorders (ASD). The symptoms of ASD such as impairments in social interaction, communication, emotion, imitation and language have been linked to the dysfunction of the mirror system (Iacoboni & Dapretto, 2006; Ramachandran & Oberman, 2006; Shields, 2012), although such a claim has been criticized (Hamilton, 2013b; Southgate, Gergely, et al., 2008; Southgate & Hamilton, 2008).

Previous studies investigating the modulation of mu rhythm activity in autistic individuals (for example, Bernier et al., 2007, 2014; Dumas et al., 2014; Martineau et al., 2008; Oberman et al., 2005, 2008, 2013) implemented observation and execution/imitation of conventional hand actions or hand-object manipulations. These studies provided evidence that individuals with ASD did not elicit significant mu desynchronization during action observation when compared to the matched controls. However, there is evidence that not all individuals manifesting ASD symptoms exhibit deficits in instrumental action understanding or imitation of goal-directed actions or facial expressions (Hamilton, 2013b; Southgate, Gergely, et al., 2008), thereby limiting the scope of instrumental action paradigms for this purpose.

Considering that gestural and communicative patterns during infancy may have a predictive role in the later diagnosis of ASD (Crais et al., 2006; Shumway & Wetherby, 2009; Watson et al., 2013; Wetherby et al., 2007), it would be reasonable to investigate whether incorporating social observation paradigms, similar to the current thesis, is more representative with this special sample. Moreover, the passive paradigms implemented in this thesis do not require any reciprocal responses. In other words, motivation and willingness to produce a response in typical interactive settings may influence subsequent behaviour, which is not the case with passive observation. Especially in the case of infants, passive paradigms may be more appropriate as it is challenging to provide instructions and to bring about the desired behaviours or responses.

The inability to attribute social or communicative goals in contextually congruent situations, if evident by means of a lack of significant mu desynchronization when compared to a baseline and to a normally functioning group, would be a better measure to establish a relationship between mu activity and ASD impairments, as opposed to presenting individualistic instrumental actions alone. Moreover, social action goals require a more complicated assessment of the social settings when compared to individual action goals, suggesting that social interactional difficulties typical of ASD could be also be explained from the contextual congruency perspective. In other words, the lack of significant mu desynchronization for the observed social action paradigms could be attributed to a weak ability in recognizing the congruency among the action, context and goal, specifically for social communicative goal attribution. It may be possible that individuals with ASD find it difficult to associate social cues such as the presence of a social partner, establishing eye contact, the social context, and the rationality of the observed action to achieve the intended goal as a congruent whole. They may possibly also find it challenging to implement the mechanisms such as emulation, action experience, drawing inferences or predict a response that facilitate the understanding of action-goal-context (social) contingencies.

Considering the challenges of conducting fMRI, recording EEG and analyzing mu desynchronization may be better suited to examine infants' online processing of social settings to investigate whether their ability to attribute communicative goals may correlate with a later diagnosis of ASD. Exploring potential early warning signs in infancy (Volkmar et al., 2005) make early intervention possible and avoid delays until a formal diagnosis is completed, especially in cases of at-risk population. Therefore, findings from EEG paradigms examining social action understanding may provide supplemental information to the typical behavioural observations of ASD predispositions.

7.5 Limitations and Future Outlook

Despite the promising findings of the current thesis, some important limitations need to be considered. Previous research has established that mu desynchronization elicited from the action observation and the action execution paradigms is representative of the mirror system functions and may be localized to the parietal and frontal regions included as part of the mirror system (Arnstein et al., 2011; Thorpe et al., 2016). However, it should be noted that the evidence in these studies has been derived from additional source localization analysis parameters. Therefore, owing to the low spatial resolution in EEG and in the absence of additional source localization analyses, caution needs to be exercised when drawing parallels from the current findings to the precise regions of the mirror system. Specifically, the results demonstrated in this thesis should be treated as proxy to the mirror system functions but they need not directly represent the activation of the IFG, the vPMC or the IPL regions of the mirror system. This is applicable to all the existing EEG mu rhythm research without the implementation of source localization or functional connectivity analyses.

The current studies were devoid of any experimental paradigms incorporating conventional actions such as grasping or button press that has been frequently reported thus far. Including such paradigms within the current social settings and additional individual settings and comparing mu activity among these conditions would have helped further reinforce the role of the right hemisphere in the social action observation settings. Moreover, the social element could also be manipulated, such that the social partner diverts her attention away from the unfolding action or is blind-folded or is pre-occupied in order to examine how such situational constraints modulate action understanding and mu rhythm activity. In addition, the current studies did not include an investigation of infants' gesture knowledge, both comprehension and production, by means of parent questionnaires or behavioural studies. Considering the novelty of the observation paradigms, such additional data would have been advantageous in reinforcing and strengthening the findings further.

As mentioned previously, the social, contextual paradigms incorporated in the current studies are novel and have not been employed before. As the findings could not be explained using existing theories, a composite perspective referred to as the contextual congruency was suggested to justify goal attribution and action understanding. However, this account needs to be further tested and confirmed using equivalent or similar procedures by implementing additional social manipulations, incorporating familiarization of goals and intentions, testing different age groups, using other methods besides EEG and converging findings across research laboratories.

Future EEG studies may also consider recruiting infants younger than 9 months of age to investigate infants' early social action understanding skills, especially to examine the earliest manifestation of inferential processes. Further, longitudinal designs combining behavioural and EEG paradigms may also provide valuable data on the relationship between infants' emerging social, cognitive and motor skills and their ability to anticipate and infer congruent action-context-goal relationships at different stages of development.

7.6 Concluding Remarks

By means of implementing novel social paradigms in the current EEG studies, I provided neurophysiological evidence of infants' early ability to process social, communicative intentions from a third-person perspective and I showed that adults also differentiated between communicative and non-communicative intentions. The findings from the infant studies were consistently localized to the right centro-parietal region, providing further support to the role of the right hemisphere in social action observation.

The data indicated that action understanding could not be explained by means of directly matching the corresponding actions available in the motor repertoire or by anticipating social responses or by emulating instrumental actions alone. The findings indicated that communicative goals were attributed by taking into account the available circumstantial cues and were not restricted only to specific mechanisms as postulated by the existing theories. This led me to propose that action understanding is contingent upon the contextual congruency among action, goal and context, where the specific mechanisms put forward by the existing theories play a supplementary role in determining this congruency. Contextual congruency is suitable to explain not only the hypothesized findings of this thesis, where the presence and position of a goal object and the social partner resulted in goal attribution of the observed back-of-hand and pointing actions but also the unexpected findings, where observing the incongruent reach action was construed as meaningful.

Further, the current findings bring to light the importance of investigating social and contextual influences that facilitate action understanding, which is only beginning to emerge in infancy research. Finally, the significant mu desynchronization exhibited for the observed communicative actions, which do not result in immediate goal attainment or touching the goal object, argues for a more flexible action understanding system than it has been assigned thus far.

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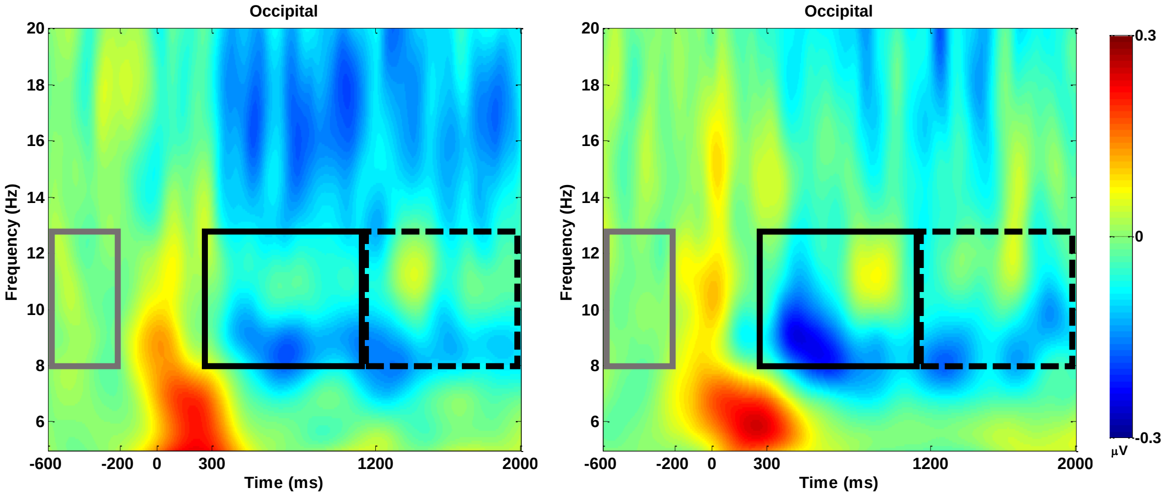
Appendix A: Study 1

Experiment 1: Occipital alpha activity for action observation



Social **Nonsocial**

Figure 18: Occipital alpha activity during action observation (experiment 1, study 1)

The areas marked in grey, solid black and dashed black boxes represent the baseline, action-unfolding and action-completion phases, respectively, in the adult mu frequency band of 8-13Hz.

Experiments 2 & 3: Activity in the other regions for action observation

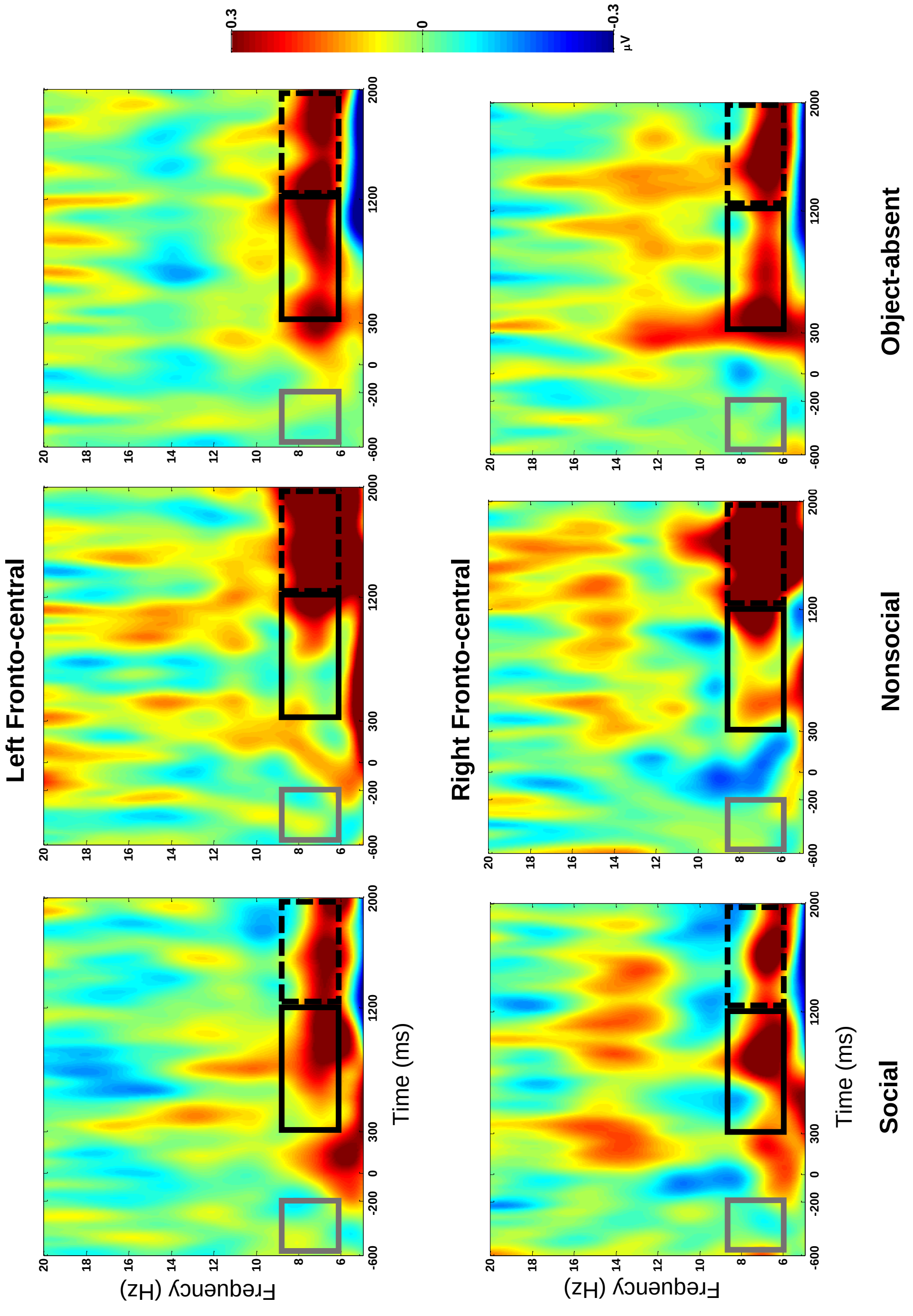


Figure 19: Left and right fronto-central activity during action observation (experiments 2 & 3, study 1)

The areas marked in grey, solid black and dashed black boxes represent the baseline, action-unfolding and action-completion phases, respectively, in the infant mu frequency band of 6-9Hz.

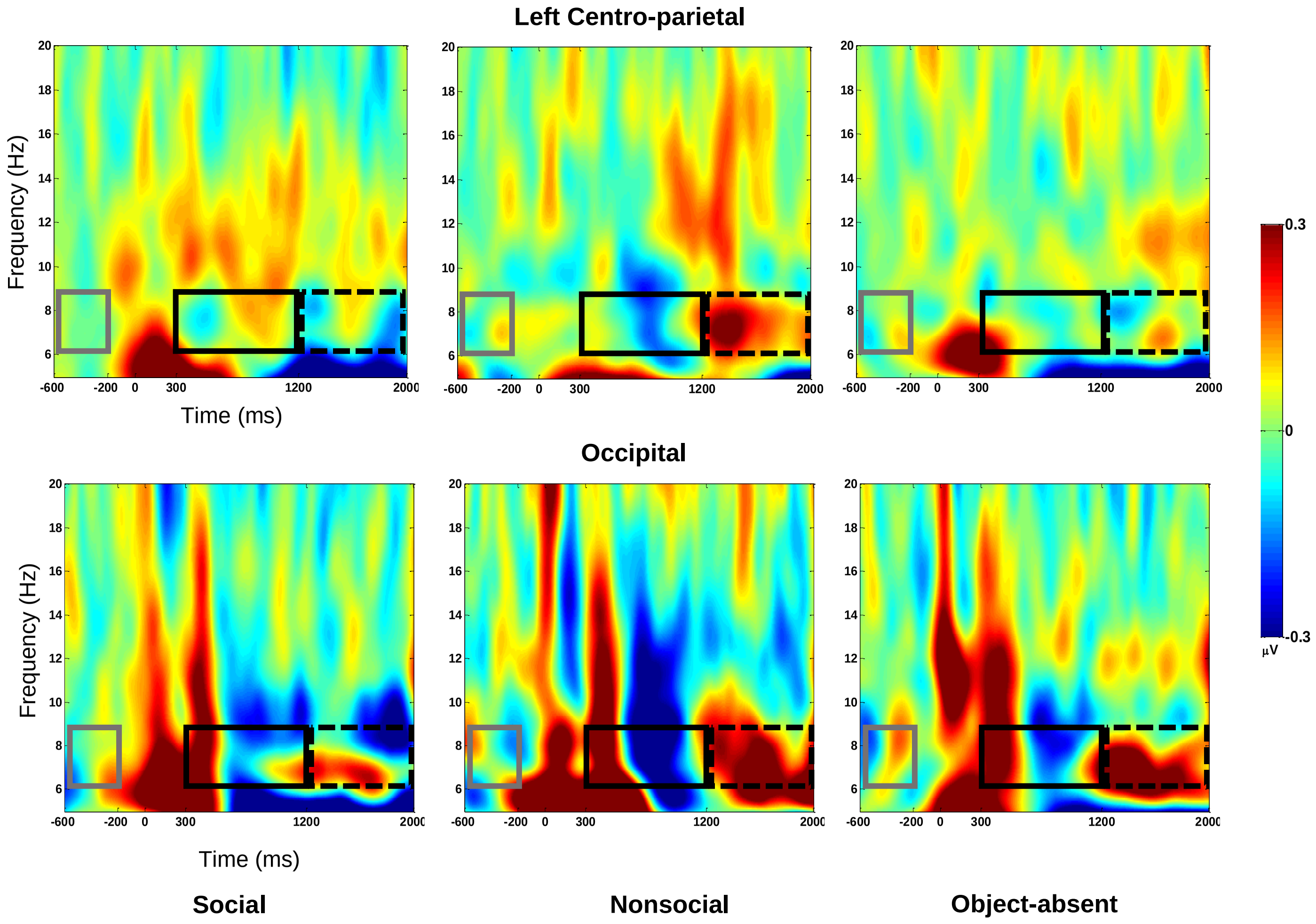


Figure 20: Left centro-parietal and occipital activity during action observation (experiments 2 & 3, study 1)

The areas marked in grey, solid black and dashed black boxes represent the baseline, action-unfolding and action-completion phases, respectively, in the infant mu frequency band of 6-9Hz.

Appendix B: Study 2

Activity in the other regions for action observation

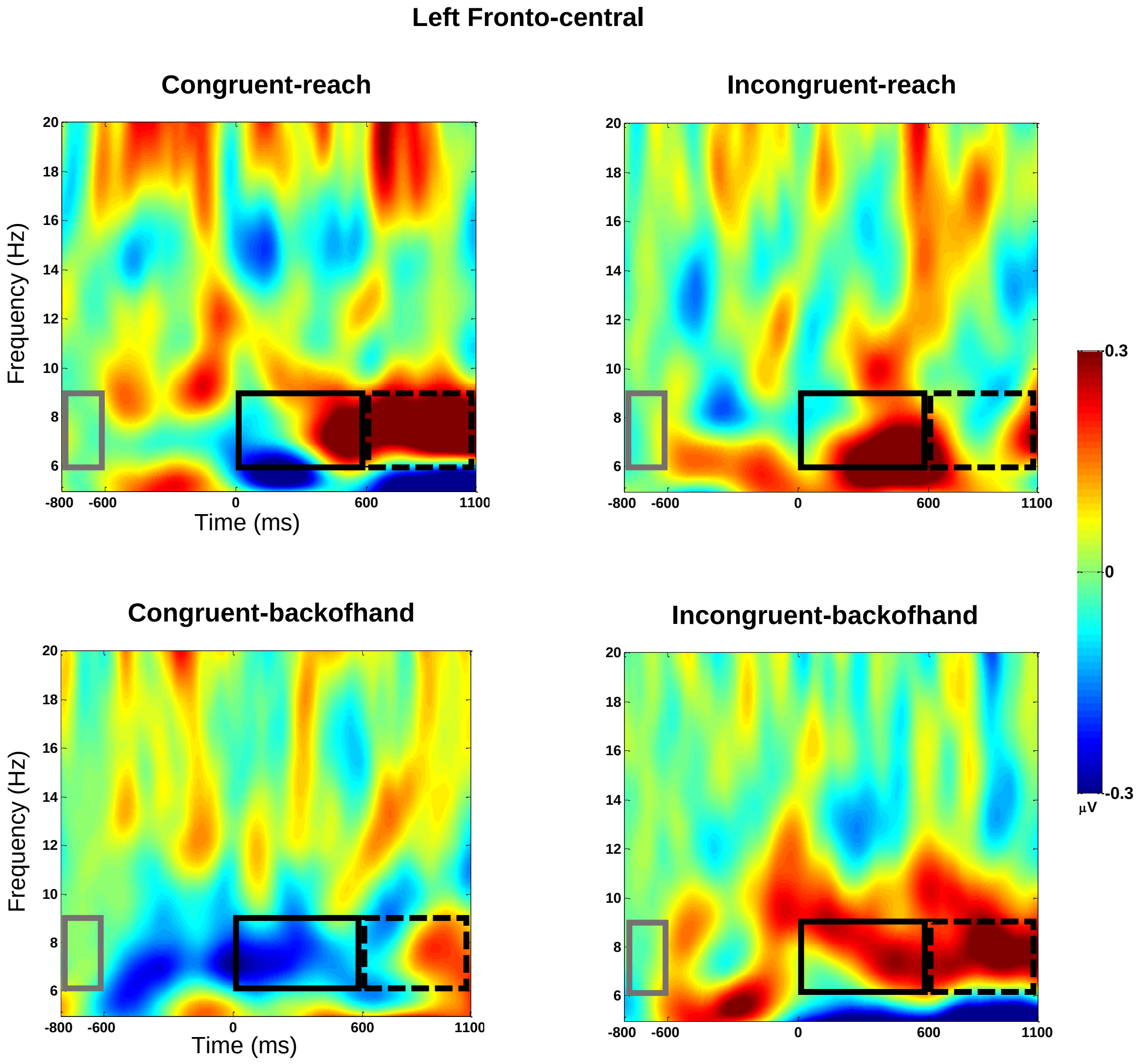


Figure 21: Left fronto-central activity during action observation (study 2)

The areas marked in grey, solid black and dashed black boxes represent the baseline, action-unfolding and action-completion phases, respectively, in the infant mu frequency band of 6-9Hz.

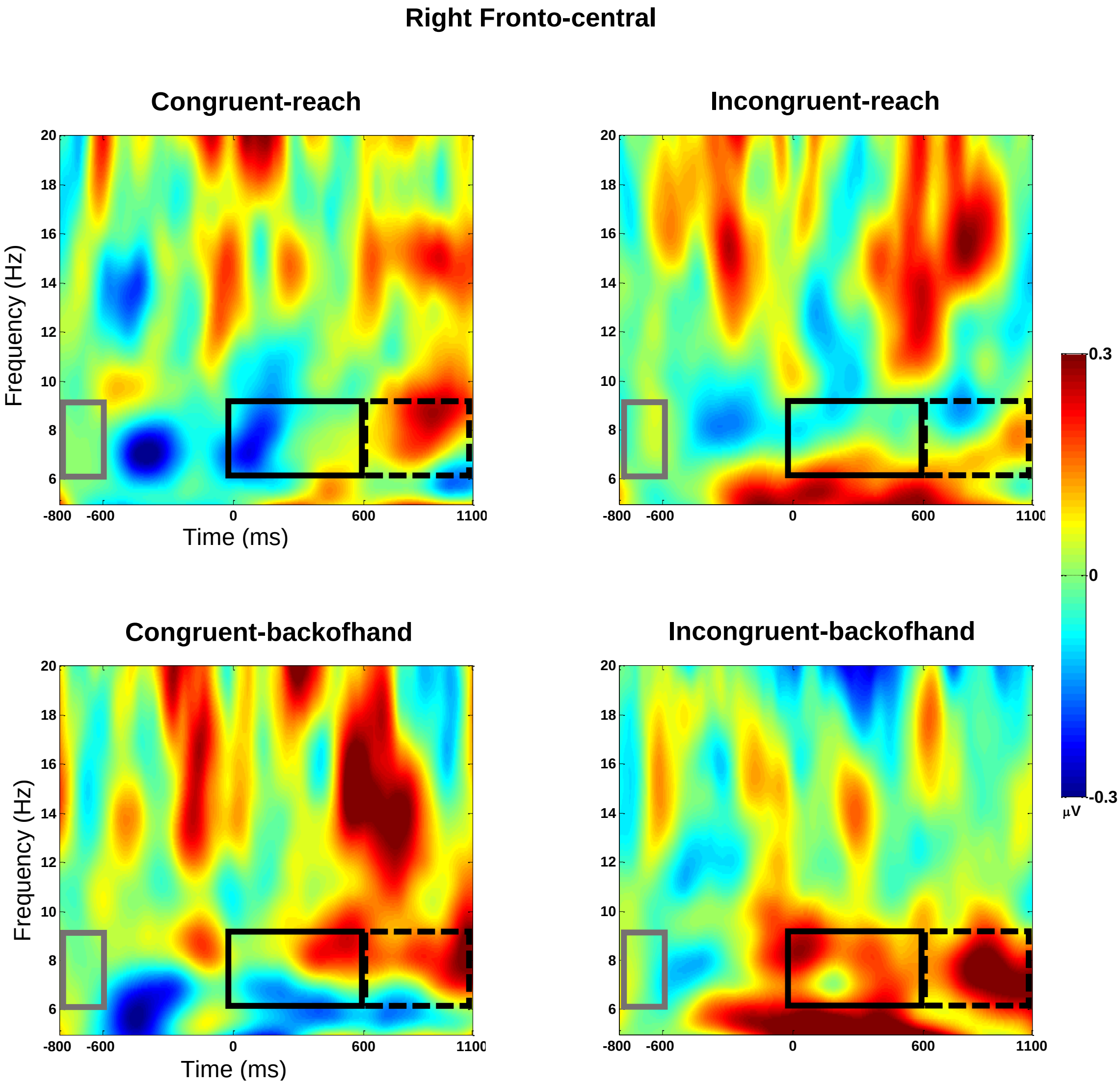


Figure 22: Right fronto-central activity during action observation (study 2)

The areas marked in grey, solid black and dashed black boxes represent the baseline, action-unfolding and action-completion phases, respectively, in the infant mu frequency band of 6-9Hz.

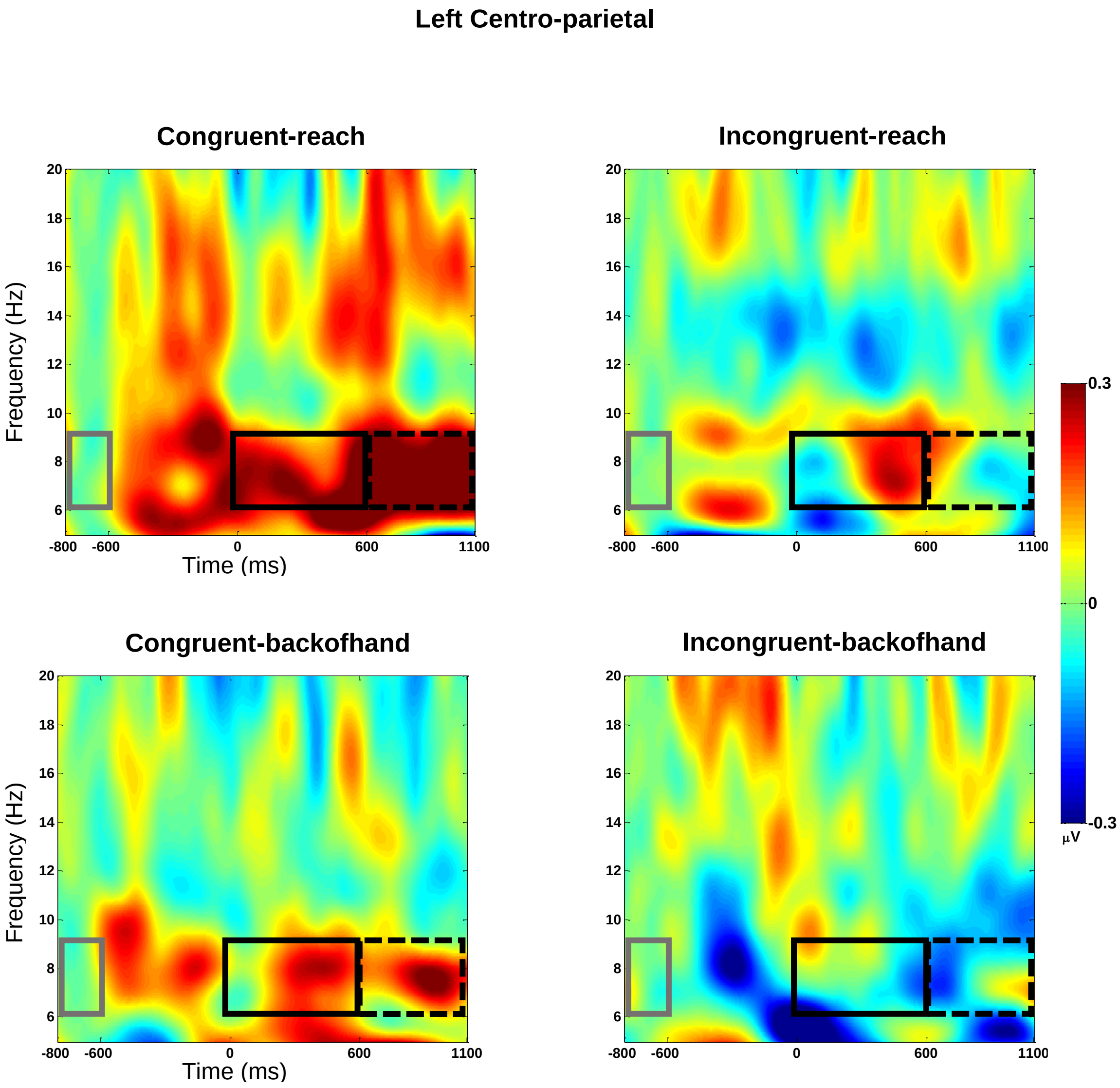


Figure 23: Left centro-parietal activity during action observation (study 2)

The areas marked in grey, solid black and dashed black boxes represent the baseline, action-unfolding and action-completion phases, respectively, in the infant mu frequency band of 6-9Hz.

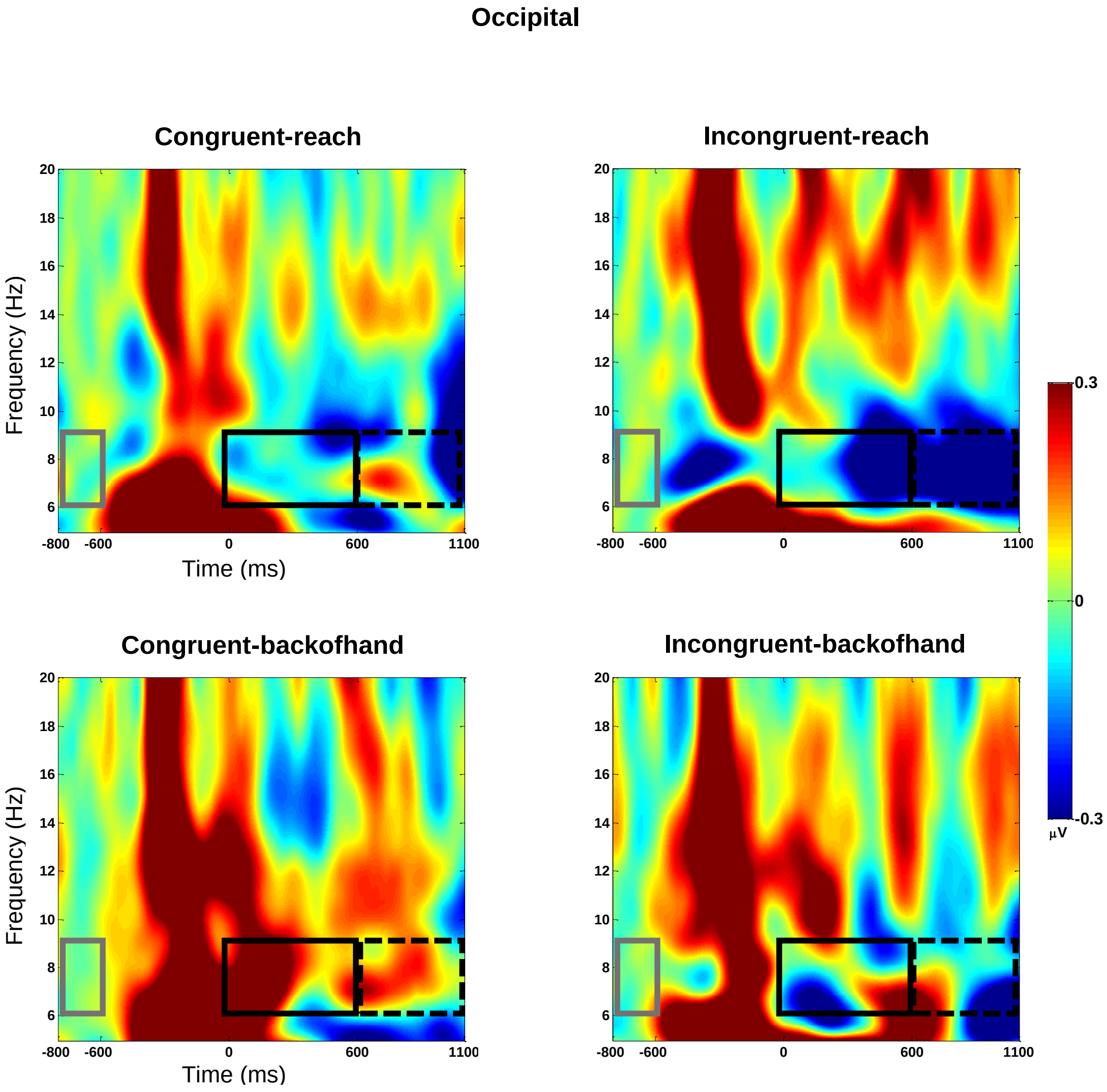


Figure 24: Occipital alpha activity during action observation (study 2)

The areas marked in grey, solid black and dashed black boxes represent the baseline, action-unfolding and action-completion phases, respectively, in the infant mu frequency band of 6-9Hz.

Appendix C: Study 3

Activity in the other regions for action observation

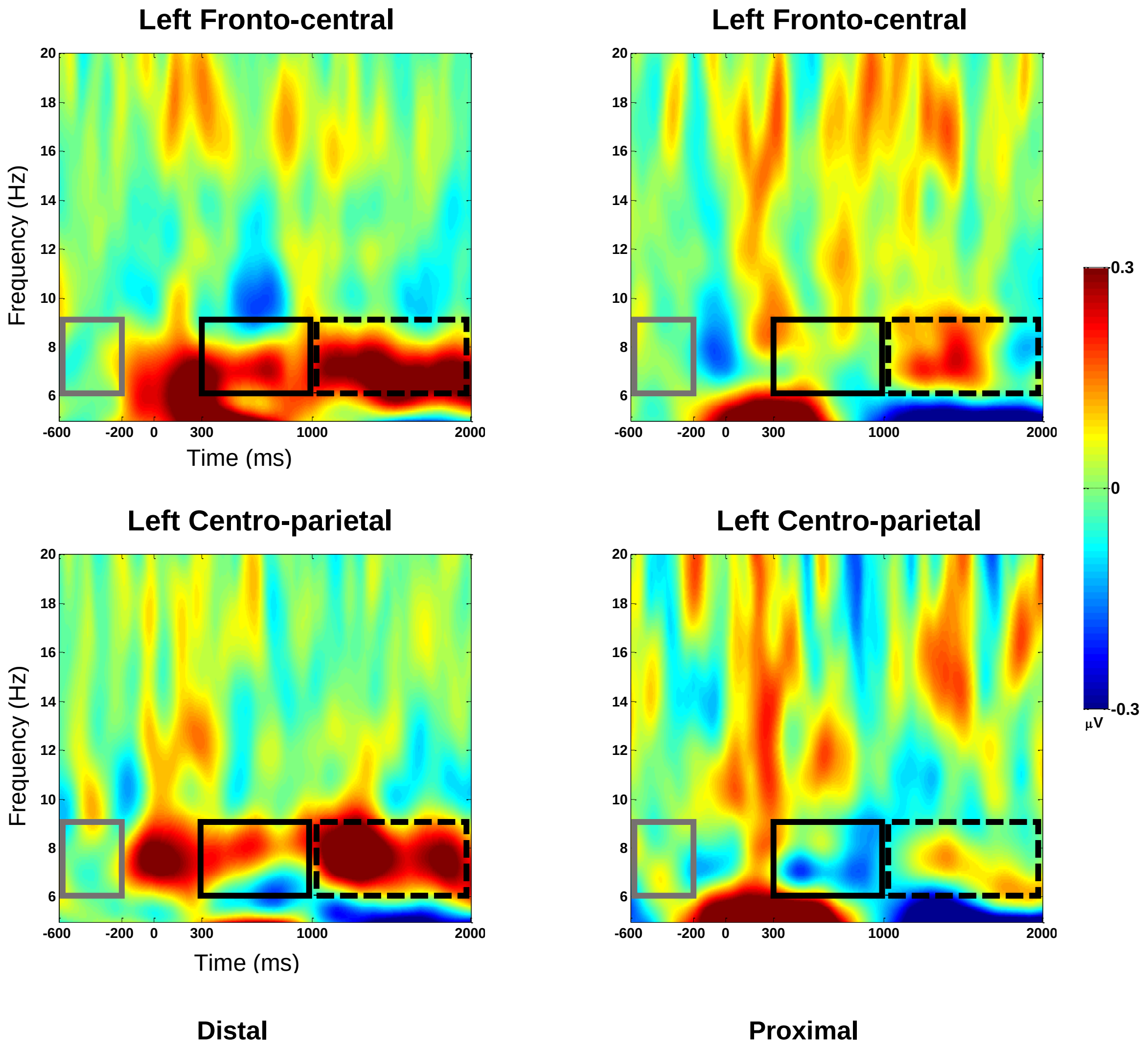


Figure 25: Left fronto-central and left centro-parietal activity during action observation (study 3)

The areas marked in grey, solid black and dashed black boxes represent the baseline, action-unfolding and action-completion phases, respectively, in the infant mu frequency band of 6-9Hz.