AN INVESTIGATION OF METHODOLOGICAL CONCERNS REGARDING GRASPING AND ITS COMPARISON WITH PERCEPTION

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Abstract

How vision is used to guide movement is a relatively new yet both fundamental and practical field of study. A recent neuroscientific interpretation of the function of the dorsal and ventral visual streams of the human brain, the perception and action model, suggests that even intrinsic visual object properties such as size and shape might be differentially computed when their purpose is to guide action rather than make a perceptual judgment (Milner & Goodale, 1995). In particular, it has often been tested whether grasping employs a more analytical rather than holistic visual processing, ignoring either visual context (such as illusory context), or dimensions of the stimulus itself which are not immediately relevant to grasping. However, the methodological challenges in comparing grasping and perceptual judgments have been substantial, in particular regarding equating task demands and correctly evaluating grasping data. The experiments detailed in this dissertation examine three further methodological difficulties when comparing grasping and perception. Study 1 investigates the appropriate amount of visual feedback to be allowed during a grasping task so it does not gain an undue advantage in accuracy over perceptual judgments. In a bimanual grasping task, grasping with visual feedback of the hands resulted in a smaller illusion effect than when vision was removed as the movement was initiated. In the latter case, the illusion effect was comparable to that found for perception. This indicates that it is the availability of online visual feedback, rather than a differential processing of visual information for action, which leads to a smaller illusion effect in grasping. Study 2 relates to an earlier claim that, unlike perception, grasping may not be subject to Weber's Law. This was based on the finding that the standard deviation of the maximum grip aperture, a measure of visual size processing in the dorsal stream, was found not to increase with object size. Further studies, however, showed that a dependency of aperture standard deviation on object size could be found earlier in the movement, indicating that a difference in visual processing may exist not only between perception and action, but between early and late stages of a movement. However, our study demonstrates a statistical artifact that arises when averaging grasping trajectories, whereby the standard deviation of the average trajectory will depend on the aperture's slope. Because the slope is dependent on size at early time points, the artifact leads to the average aperture's standard deviation also being dependent on size at early time points. Thus, the apparent adherence to Weber's law at early time points can be explained exclusively by the artifact arising from the method of analysis; an interpretation involving a differential processing of visual information is not necessary. Finally, Study 3 looks at how small differences in measurement method can affect the strength of the Müller–Lyer and Ebbinghaus illusions. We found a larger illusion effect when the two illusory figures were compared to each other directly, as opposed to comparing each to a neutral stimulus and summing the effects. However, the finding was consistent only if the illusory figures were manipulated simultaneously for the direct comparisons, instead of one figure remaining fixed while the other was adjusted to match it. Such differences in how a participant interacts with an illusory stimulus should also be considered when designing equivalent action and perception tasks, so that a difference in illusion effect due to task demands is not misinterpreted as differential visual processing. The results of all studies presented in this dissertation show that what appears to be a methodological detail can change the outcome or interpretation of a study. While Study 2 highlights an artifact that could lead to false conclusions, Studies 1 & 3 refine the conditions for making perception and action tasks most comparable. In light of these and previous methodological concerns, the current state of support for the model of Milner and Goodale (1995) is evaluated.

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Contents

Chapter 1

Introduction

More than any other sense, vision has been the object of interest of experimental psychologists for centuries. While studying vision in an abstract way is intriguing in its own right—it plays a large role in our understanding of and connection to the outside world—it is also important to consider that most likely the very reason this sense was developed was not to merely observe the world, but to interact with it. From the development of stereopsis in order to navigate a tree and branch–filled environment (Collins, 1921), to the development of color vision to find ripe fruit (Regan et al., 2001), vision has been theorized in many ways to have evolved in order to guide our movements in the world, and to direct them to particular targets.

Even when limiting oneself to the study of vision for movement, the interpretations, theories, and applications are numerous and varied. For example, consider the theory of ecological vision, which has gained a large following since its inception (Gibson, 1979a). One of its most popular tenants is that objects are perceived directly, by means of perceiving their "affordances", or the ways in which the perceiver is able to interact with them (Gibson, 1979b). But even the relatively small field of ecological vision has inspired diverse concepts such as optic flow, or the ability to use the deformation and movement of the visual environment as a whole in order to move through it (Lee, 1980). This has led to many interesting discoveries regarding navigation, such as the ability of distorted optic flow to adapt one type of movement but not another (such as walking but not kicking; Bruggeman & Warren, 2010).

This dissertation will focus on another sliver of the intersection between vision and action, namely on grasping, also known as prehension, and the use of vision to guide these movements. I will start with a historical background on theories of motor control and classic findings on grasping itself (Chapter 2). Then, I will move on to review several theories on the "division of labor" of visual processing, placing special focus on the recent yet highly influential theory that visual information is processed in a fundamentally different fashion when its goal is to direct our movements, rather than make an observation or judgment (the perception and action model; Chapter 3). After this overview, I will present several challenges to the perception and action model, including detailing my own original contributions within the context that motivated them (Chapter 4). These challenges are based primarily on methodological difficulties that have arisen from trying to compare properties of perception and action. Finally, I will summarize my findings and the current state of research, and also discuss the future outlook on the topic (Chapter 5).

Chapter 2

Fundamentals of Grasping and Motor Control

One of the earliest and most salient questions in motor control is how, given the multitude of possible combinations of muscle contractions and limb placement which would allow us to arrive at our goal, is only one selected? And also, how can a particular stimulus or goal create a neural response that allows for such a diversity of movements? This question is now known as the degrees of freedom problem or the motor equivalence problem, and served as an impetus for trying to determine how motor actions were organized and controlled (Lashley, 1930; Bernstein, 1967). Several influential explanations were advanced in the past century. One early idea was that the spinal cord produced a series of reflexes called “motor units” in order to perform an action. These motor units could be executed in a different sequence for different movements or effects (Burke, 2007; Sherrington, 1947). However, there were several problems with this idea. Lashley (1930) argues that natural movements are typically not so “stereotyped”, that is, they show variation between different execution attempts which is not compatible with reflex behavior. It was soon also questioned how corrections could be made to a motor movement once it had been initiated, which led to the conceptualization of a system that also allowed for feedback processing, rather than just feedforward impulses (Bongaardt, 2001; Bernstein, 1967). Once you believe a system utilizes feedback, a natural follow–up question is: To what reference is the current state compared? The general conclusion is that some sort of goal state must be stored as a reference, although the exact nature of the reference was—and is—disputed (e.g., Jeannerod, 1997; Bernstein, 1967; Neisser, 1976). The idea of an internal model of movement or limb position to which the current state could be compared is important because it represented one of the first claims for an internal representation guiding movement (Jeannerod, 1997). The idea is also central to this dissertation, which will focus for a large part on whether the visuomotor representation used to guide movements is unique from that used for perception.

Another line of research has examined grasping movements in particular. Initially, researchers were interested in defining different types of grasping, or identifying different components of a grasping movement. One such early distinction was the differentiation between a "power grip" and a "precision grip". A power grip is a type of grasping where the object is clasped between the fingers and the palm of the hand; a precision grip, in contrast, involves holding an object between the fingers and thumb (Napier, 1956). Within our field of study and this dissertation, we will primarily be concerned with precision grips, in particular those using only the index finger and thumb. Within the precision grip, we also distinguish between the "transportation" and "manipulation" components of the grasp (Jeannerod, 1984). The transportation component is understood as the reaching action, or the movement of the arm in the direction of the target (often measured on the wrist), while the manipulation or grasp component involves the adjustment of the fingers into position around the object. Between these two components, we will focus primarily on the manipulation aspect. This is mainly due to the established linear increase in the maximum grip aperture (MGA), or maximum distance reached between finger and thumb during the course of the movement, as object size increases (Jeannerod, 1984; Smeets & Brenner, 1999). Because the MGA is dependent on object size, it has become a useful tool in helping researchers draw conclusions about the motor–estimated size of the object. In the following chapter, we see that a recent theory has called into question whether the motor system's interpretation of the visual world is the same as our conscious perception. The MGA has been a critical tool in comparing perceived and motor–estimated size and testing this hypothesis.

Chapter 3

Two Streams of Visual Perception: The Theory

3.1 Early Models: “What” and “Where”

Initially, the study of vision advanced separately from its association with movement. It was assumed that everything we wanted to know about visual processing could be inferred from a person or animal’s conscious perception; how the response was given did not play a major role. However, some unusual findings led researchers in the mid–20th century to consider the importance of the task in visual experiments. Schneider (1969) reported a difference in deficits observed in hamsters between lesions to the superior colliculus, which impaired the hamster’s ability to visually orient to a stimulus, and lesions to visual cortex, which impaired their pattern recognition. Previously, it was assumed that hamsters with lesions to the superior colliculus, who were then unable to orient to visual stimuli, were effectually blind. However, Schneider (1969) showed that they were nonetheless able to discriminate between patterns such as stripes and spots when choosing between doors with those patterns to find water. Hamsters with damage to the visual cortex, on the other hand, retained their ability to orient themselves to a visual stimulus, but often made errors when trying to find the water behind a patterned door. Schneider (1969) therefore suggested that the superior colliculus and visual cortex represented two loci of visual processing: the first concerned with localizing and orienting oneself to a visual stimulus, and the second with visual identification. He uses the key phrases “Where is it” and “What is it” to describe the purpose of the two systems (later shortened by others to “What” and “Where”).

The second major proposal of two streams of visual processing retained the distinction in purpose of the two streams—what vs. where—but sought to clarify the anatomical locations of these two areas of processing. In particular, Mishkin, Ungerleider, and Macko (1983) proposed that the “where” visual processing is localized in the posterior partietal cortex rather than in the superior colliculus. This was primarily supported by studies on monkeys with lesions to that area, who were unable to perform a “landmark” task—that is, they were unable to select the foodwell nearest to a cylinder object “landmark” in order to receive a food reward (Pohl, 1973). Being aware of earlier theories suggesting a role of the superior colliculus in visual processing of location, Ungerleider and Mishkin (1982) also tested whether lesioning this region would have a detrimental effect in the landmark task. However, they found that even destroying the superior colliculus completely had no effect on task performance. What Schneider (1969) referred to as visual cortex, responsible for pattern recognition and other “what” processing, is now more specifically described by Mishkin et al. (1983) as the inferior temporal cortex. In a similar setup as used for the monkeys with lesions to the posterior partietal cortex, monkeys with lesions to the inferior temporal cortex were unable to select an unfamiliar object which differed from a familiar object in terms of color and shape in order to receive a food reward (Pohl, 1973). In sum, Mishkin et al. (1983) preserved the functional “What” vs. “Where” distinction established by Schneider (1969), also referring to it as “Object Vision” vs.

"Spatial Vision". However, they greatly refined the anatomical localization of these functional areas.

3.2 Vision for Perception and Vision for Action: "What" and "How"

3.2.1 Overview

Unlike the previous rethinking of the division of labor in visual processing, the most recent major interpretation accepts Ungerleider and Mishkin (1982)'s anatomical analysis, but instead takes issue with the classification of the functional purposes as "what" and "where". Instead, Goodale and Milner (1992) propose that the distinction is better described as "what" and "how". In more direct terms, they theorize that visual information is processed in a fundamentally different manner based on its purpose—in particular, different calculations of fundamental object features such as size or shape may guide goal–directed actions than those used to make more detached perceptual judgments about an object. Anatomically, the "what" processing is localized in the ventral stream (or inferior temporal cortex, as in the theory of Ungerleider & Mishkin, 1982), and the "how" processing is located in the dorsal stream (or posterior parietal cortex, in the same location as and replacing Ungerleider & Mishkin, 1982's "where" processing). Milner and Goodale's book on their theory details an extensive justification for their interpretation (Milner & Goodale, 1995). It begins by describing how even retinal projections extend to various different parts of the brain, the most prominent being the superior colliculus and lateral geniculate nucleus. They claim that this early diversity in projections indicates that even the most basic visual information—direct retinal input—it separated early on and therefore likely differentially processed at different locations in the brain. They then discuss more specifically evidence from other mammals for action–specific visual processing: for example, lesions to the superior colliculus will cause rats and gerbils to stop fleeing from threatening visual stimuli, as well as cause them to be unable to orient themselves to stimuli in their peripheral visual field. They consider this to be evidence of a strong neurological link between visual stimuli and particular actions.

Establishing that some strong, direct links between vision and motor actions exist in animals does not yet, however, prove that a similar system exists in humans. To support their argument that it does, Milner and Goodale (1995) draw on two major sources of evidence: studies on patients with brain damage, and studies with neurologically intact participants. Studies with brain damaged patients primarily aim to extend the anatomical findings of animal studies to humans; in particular, they seek to show that the processing of the posterial parietal cortex is visuomotor in nature. The studies with neurologically intact participants generally aim to support one of their strongest claims, namely that different calculations of space and size are used by the dorsal stream to guide actions. The literature regarding these two areas of study is discussed separately in the following sections.

3.2.2 Evidence from Patients

Arguably the strongest support for Milner and Goodale's theory comes from research on brain damaged patients. In essence, they report a double dissociation between vision for perception and vision for action—that is, they were able to find patients with brain damage to the ventral stream who were able to interact normally with objects, despite being unable to identify or describe them, as well as patients with damage to the dorsal stream who had trouble interacting with objects, but could identify and describe them easily.

The first case, involving damage to the ventral stream, results in a condition called visual form agnosia. Patients with this condition are unable to recognize shape or form, identify common objects by looking at them, or copy observed shapes when asked to do so (e.g., Benson & Greenberg, 1969). This condition is quite rare and has been primarily studied in one particular patient, D.F., by the Milner and Goodale research groups. Patient D.F. suffered serious damage to the lateral occipital cortex, the primary location of the proposed ventral stream, at the age of 34 due to carbon monoxide poisoning (Milner et al., 1991). Milner et al. (1991) extensively tested her vision, and found that while many of her lower–level visual abilities, such as color perception and luminance detection, remained intact, she was unable to recognize simple shapes, distinguish between rectangles of different sizes, or identify the orientation of a line. Despite her non–existent form perception, some visually guided motor actions were remarkably preserved. For example, she was able to orient a card when reaching to put it through a slot (a "posting" task, as the movement is similar to posting a letter), although she could not match the orientation of the slot with her hand (Milner et al., 1991; for an example of the posting task, see Figure 3.1). Furthermore, it was discovered that she was able to scale her grip aperture to the

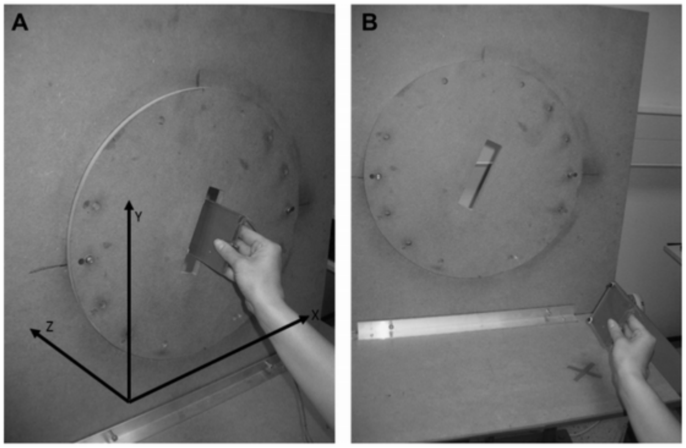

Figure 3.1: An example of the posting task used with patient D.F. On the left is the action task, where she inserted the card into the slot. On the right is the perceptual task, where she was instructed to match the orientation of the card or her hand to the orientation of the slot, which she is unable to do. Reprinted from Cortex, 54, Hesse, C. & Schenk, T., Delayed action does not always require the ventral stream: A study on a patient with visual form agnosia, 77–91, 2014, with permission from Elsevier.

size of the object she was grasping—that is, she opened her fingers wider for larger objects, and smaller for smaller objects, before coming into contact with the object (Goodale, Milner, Jakobson, & Carey, 1991). Since her ventral stream was so severely damaged, they inferred that she must be performing the actions by exclusively relying on dorsal visual processing. Later, fMRI studies confirmed that patient D.F.'s dorsal stream functioned similar to controls when performing reaching and grasping movements, but that the area typically activated in an object identification task—the lateral occipital cortex—corresponded almost precisely with the area of her lesion (James, Culham, Humphrey, Milner, & Goodale, 2003).

Complementary results come from patients who have damage to the dorsal stream. The two streams theory would predict that they would have difficulties performing goal–directed movements, but that their object and form recognition would remain intact. And that is indeed what has been found: patients with optic ataxia, stemming from damage to the posterior parietal cortex, are found to typically make pointing localization errors (e.g., Ratcliff & Davies-Jones, 1972; Jakobson, Archibald, Carey, & Goodale, 1991), and also showed reduced scaling of the MGA with object size (Jakobson et al., 1991). They also have difficulty grasping visual targets (e.g., a pencil) presented in the visual field contralateral to their lesion, and—in contrast to patient D.F.— make position and orientation errors when attempting a posting task (Perenin & Vighetto, 1988). However, their visual field and acuity are generally unaffected (i.e., their deficits are not due to low–level vision problems), and they are able to direct movements to auditory stimuli or to parts of their own body such as their thumb (i.e., they do not have an exclusively motor deficit; Perenin & Vighetto, 1988). Damage to the posterior parietal cortex therefore seems to specifically disrupt the use of visual information for motor movements. Their retained ability to identify shapes and objects (Perenin & Vighetto, 1988; Jakobson et al., 1991) completes the complementary profile to that of visual agnosia.

Taken together, this double dissociation suggests that in these patients, the dorsal stream can allow for some visual information to be processed in order to guide movement, even if the ventral stream is damaged to the point that they are unable to recognize the object they are grasping for. Likewise, damage to the dorsal stream will impair visually guided movement, but leave identification intact.

3.2.3 Evidence from Neurologically Intact Persons

While the evidence thus far shows a contribution of these areas of the brain to the general control of these tasks, the theory has also made stronger, more controversial claims regarding their role in the processing of visual information in healthy participants. This began with the claim that size and physical dimensions are dually processed by the dorsal and ventral streams, and in particular, that they are processed without influence of context, or any information not directly relevant to the movement, by the dorsal stream. This proposal has been tested extensively by studies on the grasping of illusions, but in more recent years it has also been studied whether grasping is resistant to other perceptual effects. This section will examine some of the principle findings regarding the differential processing of visual information in neurologically intact individuals, first ignoring later critiques. The rest of the dissertation will focus on methodological concerns and alternative explanations of these original findings.

Grasping Illusions

If the dorsal stream processes visual information specifically for the purpose of action, it is reasonable to think that the visual information might be processed uniquely in a way that reflects this purpose. This led Aglioti, DeSouza, and Goodale (1995) to ask whether an irrelevant context, such as the surrounding circles of the Ebbinghaus illusion, might be ignored while grasping, leading to maximum grip apertures

(MGAs) unaffected by the illusion. To test this hypothesis, they first found a set of stimuli for each participant where the two center circles of the Ebbinghaus illusion appeared to be perceptually of the same size. They then had participants grasp these perceptually identical stimuli in three conditions: either the physically smaller circle was presented in the small circle surround configuration, and the physically larger circle in the large circle surround configuration (perceptually the same, physically different); or the physically smaller circle was presented in both illusory configurations (perceptually different, physically the same); or the physically larger circle was presented in both illusory configurations (perceptually different, physically the same). Interestingly, they found that the physically larger disc was still grasped with a larger MGA than the physically smaller disc when they were placed in illusory configurations where participants had reported them to be perceptually the same. This would indicate the participants respond to the disc's physical size, rather than its perceptual size. Regarding the effect of the illusory context, Aglioti et al. (1995) found that the difference in MGA between grasping a disc surrounded by small context circles (perceived larger) and grasping a disc surrounded by large context circles (perceived smaller) was significantly smaller than the physical difference required for the participants to say the stimuli seemed to be of the same size. They therefore argue that, while the illusory context seemed to have some influence on grasping, it was smaller than its influence on perceptual judgments. They then conclude that the dorsal stream controls actions based on a more direct and accurate perception of an object's physical properties, with less influence of context.

The finding that grasping has a reduced sensitivity to the influence of illusions has been replicated for the Müller–Lyer (e.g., Daprati & Gentilucci, 1997; Otto–de Haart, Carey, & Milne, 1999), Ponzo (e.g., Brenner & Smeets, 1996; Jackson & Shaw, 2000), and diagonal (e.g., Stöttinger & Perner, 2006) illusions. These experiments have also employed a variety of methods to measure the perceptual illusion effect, from constant stimuli (e.g., Aglioti et al., 1995), to reproducing the illusion with paper and pencil (e.g., Daprati & Gentilucci, 1997), to manual size estimation (MSE), that is, when the participant is asked to adjust their finger and thumb to indicate the size of the object, without moving to pick it up (e.g., Haffenden & Goodale, 1998). However, despite these many and varied replications, whether and to what extent visual illusions affect grasping has been the subject of much contentious debate. Many of these methodological considerations will be discussed in Section 4.1.

Grasping and Garner Interference

The argument that vision–for–action evaluates size in an unbiased manner was further evaluated by means of experiments on whether Garner interference affects grasping. In order to understand the grasping experiments, it is first important to understand the original perceptual effect of Garner interference. Garner interference was first measured by means of card sorting tasks. Participants received a stack of cards which varied on either one or two dimensions; for example, in one set of cards, each card might have a dot which was either above or below center; in another set, the dots might be to the left or right of center; and in a third variation, the dot might appear in one of the four corners (i.e., varying on both the vertical (above/below) and horizontal (left/right) dimensions; Garner & Felfoldy, 1970, Exp. 4; see Figure 3.2). For each set of cards, participants were asked to sort the cards into two piles based on one of the dimensions (e.g., place all cards with a dot above center to the right, and the others to the left). Garner and Felfoldy (1970) found that participants were faster in sorting the cards when those in the deck varied only on one dimension, rather than two. They reasoned that the non–relevant dimension was automatically being processed as well, thus requiring this information to be "filtered" in order to arrive at the correct answer. (Also leading to the condition where both dimensions

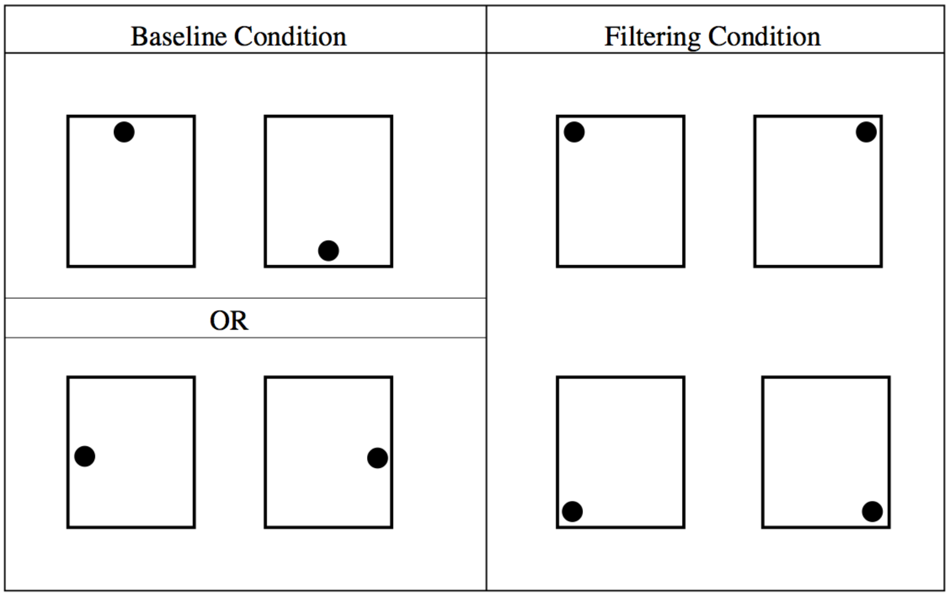

Figure 3.2: One of the original interference tasks of Garner & Felfoldy (1970). In the baseline condition (left), participants sorted decks of two cards each based on whether the dot was above or below (top), or left or right of the midline (bottom). In the filtering condition (right), participants were given the same task, but the deck contained four cards, with a dot in each corner (i.e., the position varied on both the horizontal and vertical dimension). Although they were still required to base their judgment on only one dimension, participants were found to be slower in the filtering condition, when an irrelevant dimenion was also varied.

are varied to be known as the "filtering" condition in future experiments, in contrast to the "baseline" condition where only one dimension is varied).

Ganel and Goodale (2003) hypothesized that vision–for–action may better be able to ignore irrelevant stimulus dimensions and thus not be susceptible to Garner interference. They therefore tested reaction times in both baseline and filtering conditions for perceptual and action tasks using blocks that could vary in length, width, or both dimensions. For the perception task, participants had to classify the object's width as narrow or wide as quickly as possible by pressing a button. Consistent with classical Garner interference, participants were slower to react in the filtering condition—that is, if the irrelevant dimension, the length of the object, was also varied. For the action task, participants simply had to reach out to grasp the object along its width as fast as they could. For this task, the authors found no difference between the baseline and filtering conditions for either reaction time, time to MGA, or total movement time. They therefore concluded that grasping is not subject to Garner interference, and perception–for–action processes visual information in an analytical fashion, ignoring irrelevant stimulus information.

Grasping and Weber's Law

One further distinction between perception and action that has been investigated in recent years is whether grasping may be subject to Weber's Law in a way similar to perception. Perceptually, we know that the estimates of many dimensions, from weight (Weber, 1834; as cited in Hecht, 1924) to physical distance (McKee & Welch, 1992), are subject to a rule called Weber's Law, whereby the just–noticeable difference (JND), or the difference between two stimuli necessary in order for a person to consistently notice this difference, increases with the magnitude (also known as intensity) of the stimuli to be judged. Mathematically, this is expressed as:

$\frac{\Delta I}{I} = k$

where I represents the stimulus intensity, ΔI is the JND, and k is a constant, the Weber fraction, which indicates at what rate the JND will increase with stimulus intensity (Hecht, 1924).

Ganel, Chajut, and Algom (2008) asked whether motor–estimated size would also be subject to Weber's Law. Because the MGA scales linearly with object size, it is often used as a measurement of the motor–estimated size. It would thus be reasonable to believe that, if motor–estimated size is affected by Weber's Law, this would be reflected in the MGA. Ganel et al. (2008) therefore had participants grasp objects of varying sizes, as well as make perceptual judgments by adjusting the length of a line on a computer screen to match the size of the same stimuli. As a consistent way of measuring the JND for both tasks, they looked at the standard deviation of each participant's perceptual adjustments or MGAs, with the hypothesis that if Weber's

Law were followed, the standard deviations of both measures should increase with object size. While this was true for the perceptual adjustments, this relationship was not found for the standard deviation of the MGA, where the standard deviations were constant across all object sizes used. The authors therefore conclude that motor–estimated size does not follow Weber's law. They speculate that the reason for this may be due to the limited range of graspable sizes; Weber's Law has been theorized to result from a neurological logarithmic encoding for magnitude in other modalities (e.g., Dehaene, 2003). If only a limited range of motor–estimated sizes must be encoded, due to larger sizes being physically unable to be grasped, such a logarithmic encoding mechanism would no longer be necessary.

3.2.4 Clarifying the theory: Necessary conditions for dorsal control

As research on the perception and action theory has progressed, it has been necessary to further define the borders between perception and action. Which tasks would be expected to engage the dorsal stream, and which the ventral stream? One of the first gray areas examined is what is known as pantomimed grasping. In these experiments, both healthy participants and the patient D.F. grasped objects after a delay of 2 seconds, during which the object was removed, or with no delay, but next to the actual object, without actually touching it (Goodale, Jakobson, & Keillor, 1994; see Figure 3.3 for an example of grasping next to the object). The healthy participants showed abnormalities in several movement parameters of their grasp in these conditions (namely lower movement velocities, longer movement times, and smaller MGAs), and, most notably, the patient D.F. no longer showed any recognizable grip scaling to object size. From these results, Goodale et al. (1994) label these conditions—grasping from memory, or to a different location from the physical target—as pantomimed grasping, and suggest that they are most likely controlled by the ventral stream, which is destroyed in D.F. Here again, a double dissociation with patients with optic ataxia was found: the optic ataxic patient I.G. was found to be able to scale her MGA to object size when grasping after a delay, but not when directly grasping a visible object (Milner et al., 2001).

More recent fMRI studies have also investigated the neural basis of this proposition, but support for these actions being controlled by the ventral stream has been difficult to find. In particular, Króliczak, Cavina-Pratesi, Goodman, and Culham (2007) tested healthy participants in an fMRI study, where they were asked to perform normal or pantomimed grasping and reaching movements, where a reach is understood to mean tapping the location with one's knuckles. In the pantomimed task, participants reached or grasped a location next to the presented stimulus. When they evaluated the activation of the lateral occipital cortex (that is, the proposed location of the ventral stream), they found no difference in activation between the four different tasks. They did, however, find some differences between normal and pantomimed grasping—namely that the difference between normal reaching and grasping in the anterior intraparietal area was greater than the difference in that area between

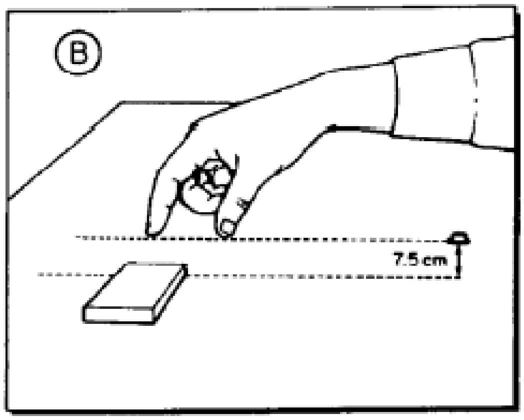

Figure 3.3: One of the original two pantomimed grasping tasks. Participants viewed both their hands and the stimulus during the movement, but grasped a location next to the object. Reprinted from Neuropsychologia, 32(10), Goodale, M. A., Jakobson, L. S., & Keillor, J. M., Differences in the visual control of pantomimed and natural grasping movements, 1159–1178, 1994, with permission from Elsevier.

pantomimed reaching and grasping, and pantomimed movements showed a greater activiation of the right medial temporal gyrus and superior temporal sulcus. But these areas are not part of the ventral stream, and given the lack of differential activity in the lateral occipital cortex, this seems to indicate that while grasping next to an object may indeed be processed in a different manner from normal movements, it does not recruit the ventral stream for visual processing.

The other form of pantomimed grasping, grasping from memory, has produced some more mixed results. One group was able to show that the lateral occipital cortex was active while viewing an object, less active when vision of that object was removed, then reactivated when grasping from memory (Singhal, Kaufman, Valyear, & Culham, 2006; Singhal, Monaco, Kaufman, & Culham, 2013). However, they did not compare the degree of activation between grasping from memory and immediate grasping. Fiehler et al. (2011) did make such a comparison. Their participants grasped a small bar after either no delay, or a delay ranging from 2–12 seconds. Similarly to Króliczak et al. (2007), they found no evidence for involvement of the lateral occipital cortex in the control of this pantomimed movement. However, it should be noted that the form of grasping from memory used in these experiments did differ somewhat from that of Goodale et al. (1994). While Fiehler et al. (2011) and Singhal et al. (2013) removed vision but left a haptic stimulus for the participants to grasp, Goodale et al. (1994) removed the object but had participants open their eyes and grasp the location where the object had been. This distinction was also noticed by Hesse and Schenk (2014) and is discused in more detail in Section 4.4.2.

Apart from pantomimed grasping, it has also been suggested that awkward or cumbersome grasping (Gonzalez, Ganel, Whitwell, Morrissey, & Goodale, 2008), left handed grasping (even in left–handed persons; Gonzalez, Ganel, & Goodale, 2006), and even extremely slow or deliberate movements (Króliczak, Heard, Goodale, & Gregory, 2006) may be controlled by the ventral rather than the dorsal stream. This was primarily due to apparent pattern in those experiments that awkward, left handed, or deliberate movements were susceptible to visual illusions, while rapid, practiced movements with the right hand were not. While later experiments have shown no difference between cumbersome and unencumbered movements (Franz, Hesse, & Kollath, 2009; Janczyk, Franz, & Kunde, 2010; Eloka, Feuerhake, Janczyk, & Franz, 2014) or left and right handed grasping (Dewar & Carey, 2006; Foster, Kleinholdermann, Leifheit, & Franz, 2012), practiced, right–handed grasping is generally used to test the perception and action model, as that type of movement would be unquestionably controlled by the dorsal stream according to the theory.

Chapter 4

Two Streams of Visual Perception: Criticism

In the previous chapter, an extensive case was presented for the argument that different calculations of fundamental visual properties are utilized by the dorsal stream in order to guide action. Grasping was shown to be resistant to several different illusions, it seemed to ignore irrelevant dimensions by not being subject to Garner interference, and even seemed to defy following Weber's law. However, this is only half of the story: since their publication, many methodological criticisms have been raised against the original studies. These methodological criticisms will be the focus of this chapter. Because the original experiments conducted for this dissertation tie in so closely to particular points of criticism, they are discussed in their relative context (Sections 4.1.1, 4.1.3, and 4.2.1).

4.1 Criticism of Experiments on Grasping Illusions

4.1.1 Matching Task Demands

One of the first criticisms raised against the studies showing a smaller illusion effect on grasping than perception concerned the task demands placed on the participants for each of the two tasks. If the grasping and perceptual tasks required the participants to interact with the illusion differently, such that this altered the strength of the illusion itself, the difference in illusion effect shown between grasping and perception could be a reflection of those different task demands, and not of a fundamentally different size processing utilized by the dorsal stream in order to guide motor movements.

In particular, Franz, Gegenfurtner, Bülthoff, and Fahle (2000) examined the task demands placed on participants in the experiment of Aglioti et al. (1995). In this study, a perceptual match was found for participants by asking them to compare the inner circle of one half of the illusion (e.g., small circle surround) to the inner circle of the opposite half of the illusion (e.g., large circle surround). However, during the grasping task, they were only required to interact with the center circle of one of the figures. If this comparison between the two illusory figures causes the illusion to be greater than if each figure were observed individually—a "superadditive" effect—then we would predict the illusion effect to be greater in Aglioti et al. (1995)'s perceptual task, merely due to this mismatch in task demands.

To test this, Franz et al. (2000) measured the illusion effect when the two figures of the Ebbinghaus illusion were adjusted to match each other by a direct visual comparison, and contrasted this with the illusion effect found when a neutral figure was adjusted to match each illusory figure separately, and these illusion effects summed. And indeed, they found a greater illusion effect when the two illusory figures were directly compared (i.e, a superadditive effect). Additionally, when they used single–

figure displays, they found the same illusion effect magnitude for both the perceptual adjustment and the grasping tasks. In parallel, two other research groups tested the same hypothesis and came to similar conclusions (Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999; Vishton, Rea, Cutting, & Nuñez, 1999).

This criticism ties in directly to one of the original projects in this dissertation. First, while many researchers have since followed Franz et al. (2000)'s example by using displays with only single illusory figures, others have also attempted to induce a direct comparison in grasping by means of bimanual grasping (e.g., Dewar & Carey, 2006). However, unlike Franz et al. (2000), Dewar and Carey (2006) used the Müller–Lyer illusion. In **Study 3**, we investigate whether the Müller–Lyer illusion is subject to the same superadditive direct comparison effects as the Ebbinghaus illusion (for examples of both illusions, see Figure 4.1). We furthermore investigate

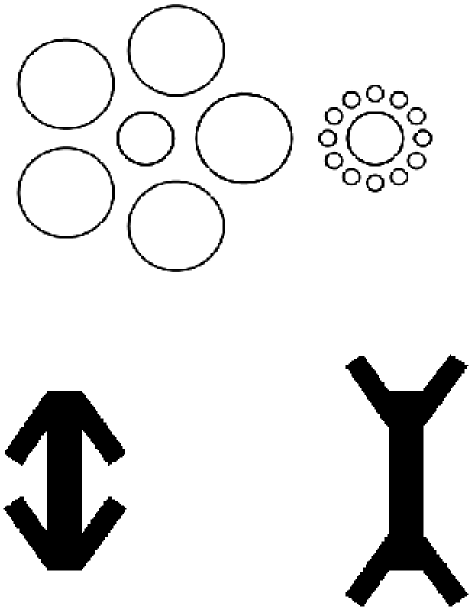

Figure 4.1: Examples of the Ebbinghaus (top) and Müller–Lyer (bottom) illusions, as used in our **Study 3**. The inner circle of the small–circle surround figure should appear larger, and the fin out shaft longer, although they are in fact the same size as the large–circle surround center circle and fin in shaft.

two methods of comparing two figures comprising these bipart illusions: simultaneous adjustment, whereby increasing the size of one figure results in an equivalent decrease in the other; and independent adjustment, where one figure remains stationary while the other is adjusted to match it. Both were previously used to investigate superadditivity of illusions, with Franz et al. (2000) using simultaneous adjustment, and Gilster and Kuhtz-Buschbeck (2010) using independent adjustment. Franz et al. (2000) had found a superadditive effect for the Ebbinghaus illusion using simultaneous adjustment, but Gilster and Kuhtz-Buschbeck (2010) had failed to find one for the Müller–Lyer illusion using independent adjustment. We therefore wanted to test whether this difference was due to the method of adjustment or differences in the illusions themselves. Our results indicate that for both the Müller–Lyer and Ebbinghaus illusions, simultaneous adjustment direct comparisons result in a superadditive illusion effect, but independent adjustment direct comparisons only cause superadditivity under limited experimental conditions (Foster & Franz, 2014). We therefore conclude that merely interacting with both illusory elements is not sufficient to achieve a superadditive illusion effect. Due to this uncertainty, it is also unclear whether bimanual grasping involves a comparison of the stimuli that would result in a superadditive illusion effect. Experiments comparing bimanual grasping of illusions to a perceptual task are thus difficult to interpret, as they may not solve the problem of different task demands occuring in the perception and action conditions.

4.1.2 Manual Size Estimation as a Perceptual Measure

The intriguing prospect that grasping might show a resistance to visual illusions resulted in the hypothesis being tested with a variety of different illusions, using a variety of methods for measuring the perceptual effect. While the original study of Aglioti et al. (1995) used a visual comparison technique, another early study introduced a new method of measuring the perceptual illusion effect, namely by opening the finger and thumb to indicate the perceived size of the object, while keeping the hand in place (Haffenden & Goodale, 1998). This technique is now commonly referred to as manual size estimation (MSE), and was also considered a ventral, perceptual task due to visual agnosic D.F.'s inability to complete the task (e.g., Westwood, Danckert, Servos, & Goodale, 2002). On the surface, MSE seems like an ideal perceptual task to compare to grasping, due to their similarities—both result in a measurement of the distance between finger and thumb, for example. However, not only has the question been raised how truly "perceptual" this action of moving the finger and thumb really is (Franz, 2001; Bruno, 2001), but furthermore whether the ease of comparison between conditions may be deceptive. The dependent variable may in both cases be the distance between finger and thumb, but is a 1 mm difference in grasping equivalent to a 1 mm difference in MSE? That is, do they represent the same difference in estimated size?

To investigate this question, Franz, Fahle, Bülthoff, and Gegenfurtner (2001) suggested looking at how the response measures respond to *physical* differences in stimuli. For example, if stimulus A is 35 mm, and stimulus B is 40 mm, the difference in MGA measured when grasping these stimuli may nevertheless be only 4 mm. If a particular measure does not respond to changes in physical size on a 1:1 basis, it should not be expected that it would respond to illusory size in that way, either. Instead, the responsiveness slope should then be determined (as response difference/physical difference, or in the above example, 0.8). If both grasping and perceptual illusion effects each are divided by that response measure's slope, only then can they be considered representative of differences in estimated size, and rightfully compared.

Franz (2003a) applied this correction procedure to MSE. Interestingly, MSE showed a much stronger responsiveness to changes in physical size than either perceptual adjustments or grasping (slope of 1.57 relative to .97 and .95, respectively). When the illusion effects are uncorrected, there appears to be a larger illusion effect for manual size estimation. After correcting the illusion effects by the responsiveness slopes, however, there was a similar illusion effect for all three methods of measurement. Taking into consideration the measurement's responsiveness to physical size typically results in illusion effects indistinguishable for grasping and perception or MSE (e.g., Franz & Gegenfurtner, 2008; Franz et al., 2009; Foster et al., 2012; Duemmler, Franz, Jovanovic, & Schwarzer, 2008).

4.1.3 Use of Visual Feedback

In Section 3.2.4 I discussed pantomimed grasping, where certain actions, such as grasping from memory, were thought to be controlled by the ventral stream because they were unable to be performed by patient D.F. If current visual information is key to her being able to grasp normally, it therefore initially seems ideal to include as much visual information as possible in a trial, also in experiments using healthy participants. However, there has also been a longstanding concern that participants may correct their aperture while approaching the target based on visual feedback, thus reducing or eliminating the illusion's effect on grasping (e.g., Haffenden & Goodale, 1998). The amount of visual feedback to allow is therefore a balancing act: How can we allow enough vision of the stimulus to prevent pantomimed grasping, yet not allow for online corrections?

The most common compromise that has emerged is to remove sight of the object as soon as the participant begins their movement. Westwood and Goodale (2003) tested participants' grasping of a size contrast illusion and found it to have an effect on grasping if vision was removed immediately after the go signal tone, but not if it was removed just after the participant began to move. They interpret this result to mean that the dorsal stream has a very short, limited "memory", whereby the information is simply no longer available by the time the person begins the movement if vision was already removed with the go signal tone. In that case, they contend that the brain reverts to ventral visual processing to control the movement. However, in contrast to this view, Franz et al. (2009) found a clear decrease in the illusion effect on grasping when increasing visual feedback over multiple steps, from grasping after a delay to full vision throughout the entire movement (with intermediate steps of removing vision after the signal tone, after the participant has begun moving, or after the participant had moved 1/3 or 2/3 of the distance to the object). They argue that this slow decrease in illusion effect as more visual information is made available is more indicative of online corrections than a fundamental shift in processing. Nevertheless, both proponents and challengers of the two stream theory have generally agreed upon removing visual feedback as the participant begins to move as an acceptable condition for testing whether grasping may be resistant to illusions.

When vision was removed as soon as the movement was started, illusions were nevertheless often shown to have an effect on grasping. The illusion effect in this case was also stronger than when participants were allowed full view of their hands and the stimulus (Heath, Rival, Westwood, & Neely, 2005; Heath, Rival, & Neely, 2006). A meta–analysis also showed that the effect of the Müller–Lyer illusion on grasping was smaller when participants had full view of their hand compared to when vision was removed at the start of the movement (Bruno & Franz, 2009). We also tested the effect of visual feedback on grasping in one of the studies included in this dissertation (**Study 1**). While the importance of visual feedback on grasping illusions had already gained much support, previous studies had used only single figure illusory configurations. We decided to test whether visual feedback would also be the deciding factor in an experimental design such as that of Dewar and Carey (2006), who used bimanual grasping of the Müller–Lyer illusion, hoping to increase the illusion effect by inducing a direct comparison. (From Section 4.1.1 and **Study 3**, we now know that it is difficult to know whether the bimanual grasping task did induce a direct comparison, and if so, whether it increased the illusion effect).

Dewar and Carey (2006) found a larger illusion effect for a bimanual perceptual task (MSE) than a bimanual grapsing task under full vision conditions. In **Study 1**, we replicate the findings of Dewar and Carey (2006) with full visual feedback, but also included a condition where we removed vision of the hands as participants began their movement. In the latter case, we found no difference in illusion effect between the perception and grasping tasks (Foster et al., 2012). This finding further underscored that visual feedback is a critical factor in reducing the illusion effect on grasping, even in a bimanual design.

4.1.4 An Alternative Interpretation: Planning and Control

A further alternative to the perception and action model of Milner and Goodale (1995) was proposed by Glover (2004). Called the planning—control model, it suggests a further subdivision of visual information processing in the posterior parietal cortex or dorsal stream, whereby the inferior parietal lobe is responsible for the planning of a movement, and the superior parietal lobe is concerned with the control of a movement. When referring to planning, Glover (2004) considers this to be the initial determination of both spatial and non–spatial properties (non–spatial properties being attributes such as weight or fragility), as well as the higher–level goals of the one performing the movement. When referring to control, he considers this to encompass the on–line correction during the course of a movement of spatial characteristics only.

Relative to the perception and action model of Milner and Goodale (1995), the planning and control model distinguishes itself by predicting differences between early (handled by planning) and late (handled by control) phases of the movement. However, it shares the prediction that in late phases of a movement, spatial characteristics should be processed more analytically and be less susceptible to context. It therefore seemed natural to test the planning—control model by examining whether illusion effects might be greater at earlier rather than later points in the movement.

Glover and Dixon (2002) tested this by having participants grasp the Ebbinghaus illusion, and calculated illusion effects at different time points in the grasp (40%, 60%, 80%, and 100% of movement time). They did this by first finding the responsiveness rate of the grip aperture to actual size by dividing the grip aperture at that point in time by physical size (i.e., by finding the slope). The illusion effect (difference in grip aperture between small context and large context circle configurations) at each point in time was subsequently divided by this responsiveness rate in order to find a corrected illusion effect (as suggested by Franz, 2003a; Franz et al., 2001). Analyzing the data in this way, they found a decrease in the illusion effect at later movement times, which they attribute to the more accurate control processing taking over.

However, it was soon argued that several characteristics of this data make it difficult to analyze. One of the first arguments against their analysis was that because they divided a participants illusion effect by the average slope at that time point, this would cause their confidence intervals to be underestimated, because such an analysis assumes that the denominator has no variance (Franz, 2003b, 2004). On the other hand, simply dividing a participant's illusion effect by their individual slope is also problematic, as if the slope is small enough (as is common at early time points), this can lead to arbitrarily large values (Franz, Scharnowski, & Gegenfurtner, 2005). Analyzing the ratio of two variables and determining their confidence interval is a problem not unique to psychology, however, and a general statistical technique for this does exist, called Fieller's theorem (Fieller, 1954; Franz, 2007). When this method of evaluating the data and determining the confidence intervals was applied, no decrease in illusion effects over time was found (Franz et al., 2005). This suggests that dynamic illusion effects do not exist and should not be taken as evidence for the planning—control model.

4.2 Criticism of Weber's Law Experiments

When Ganel, Tanzer, and Goodale (2008) published their finding that contrary to what one would expect from Weber's Law, MGA standard deviations did not increase with object size, it was nearly immediately met with an alternative explanation. While Ganel et al. (2008) concluded that their findings could be seen as evidence for differential processing of visual size for perception and action, Smeets and Brenner (2008) instead claimed that one would only expect the standard deviation to increase with object size if the relevant property being estimated is *size*; however, they had previously put forward a model which proposes that grasping is more akin to directing the finger and thumb to a particular *position* (Smeets & Brenner, 1999). Because position does not increase in magnitude the way size does, rather remaining isolated points regardless of the distance between them, they contend that there is no reason to expect the variability of MGA to reflect Weber's Law at all.

Some further research has attempted to test these two theories. Together with my M.Sc. student, Philipp Taesler, we examined the variability of the MGA when grasping a partially obscured stimulus.[1] We theorized that participants would have to mentally estimate where the obscured edge of the stimulus most likely lie (the proportion of the stimulus which was covered was consistent at one half). Our motivation was that in this case, both the perception and action account as well as the reasoning of Smeets and Brenner (2008) would predict an effect of Weber's Law on grasping. In the first case, we reasoned that grasping such a non–visible, mentally estimated stimulus would be interpreted in the perception and action framework as engaging the ventral stream, and should therefore be susceptible to Weber's Law. In the latter case, if participants were grasping based on position, they could still not determine the points to aim to by vision directly, having to mentally double the size

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[1] This study was presented as a poster at the Tagung experimentell arbeitender Psychologen (TeaP), but is not included in the dissertation.

of the visible stimulus to determine where the other edge must be. Because they are required to work with size to direct their grasp, we would expect an effect of Weber's Law even under the interpretation of Smeets and Brenner (2008). However, we still did not find the expected increase of standard deviation of the MGA with object size (Taesler, Foster, Floss-Loewenkamp, & Franz, 2014). Another experiment examined an extreme case—grasping without visual information at all, only to an auditorally presented number—and also could not find such a relationship (Floss & Franz, 2012). These results indicate that it cannot be a differential processing of visual information that leads to the inability to find evidence for Weber's Law in grasping. This lack of Weber's law for grasping, even in situations where both proposed explanations of the original effect would predict it, has led researchers to consider whether there might be some other, as of yet unconsidered factors in grasping, which cause it to not reflect Weber's Law. However, a counter explanation has yet to be concretely proposed.

4.2.1 Do the Weber's Law Findings Support the Planning—Control Model?

Apart from these criticisms, the absence of Weber's Law at the MGA offered another opportunity to test the planning—control model of Glover (2004). Heath, Mulla, Holmes, and Smuskowitz (2011) asked whether a dependency of the standard deviation of grip aperture on object size might be found earlier in the grasping movement, indicating that Weber's Law can be found at earlier time points but not late, due to processing for planning versus control. They performed an experiment similar to the one of Ganel et al. (2008), having participants grasp objects of varying sizes and measuring their grip aperture. However, instead of looking only at the variability of the MGA, they found the average grip aperture at different points of the movement (from 10% to 100% movement time), and calculated the standard deviation of the aperture at each of these time points. They found that the aperture standard deviation increased with grasped object size at early time points (from 10% to 50% movement time), but not at later time points. They interpreted this as evidence for the planning and control model, whereby planning processing was susceptible to Weber's Law, while control processing was not (see also Holmes, Mulla, Binsted, & Heath, 2011).

However, our analysis in **Study 2** reveals a flaw in their reasoning. When Heath et al. (2011) averaged their grasping trajectories, they failed to take into account the impact of noise arising from misalignment on their estimated standard deviations. We show that because the trajectories had a greater slope at early time points for larger objects, due to opening the fingers more quickly for larger objects, averaging them would necessarily cause the standard deviations to be dependent on size. This is true simply due to a relationship between slope and standard deviation, which we derive analytically, and does not require the contribution of an effect like Weber's law **Study 2**; Foster & Franz, 2013).

Recently, our argument was tested in an experimental setting. Ganel, Freud, and Meiran (2014) reversed the usual size/velocity relationship by having participants assume a start position with their finger and thumb open as wide as possible, instead of closed together, as in most other studies. This means that participants would have to close their fingers faster to grasp smaller objects in the same amount of time. As we would predict, under this manipulation, not only did aperture velocities decrease with object size at early time points, but standard deviations did as well. This demonstrates experimentally our argument that standard deviation will be directly related to the aperture velocity at a given time point. To circumvent this problem, Ganel et al. (2014) manipulated the start position of the participants' fingers, such that the start position was wider for larger objects. The intent was to maintain an equal velocity for all object sizes, even at early time points, which they also measured and confirmed to be the case. Controlling for velocity, they found that the aperture standard deviation remained constant for all object sizes. Thus, the finding that Weber's law exists only at early time points has been shown to be both theoretically and experimentally due to the relationship between aperture velocity and standard deviation, and should not be taken as evidence for the planning—control model.

4.3 Criticism of Resistance to Garner Interference

The finding that grasping is immune to Garner interference, with the conclusion that dorsal stream processing considers only the relevant dimensions of the stimulus to be grasped (Ganel & Goodale, 2003), has been subject to criticism of both internal consistency with the perception and action model, as well as the methods used in the original experiments. Regarding internal consistency, Janczyk et al. (2010) tested several movements considered to be subject to ventral control—grasping with the left hand, using a tool, and grasping awkwardly—to see whether influence of Garner interference could be identified in those cases. They used a similar paradigm to the study of Ganel and Goodale (2003), measuring reaction time and movement time when grasping blocks in both baseline and filtering conditions, where the stimuli varied in either one or two dimensions, respectively. The expectation was that, if these actions relied on the ventral stream, they would find slower reaction times or movement times in the filtering condition, due to the inability of the ventral stream to ignore the extraneous information of the changing irrelevant dimension. However, they found no difference in reaction or movement times between the baseline and filtering conditions for any of the actions they tested. Since these actions were apparently also not susceptible to Garner interference, Janczyk et al. (2010) conclude that even awkward, left–handed, or tool–based grasping must be controlled by the dorsal stream. Eloka et al. (2014) similarly tested the extreme case of grasping that was both awkward and left–handed (grasping with the thumb and ring finger of the left hand), and also failed to find any evidence of Garner interference for the task.

However, an alternative explanation has recently been offered by Hesse and Schenk (2013). In particular, they argue that reaction and movement times are not an appropriate way to judge whether Garner interference affects motor estimated size, as there is ample time for correction between the start and the end of the movement. Therefore, for grasping, it would not be required to have completed visual processing before beginning the movement. They tested this hypothesis in two ways. First, they showed that it is possible to design a perceptual experiment that does not show evidence of Garner interference. They did this by having participants reach to a virtual button on a touchscreen in order to classify the object, rather than placing their left and right index fingers directly on two separate response buttons. This allowed participants time to adjust which button they are aiming for in flight. And in fact, they found no difference in movement or response times (i.e., no Garner interference) in this perceptual judgment task. Additionally, they also designed a grasping experiment that had less room for online correction, namely by taking away vision of the hand as soon as the movement was initiated. Using this visual condition, they were able to find slower reaction times in the filtering condition than in the baseline condition even for grasping. These results provide strong support for the hypothesis that any response, whether grasping or perceptual, that provides opportunity for on–line correction, will not show Garner interference in its reaction times. Because Garner interference can also be induced in grasping if the opportunity for correction is removed, it does not provide evidence for a differential processing of object attributes by the dorsal stream.

4.4 Alternative Explanations of D.F.'s Behavior

The previous sections have called into question whether a qualitative difference in visual processing can be found in healthy participants for perception and action. That dorsal processing of visual information should be analytical rather than holistic constitutes a major portion of the perception and action model, and a lack of reliable evidence to support this claim has also caused scientists to revisit one of its other major sources of inspiration, namely the behavior of visual form agnosic patient D.F. Her ability to correctly grasp objects, but not judge their form, size, or orientation, has been replicated successfully many times (e.g., Schenk, 2012a; Goodale et al., 1991, 1994; Schenk & Milner, 2006). If not due to a unique visual processing by the dorsal and ventral streams for the purposes of perception and action, what might explain her behavior? In the following, two other contributing factors are discussed, namely haptic feedback received at the end of a movements, as well as the role of contextual visual information.

4.4.1 The Role of Haptic Feedback

As discussed in Section 3.2.4, some conditions of pantomimed grasping—where grasping movements were thought to be controlled by the ventral stream—were established very early on in the model's history. These included grasping from memory, or grasping next to the target object (Goodale et al., 1994). However, as experiments began using virtual stimuli and mirror setups to investigate grasping (e.g., Foster, Fantoni, Caudek, & Domini, 2011; Bingham, Coats, & Mon-Williams, 2007), this enabled a further, more ambiguous condition, where participants direct their movements directly to a target's location (i.e., not next to it), and while the visual presentation of the virtual object is still present (i.e., not from memory), but nevertheless do not actually touch an object and receive haptic feedback. It was thus not immediately clear from previous research whether the two streams theory would expect this type of action to be processed dorsally or ventrally. One clear way to test this would be to see whether patient D.F., whose dorsal stream is destroyed, is still able to correctly grasp objects without haptic feedback.

Schenk (2012a) tested patient D.F. under several different haptic feedback conditions using a mirror setup (for a visual depiction of the mirror setup used, see Figure 4.2). In addition to the more common size discrimination, manual size estimation, and grasping with full haptic feedback conditions, he also tested patient D.F.'s grasping performance when there was no haptic feedback, and when haptic feedback was only available in 50% of trials (although a small light indicated whether haptic feed-

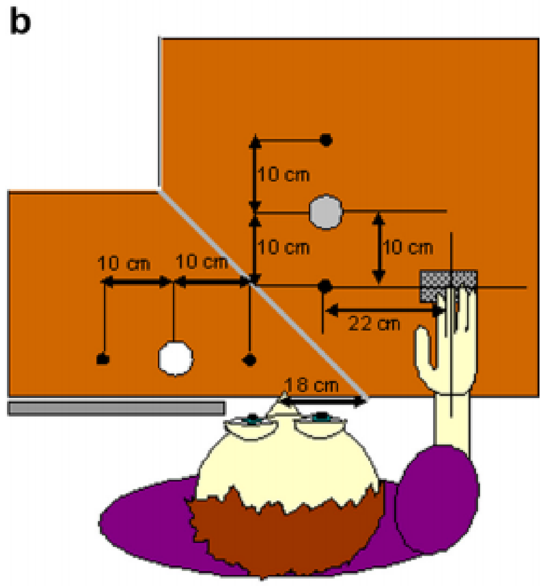

Figure 4.2: The mirror setup used by Schenk (2012a). The participant is seated in front of a slanted mirror such that an object placed to the participant's left appears to be located in front of them. By placing a different object behind the mirror, or no object at all, this allows haptic feedback to be inconsistent with the visual image. Republished with permission of Society for Neuroscience, from The Journal of Neuroscience, 32(6), Schenk, T., No dissociation between perception and action in patient DF when haptic feedback is withdrawn, 2013–2017, 2012; permission conveyed through Copyright Clearance Center, Inc.

back would be available in a particular trial). For the size discrimination, manual size estimation, and grasping with full haptic feedback tasks, Schenk (2012a) replicated the typical findings with patient D.F., namely that she was much better at scaling her her grasp than either discriminating between sizes or manually estimating. For the condition where she grasped without haptic feedback, however, her performance severely deteriorated. For the intermittent haptic feedback condition, patient D.F. showed some decline in performance compared to the full haptic feedback condition, but was still able to scale her grasp. Furthermore, within the intermittent haptic feedback condition, Schenk (2012a) found no difference in scaling between trials with and without haptic feedback. This indicates that knowledge of the feedback condition made no difference for patient D.F.'s performance. Schenk (2012a) interprets these results to mean that patient D.F. does not rely on visual information alone, but that other cues, in particular from haptic information, also play a role in her grasping success. He believes this extraneous information can be used to bolster remaining, impoverished visual information in order to improve her performance.

However, Milner, Ganel, and Goodale (2012) argue that an equally reasonable explanation is that grasping without haptic feedback represents another form of pantomimed grasping, which would be expected to engage the ventral stream. As this area of patient D.F.'s brain is damaged, it is natural that she would not be able to perform the task. Only grasping with haptic feedback would therefore be expected to activate the dorsal stream. Schenk (2012b) argues that he included a condition which tests this possibility in his original study, namely the condition of intermittent haptic feedback, where the presence of haptic feedback was indicated by a small light. In this case, patient D.F. knew whether or not haptic feedback would be present, and was still able to scale her grasp to the size of the object even when she knew there would be no haptic feedback. However, Milner et al. (2012)'s interpretation is also supported by a study showing that, for uninformative haptic feedback—that is, where the physical object is always the same size, regardless of visual display—patient D.F. was still able to scale her aperture to the visually presented object size (Whitwell, Milner, Cavina-Pratesi, Byrne, & Goodale, 2014). The authors interpret this to mean that while consistent haptic feedback is necessary for dorsal control of grasping, it does not determine aperture size, which is reliant on visual information. Although Schenk (2012b) argued that patient D.F. could be associating impoverished visual information, such as that of edges, rather than size, with the haptic feedback, it is nevertheless difficult to explain how even uninformative haptic feedback could improve her estimates in such a way as to produce acceptable performance.

One study has also attempted to relate grasping without haptic feedback to pantomimed grasping in healthy participants. Byrne, Whitwell, Ganel, and Goodale (2013) showed that similar changes to grasping parameters (e.g., smaller MGAs, lower peak hand velocity) occur when healthy participants grasp without haptic feedback as when they grasp from memory or next to an object (the classic cases of pantomimed grasping). However, this alone cannot prove that the dorsal stream is not being used in healthy participants to perform this task. The topic of haptic feedback in grasping is one of the newest and most unresolved areas regarding the two streams theory and the perception and action model. It will likely continue to be the focus of much research and debate in coming years.

4.4.2 Egocentric vs. Allocentric Visual Processing

A further alternative is that the proposed purpose of the dorsal and ventral streams as being responsible for action and perception, respectively, should be revised. Schenk (2006) suggested that the roles of the dorsal and ventral streams would be better described as responsible for egocentric (relative to the actor) and allocentric (relative to the scene) visual processing, respectively. Under this interpretation, patient D.F. should have preserved egocentric visual processing, but impaired allocentric visual processing, regardless of whether a perception or action task is used to test each case. Schenk (2006) argues that in a typical study, the "action" task used requires egocentric processing, while the "perception" task requires allocentric processing, and these studies are therefore not capable of distinguishing between the two interpretations. He therefore devised both an allocentric action task and an egocentric perception task, such that he could test both allocentric and egocentric processing in both perception and action tasks (for a visual depiction of all four tasks, see Figure 4.3). For the allocentric perception task, he asked patient D.F. and controls to indicate which of two points was closer to a cross. For the egocentric perception task, the partici-

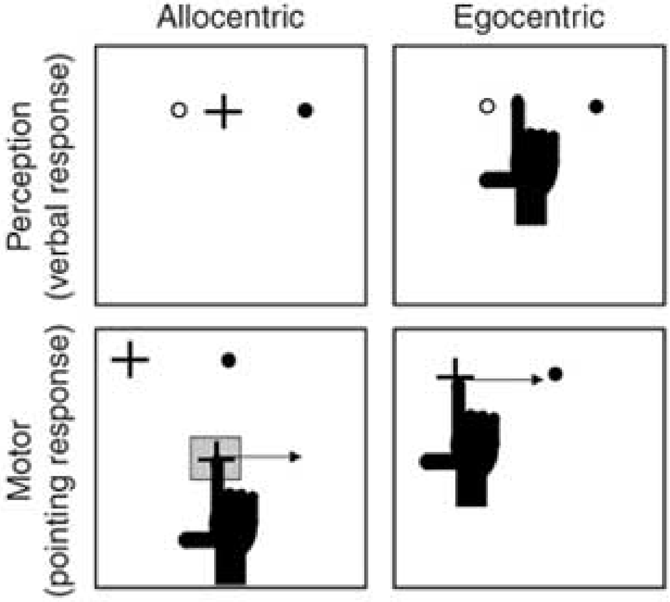

Figure 4.3: Allocentric and egocentric tasks for both perception and action. The allocentric perception task (determine which point is closer to a cross) and egocentric motor task (move finger from a cross to a point) were considered typical. The egocentric perceptual task (determine which point is closer to one's own finger) and allocentric motor task (move finger the distance between the cross and point, in a different direction) intended to remove this confound when comparing perception and action tasks. Schenk (2006) found that patient D.F. was able to perform both egocentric tasks, but neither allocentric task. Republished with permission of Nature Publishing Group, from Nature Neuroscience, 9(11), Schenk, T., An allocentric rather than perceptual defect in patient DF, 1369–1370, 2006; permission conveyed through Copyright Clearance Center, Inc.

pant's finger provided the middle reference point instead of the cross, and they had to indicate which of two visible points was closer to their finger. For the egocentric action task, participants moved their finger from a starting point to a target cross. For the allocentric action task, a start and end point were displayed, and participants were instructed to move their finger the same distance, but at a location below the visually presented points, and in the opposite direction. In accordance with Schenk (2006)'s allocentric/egocentric hypothesis, patient D.F. was able to perform the both the egocentric perception and action tasks, but was unable to perform either allocentric task. However, Milner and Goodale (2008) argue that the allocentric motor task was requiring patient D.F. to act out her perception, similar to a pantomimed grasping task. As for the egocentric perceptual task, they argue she may have used a motor strategy for her decision, as she could have imagined pointing to each of the targets.

Recently, the distinction between allocentric and egocentric visual processing has also been offered as an explanation for patient D.F.'s poor performance in pantomimed grasping. Specifically, Hesse and Schenk (2014) tested patient D.F.'s ability to perform a card–posting task under two different delay conditions: in one case, her vision was obscured completely using shutter glasses, and in the other, only the stimulus was removed (by presenting a virtual slot on a monitor). They found that, although her ability to orient the card to the slot was impaired when only the stimulus was removed and environmental cues were present, her performance was indistinguishable to that of controls when her vision was obscured completely, even after a 3–second delay. This seems to indicate that it is at least possible for delayed action to still be controlled by the dorsal stream. Hesse and Schenk (2014) claim that healthy participants likely use contextual landmarks to aid memory–guided grasping when the scene is still present. If patient D.F.'s allocentric processing is impaired, this would explain why she is unable to use these contextual landmarks in order to grasp from memory when the environmental context is present. However, in order to explain why her performance is even *worse* when environmental cues are present, as opposed to simply lacking helpful information, one would have to go one step further and suppose that the missing or distorted allocentric processing, when it is otherwise expected to be present, actively impairs her performance in the task.

Chapter 5

Conclusion

5.1 Summary of Current Projects

I have thus far reviewed several theories of how motor actions are controlled via visual information, as well as the recent surge of interest in the topic, aided by advances in cognitive neuroscience. As the field has been flooded with new techniques and methods in order to tackle this problem, it is only natural that some of the finer points of their usage remained to be clarified. In particular, standardizing the visual content so that motor and perceptual tasks can be adequately compared has been a challenge. Our **Study 1** shows that allowing participants to view their hands while grasping affords them visual information—most likely from comparing the position of the fingers relative to the object—which is not available in a traditional perception experiment. Removing vision as participants began their movement equalized the information available in the two tasks, as well as the illusion effects measured. Our analysis in **Study 2** also exposes a complication when trying to examine the entire time course of a grasping trajectory: simply averaging the trajectories will lead to an artifact in the estimated standard deviations, whereby they will be dependent on the trajectory's velocity. If this artifact is interpreted as a legitimate effect, it can lead to erroneous conclusions. Being aware of the artifact can allow researchers to work around it in their experimental design (as did Ganel et al., 2014). Finally, our **Study 3** shows that we still have much to learn about the subtleties of even long–studied illusions. We found that even when comparing one illusory figure to the other, small changes in the way participants adjusted the stimuli affected their perceived illusion effect. That such fine variations have such a critical effect underscores the difficulty of designing perception and action tasks with balanced task demands.

5.2 Future Outlook

In this dissertation, I have discussed many criticisms of the founding pillars of the perception and action model of Milner and Goodale (1995). The criticisms leave serious doubts about the veracity of some of their central claims, in particular whether fundamental visual properties receive different treatment when processed for the purpose of action. However, they also raise several new questions. In particular, should Milner and Goodale (1995)'s theory be rejected completely, or can some of their ideas be retained? In particular, what is precisely the role of the dorsal stream? Does it indeed play a crucial role in action, but use same fundamental visual processing as the ventral stream? In the future, it would be worthwhile to compare the predictions of the perception and action model more directly to alternatives such as Schenk (2006)'s allocentric/egocentric interpretation, or even by revisiting the "what" and "where" theory of Ungerleider and Mishkin (1982). In particular, a contrast between "what" and "where" and "allocentric" and "egocentric" would be especially interesting. For example, Pohl (1973)'s landmark task, where the monkey participants were required to choose the foodwell closest to an object "landmark", was very clearly meant to be an allocentric task (as even stated explicitly in the paper), yet performance in this task was disrupted by damaging the posterior parietal cortex (dorsal stream).

However, when patient D.F., whose dorsal stream is intact, is faced with the very similar (allocentric) task of determining which point is closer to a cross, she is unable to do so. How can these results be reconciled? Would patient D.F. have had more success in the task if she was required to touch the point closest to the cross rather merely make a verbal selection?

Another promising area of future research concerns the role of haptic feedback in grasping. The importance of haptic feedback for the guidance of motor movements, also in healthy participants, is becoming ever more clear. It has been shown to be necessary for accurate and precise visually guided grasping (Bingham et al., 2007), and will also bias grasping when it is in conflict with visual information (Coats, Bingham, & Mon-Williams, 2008). Hopefully any new theory on the way visual information is processed and translated into grasping will more strongly incorporate this influence, possibly by considering a calibration mechanism.

Understanding the influence of haptic feedback on grasping is also important for comparing perceptual and grasping responses in a methodologically sound way. Since we know that haptic feedback that is not compatible with what one sees can cause that person to grasp more in line with the haptic feedback, we must be careful that this influence does not result in a difference between perception and action tasks being found which has nothing to do with vision. In particular, mirror setups and virtual presentations have allowed much more freedom in the visual conditions to be used, as well as what type of haptic feedback should be presented, if at all. For example, Foster et al. (2011)[1] tested whether grasping in depth would follow the rules for the combination of motion and binocular disparity information for depth perception, whereby a stimulus rendered by two cues is perceived deeper than either in isolation (Domini, Caudek, & Tassinari, 2006; Tassinari, Domini, & Caudek, 2008). We found a similar pattern for manual size estimation and grasping as we did for perception, but

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[1] This study was the subject of my B.Sc. thesis, and is not included in this dissertation.

did not include haptic feedback. However, it is possible that including accurate haptic feedback would obscure the perceptual distortion. To test a dissociation between perception and action, it would be ideal to find a level of haptic feedback that does not bias grip aperture, but still allows for normal movement parameters. Together with my M.Sc. student Annika Januszewski, we tested whether providing incorrect haptic feedback on only 50% of trials would be sufficient to bias participants' grip aperture.[2] We did this by using a mirror setup where the grasped object was always 5 mm smaller or larger than the viewed object. However, we found that participants did alter their grip aperture in the expected direction, which means this amount of haptic feedback does not represent a case where grasping may be calibrated, but not biased. Future research may show that there is some level of haptic feedback that can be provided where grasping does not drift, but is also not biased; however, it is also possible that the calibration mechanism is too strong for such a condition to be found.

The study of how visual information is used to guide action has come a long way since Sherrington's reflexive motor units, and the methods used to compare action to perception have been much refined. However, we are still far from a consensus on the role of some of the higher levels of visual processing, in particular that of the dorsal stream or posterior parietal cortex. In the future, the field would likely benefit by introducing and testing alternative ideas of its purpose, preferably using neuroscientific methods such as fMRI. How haptic information is incorporated and integrated with visual information is also a very new question that should be addressed, including its neurological underpinnings. And in all cases, new methods should be carefully examined for their validity in order to avoid the misinterpretation of results.

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[2] This work has not yet been published, and is not included in this dissertation.

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List of Publications

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Taesler, P., Foster, R. M., Floss–Loewenkamp, C. & Franz, V. H. (2014). Grasping does not obey Weber's law—even if perceptual processes are involved. Poster presented at the 56th annual TeaP (Tagung experimentell arbeitender Psychologen) in Giessen, Germany.

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Foster, R. M., & Franz, V. H. (2011). A comparison of methods for testing the superadditivity of visual illusions: Evidence from the Müller–Lyer illusion. Poster presented at the 34th annual European Conference on Visual Perception (ECVP) in Toulouse, France.

Foster, R. M., Fantoni, C., Domini, F., & Caudek, C. (2009). Integration of stereomotion information for guiding calibrated reach-to-grasp movements. Poster presented at the 9th annual conference of the Vision Sciences Society (VSS) in Naples, Florida.

Study 1

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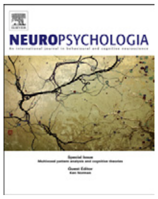

Research Report

Does bimanual grasping of the Müller-Lyer illusion provide evidence for a functional segregation of dorsal and ventral streams?

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ABSTRACT

Studies claiming a differential processing of visual illusions for perception and action have been subjected to many challenges. One criticism is that attentional demands were mismatched between the perception and action tasks. Dewar and Carey (2006) reexamined this argument by comparing bimanual grasping to bimanual size estimation and concluded that manual size estimation (ManEst) was affected by the illusion to a greater extent than grasping, supporting the case for two functionally distinct streams of visual processing. We tested whether this result may be due to their use of closed loop visual conditions by replicating their study under both closed and open loop conditions. We found that the difference in illusion effects between grasping and ManEst disappeared under open loop conditions, indicating that Dewar and Carey's findings can be explained by the availability of visual feedback and not a perception/action dissociation. We also discuss potential shortcomings of bimanual designs.

1. Introduction

The perception and action model of visual processing (Goodale & Milner, 1992; Milner & Goodale, 1995) has generated a flurry of interest, primarily due to its potential to answer one of vision science's driving questions: how, when faced with so many visual distortions, do we manage to interact with our world so seamlessly? In particular, the theory proposes that action operates on an internal size representation separate from that used for perception. It could then be possible that visual information is processed for action such that the many perceptual illusions and distortions (e.g., Coren & Girgus, 1978; Tittle, Todd, Perotti, & Norman, 1995) simply do not apply. With access to an undeceived map of our physical world, it would no longer be surprising that action is so accurate and precise. In line with this theory, several studies have indeed reported that visual illusions such as the Ebbinghaus (e.g., Aglioti, DeSouza, & Goodale, 1995; Haffenden & Goodale, 1998) or Müller-Lyer illusions (e.g., Daprati & Gentilucci, 1997; Westwood, McEachern, & Roy, 2001) have a reduced or no effect on grasping.

However, these results have been highly contentious, especially with regards to the methodology used (see Franz & Gegenfurtner, 2008, for a review). Nevertheless, a study by Dewar and Carey (2006) conforms quite well to these methodological concerns, yet still shows a smaller effect of the Müller-Lyer illusion on grasping than on a perceptual measure. This study specifically expands on the argument of Franz, Gegenfurtner, Bülthoff, and Fahle (2000) that task demands for perception and action must be matched in order for the illusion effects to be comparable. In particular, Franz et al. (2000) had found that a direct matching of the two illusory configurations of the Ebbinghaus illusion elicited an illusion effect on perception greater than the sum of the illusion effects measured when adjusting a neutral circle to each half of the illusion independently. They solved for this mismatch by using stimulus configurations consisting of only one of the two illusory figures. Consequently, when perceptual matching of a neutral circle and a single illusory configuration was compared to grasping of a single illusory configuration, the magnitude of the illusion effect was found to be equivalent for perception and action (cf. Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999; Vishton, Pea, Cutting, & Nunez, 1999).

Dewar and Carey (2006) took another approach. As a mismatch of task demands arises if the action task requires consideration of only one half of the illusion while the perceptual task forces a direct comparison of both illusory components, there are two potential solutions. The first is that the perceptual task be designed to require consideration of only one half of the illusion (the approach taken by Franz et al., 2000). The alternative would be to somehow force a direct comparison of both halves of the stimulus in the action task. To achieve this, Dewar and Carey (2006) kept the bipart display, but expanded the action to both

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halves by using bimanual grasping. Using a direct comparison for both action and perception tasks has the potential advantage of maximizing the illusion, thus reducing the likelihood of missing an effect (a concern raised by Jacob & Jeannerod, 1999 and adopted by Carey, 2001). When Dewar and Carey (2006) compared the effects of the Müller-Lyer illusion on bimanual grasping and bimanual size estimation (ManEst), they found a smaller effect of the illusion on grasping than on ManEst. They therefore concluded that visual illusions do, in fact, have a reduced effect on grasping, and that this is furthermore evidence for two streams of visual information processing in neurologically intact persons.

This conclusion is, however, obviously at odds with that of Franz et al. (2000) and Franz and Gegenfurtner (2008), who did not find differences in illusion effects for grasping and perception. What might have caused this difference? As previously mentioned, Dewar and Carey (2006) used an overall careful methodology, and calculated corrected illusion effects based on the baseline slopes for grasping and ManEst found for non-illusory stimuli (cf. Franz, Fahle, Bülthoff, & Gegenfurtner, 2001; Franz, 2003; Schenk, Franz, & Bruno, 2011). However, there is one notable aspect of their study we suspected to have caused the difference between perception and action in their case: all trials were performed closed loop. That is, participants had full view of their hands and the stimulus throughout the grasp. It has previously been shown that illusion effects on grasping are typically smaller under closed loop conditions (Bruno & Franz, 2009; Heath, Rival, Westwood, & Neely, 2005; Heath, Rival, & Neely, 2006; Westwood et al., 2001), and also systematically decrease as more visual feedback is allowed (Franz, Hesse, & Kollath, 2009). If we find that removing visual feedback leads to comparable illusion effects in perception and action under Dewar and Carey's (2006) bimanual conditions as well, it would show that their study provided no evidence that action engages a veridical, undeceived size perception (Post & Welch, 1996). We therefore attempted to replicate the study of Dewar and Carey (2006) and test whether the difference in illusion effects persists if open loop conditions are used.

2. Experiment 1: the effect of the Müller-Lyer illusion on bimanual, closed loop grasping and ManEst

Using bimanual grasping and ManEst tasks, we compared the effect of the Müller-Lyer illusion on perception and action. As in the study of Dewar and Carey (2006), we used full vision of the hand and stimulus.

For exploratory purposes we added another factor: half of the participants were presented with the two Müller-Lyer figures relatively close together (near condition) and the other half with the figures relatively far apart (far condition). We were interested in this manipulation for two reasons. First, we knew from other studies on bimanual grasping that perceiving items to be grasped as part of one unified object causes the programming of the two hands to be dependent on each other, leading to a sort of averaging of the apertures (Jackson, German, & Peacock, 2002). Second, the distance between illusion elements has long been known to play a role in the strength of visual illusions and can even lead to an inversion of the illusion effects (pool-and-store model; Coren & Girgus, 1978; Girgus & Coren, 1982). We will see that this stimulus-separation factor indeed has an effect (the illusion is stronger in the far condition for both grasping and ManEst, consistent with the pool-and-store model). However, because there were no interactions with any other factors, this additional factor did not complicate the interpretation of our other results.

2.1. Methods

2.1.1. Participants

The sample consisted of 48 participants (20 male, mean age 24 years). They were recruited via public announcement and were mostly students of the University of Gießen. All participants were right-handed as confirmed by a handedness inventory (Oldfield, 1971) and had normal or corrected-to-normal vision. They received compensation of 8 Euro/h and gave informed consent according to the 1964 declaration of Helsinki. They were naive to the hypotheses of the experiment.

2.1.2. Apparatus

Participants were seated in front of a small table with their head resting on a chinrest (Fig. 1). The object holders for the two targets were mounted such that the targets' centers were at a distance of 41 cm from the edge of the table where the chinrest was mounted. The centers of the two object holders were either 8 cm (near condition, Fig. 1) or 20 cm (far condition) apart. Small plastic knobs which served as starting points for the movements were placed at a distance of 34 cm from the object holders, separated by 20 cm and in line with the grasp targets in the far condition.

Movements were measured with an Optotrak 3020 infrared tracking system (Northern Digital Inc., Waterloo, Ontario, Canada; frame-rate: 100 Hz). One infrared marker was attached to the nails of the index finger and thumb of the participant's right and left hands, for a total of four markers used. Participants wore liquid-crystal shutter glasses (Plato, Translucent Technologies Inc., Toronto, Ontario, Canada) that enabled us to obscure vision of the stimuli and the setup arrangement while not significantly changing the level of dark adaptation (Milgram, 1987).

The experiments were programmed in Matlab (MathWorks Inc., Natick, MA, USA) using the Psychophysics Toolbox (Brainard, 1997; Pelli, 1997) and our Optotrak Toolbox (URL http://webapp6.rrz.uni-hamburg.de/allpsy/vf/OptotrakToolbox).

2.1.3. Stimuli

Bars of black plastic were used as targets (length: 39 or 43 mm; width: 8 mm; height: 5 mm). They were placed on small cards on which a printout of the Müller-Lyer illusion was laminated. The central bar of these printouts corresponded in

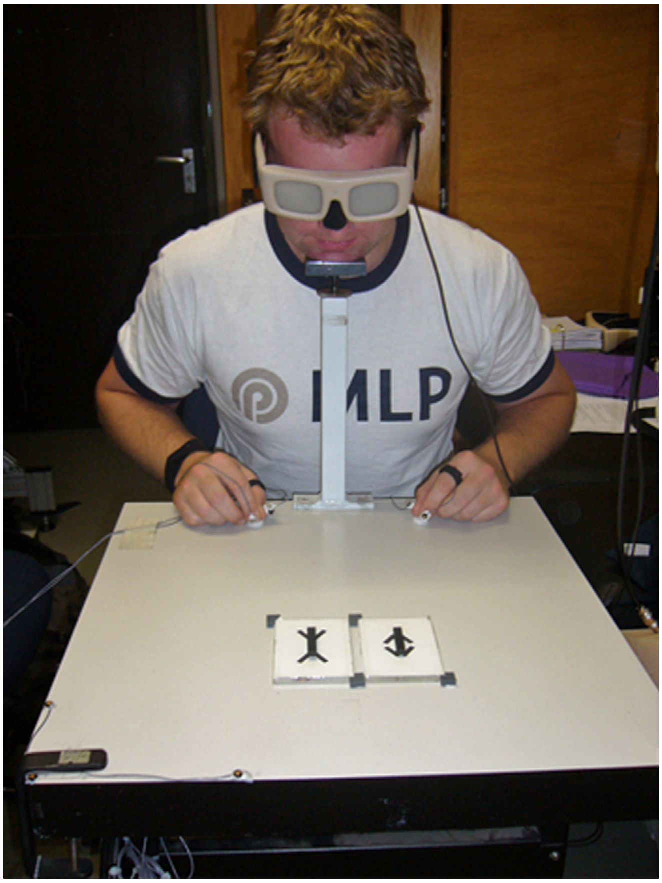
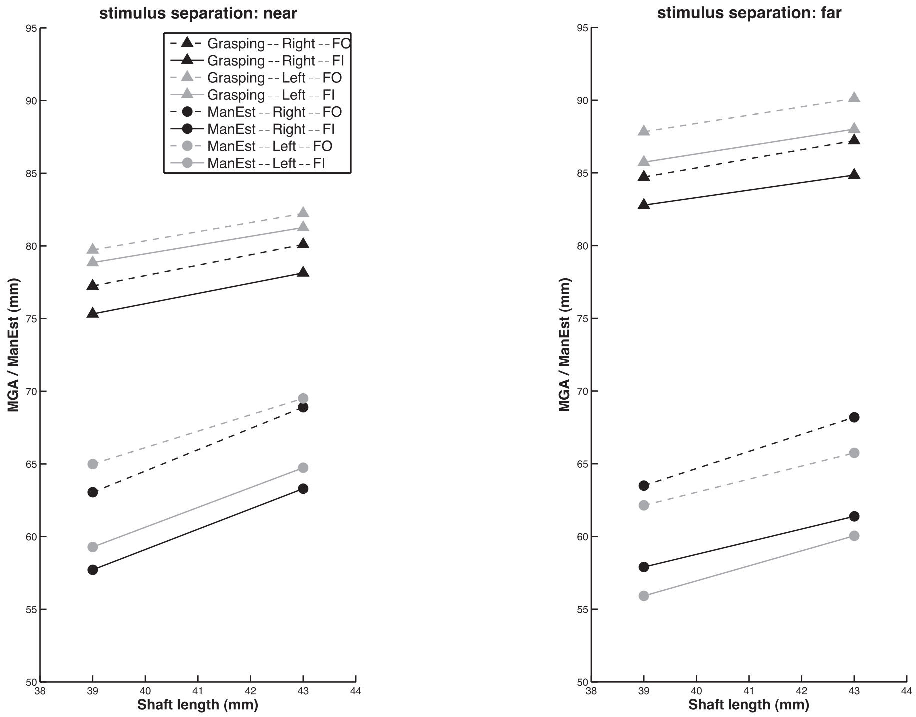


Fig. 1. A participant with hands in the starting position and shutter glasses opaque. Stimuli are presented in the near condition.

width and length to the plastic bar placed onto it. The fins of the printout could either point inwards (Fin In) or outwards (Fin Out) and the smaller angle between the fins was 70° in both cases. The longest extent of the fin measured 18 mm. For 24 participants (10 male, mean age 24 years), the distance between the centers of the object holders was 8 cm (near condition). For the remaining 24 participants (10 male, mean age 24 years), the centers were 20 cm apart (far condition).

Experiment 1: Closed Loop



Experiment 2: Open Loop

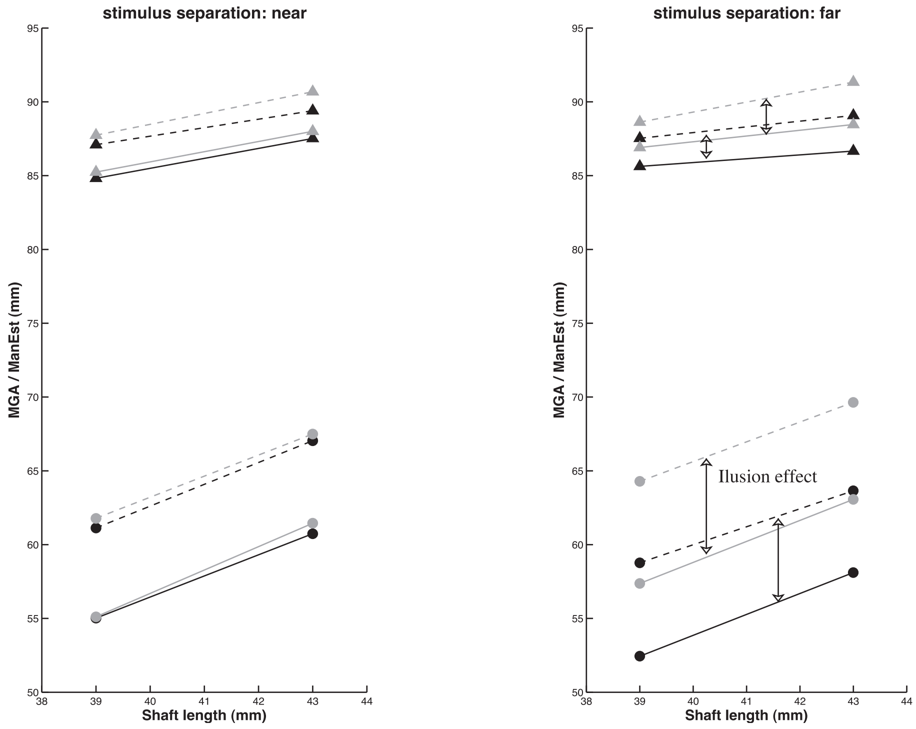


Fig. 2. Mean MGA and ManEst by experiment, stimulus separation (near/far), bar length (39/43), figure type (FO = Fin Out/FI = Fin In), and hand (left/right). Circles indicate ManEst, triangles indicate MGA. Gray lines correspond to the left hand, and black lines correspond to the right hand. Dashed lines correspond to Fin In figures, and solid lines correspond to Fin Out figures. The illusion effect is therefore the difference between the dashed and solid lines, as indicated by the arrows in the lower right panel.

2.1.4. Procedure

The experiment consisted of two blocks: a grasping task and a ManEst task, with order counterbalanced across participants. Participants typically completed the experiment within 1 h.

In the grasping task, participants were instructed to make a speedy simultaneous movement of both hands to pick up the targets lengthwise with a precision grip of index finger and thumb. Prior to every trial, participants placed their index fingers and thumbs on the starting points. The trial started with the shutter glasses being switched from opaque to clear. Participants had 1 s of preview and then heard a .1 s long 100 Hz beep as go signal to grasp the targets within 3 s under full vision of hands and stimuli. Participants picked up the target objects, lifted them away from the target area, placed them on the table and moved their fingers back to the start positions. The experimenter picked up the objects and prepared the next trial. For each of the left and right figures there were 4 experimental conditions: two bar lengths (39/43 mm) × two fin orientations (inward/outward). These 4 conditions were completely crossed, resulting in $4 \times 4 = 16$ conditions. Each condition was repeated 4 times, yielding 64 grasps per participant. At the beginning of the grasping task, participants completed five practice trials randomly selected from the experimental conditions.

In the ManEst task, participants followed the same procedure, but instead of grasping, they lifted their hands and estimated the targets' sizes by opening their index fingers and thumbs as wide as they perceived the targets (again within 3 s and under full vision of hands and stimuli). The size estimate was recorded by the experimenter by means of a button press when participants gave a verbal indication that they had finished adjusting their fingers. Experimental conditions, number of trials, and practice trials were analogous to those of the grasping task.

2.1.5. Data analysis

Reaction time (RT) in grasping and ManEst was defined as the time when the velocity of finger or thumb exceeded .025 m/s. Movement time (MT) was defined as the difference between RT and the endpoint of the movement. The endpoint of grasping was determined as the time when the minimum height above the table was reached within a 60-mm radius around the object. This minimum-height criterion has been shown to be a good measure of movement endpoint, as participants typically touch the table just before or as they make contact with the object (Franz, Scharnowski, & Gegenfurtner, 2005). For ManEst the endpoint was considered to be when the experimenter pressed the response button.

Trials were considered an error and excluded if RT was less than 100 ms or greater than 1200 ms, or if MT was less than 250 ms or greater than 2700 ms. Also, very few trials had to be excluded due to errors of the experimenter when preparing the trials. On this basis, 1.63% (1.43%) of the grasping trials and 2.34% (3.65%) of the ManEst trials were excluded in the near (far) conditions.

MGA was defined as the maximum difference of thumb and index finger between RT and end of the movement. From the MGA and ManEst values, found the illusion effects as follows: for each participant, the average MGA or ManEst for the Fin In figure was subtracted from the average MGA or ManEst for the Fin Out figure, with data pooled for the short (39 mm) and long (43 mm) lengths. This was done separately for each task (grasping/ManEst) and hand (left/right). This is the raw illusion effect.

To correct for the different responsiveness of grasping and ManEst to changes in physical size, we calculated slopes of the MGA and ManEst for each hand (left/right) and stimulus figure (Fin In/Fin Out). The slopes for the Fin In and Fin Out figures were subsequently averaged, giving us one value per hand per participant per task. Corrected illusion effects were calculated by dividing the raw illusion effects by the slopes. Standard errors for these corrected illusion effects were calculated using the Taylor-approximation: $\mathrm{SEM} = i/s\sqrt{(\sigma_s^2/s^2)+(\sigma_i^2/i^2)-(2(\sigma_{is}/is))}$ (with: i: mean raw illusion effect, s: mean slope, σ_i^2: SEM of the illusion effect, σ_s^2: SEM of the slope, σ_{is}: covariance of illusion effect and slope). This approximation is valid because the slopes were significantly different from zero (cf. Bruno & Franz, 2009; Buonaccorsi, 2001; Franz et al., 2005; Franz, 2007; von Luxburg & Franz, 2009.

A significance level of $a = .05$ was used for all statistical analyses. p-values above .001 are given as exact values. For parameters which are given as $A \pm$ SE, SE is the standard error.

2.2. Results

Average MTs for grasping for the near condition were 762 ± 23 ms for the right hand and 746 ± 26 ms for the left hand. For the far condition, average MTs were 813 ± 23 ms and 813 ± 22 ms for the right and left hand, respectively. For ManEst, average MTs for the near condition were 1306 ± 63 ms for the right hand and 1312 ± 65 ms for the left hand. For the far condition, average MTs were 1312 ± 79 ms and 1313 ± 78 ms for the right and left hand, respectively.

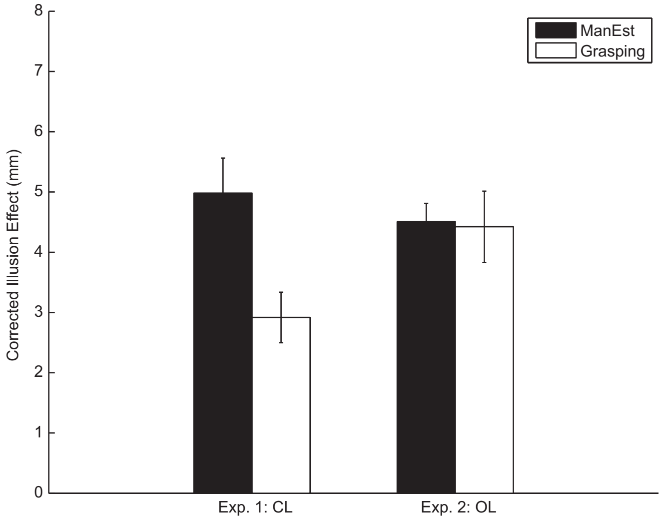


Fig. 3. Combined data from both experiments. If the tasks are performed with full vision of hand and stimuli (closed loop, CL), then grasping shows smaller illusion effects because participants can exploit visual feedback (Exp. 1; this replicates the results of Dewar & Carey, 2006). If the tasks are performed such that just after the start of the movement, vision of the hands and stimuli is suppressed (open loop, OL), then grasping and manual estimation show similar illusion effects (Exp. 2). Error bars represent ±1SEM.

Fig. 2 shows the average ManEst and MGA values, and Fig. 3 shows the corresponding corrected illusion effects. An ANOVA on the corrected illusion effects for the factors hand (left/right), stimulus distance (near/far), and task (ManEst/grasping) revealed a main effect of task ($F(1,46) = 14$, $p = .001$) and a main effect of stimulus distance ($F(1,46) = 5.3$, $p = .027$), with illusion effects being larger for ManEst compared to grasping, and for the far stimulus configuration. There was no main effect of hand ($F(1,46) = .58$, $p = .45$). All interactions also failed to reach significance (all $p > .23$).

2.3. Discussion

The most important result is the main effect of task, as this shows ManEst was more susceptible to the illusion than grasping, thereby replicating the results of Dewar and Carey (2006). We also found a main effect of stimulus distance, with the illusion effect being greater for both grasping and ManEst when the stimuli were placed further part. This is consistent with other reports on the effect of stimulus separation on the strength of the Müller-Lyer illusion (Pressey & Di Lollo, 1978), and possibly due to increased contrasting when the stimuli must be stored in memory, rather than observed in a single glance (pool-and-store model; Coren & Girgus, 1978; Girgus & Coren, 1982). As there was no task × stimulus distance interaction, there seem to have been no grasping-specific effects of stimulus distance.

3. Experiment 2: the effect of the Müller-Lyer illusion on bimanual, open loop grasping and ManEst

Experiment 2 was designed to be identical to Experiment 1, with one important modification: both ManEst and grasping tasks were now performed open loop. As soon as the participants started to move their hand, the shutter glasses prevented vision of hand and stimuli.

3.1. Methods

Because the same apparatus and stimuli as in Experiment 1 were used, we describe only differences between the experiments.

3.1.1. Participants

We tested 48 participants (20 male, mean age 24 years). As in Experiment 1, one group of participants ($n=24$, 10 male, mean age 25 years) was presented the near condition, and the other group ($n=24$, 10 male, mean age 22 years) the far condition.

3.1.2. Procedure

Experiment 2 differed from Experiment 1 only with respect to the duration of stimulus presentation: in Experiment 2, the shutter glasses turned opaque as soon as participants started their movement (defined as the point where one of the fingers moved 40 mm from the starting point) and remained so until the start of the next trial. The movement was thus carried out under open loop conditions for both grasping and ManEst tasks.

3.1.3. Data analysis

Exclusion based on RT, MT, and experimenter error (same criteria as in Experiment 1), resulted in exclusion of 2.28% (1.30%) of the trials in grasping and 4.69% (4.56%) in ManEst in the near (far) conditions.

3.2. Results

3.2.1. Experiment 2 alone

Average MTs for grasping in the near condition were 865 ± 40 ms for the right hand and 837 ± 36 ms for the left hand. In the far condition, average MTs were 863 ± 36 ms and 843 ± 32 ms for the right and left hand, respectively. For ManEst, average MTs for the near condition were 1173 ± 47 ms for the right hand and 1174 ± 47 ms for the left hand. For the far condition, average MTs were 1064 ± 49 ms and 1074 ± 48 ms for the right and left hand, respectively.

Figs. 2 and 3 show average MGA/ManEst values and corrected illusion effects, respectively. As in Experiment 1, an ANOVA was calculated on the corrected illusion effects for the factors task, stimulus distance, and hand. In contrast to Experiment 1, we did not find a main effect of task ($F(1,46)=.017$, $p=.9$). The effect of stimulus distance approached but did not reach significance ($F(1,46)=3$, $p=.09$). All other effects and interactions were not significant, as in Experiment 1 (all $p>.24$).

This suggests that visual feedback is the deciding factor. In order to ascertain this conclusion, we analyzed the data from both experiments together to see if the vision × task interaction would be significant.

3.2.2. Combined Experiment 1 and Experiment 2

An overall ANOVA was performed on the data from both experiments with the factors vision (closed loop/open loop), stimulus distance (near/far), hand (left/right), and task (ManEst/Grasping). Stimulus distance was again found to have a significant main effect ($F(1,92)=8.2$, $p=.005$). A main effect of task ($F(1,92)=6.4$, $p=.013$), and, more importantly, a vision × task interaction ($F(1,92)=5.4$, $p=.022$, cf. Fig. 3) were also observed. All other main effects and interactions were not significant (all $p>.14$). Separate t-tests on the average corrected illusion effects for grasping and ManEst (averaged over hand and stimulus distance) further clarified the vision × task interaction: the difference between the tasks was significant in Experiment 1 (Closed loop; $t(47)=3.7$, $p<.001$) but not Experiment 2 (Open loop; $t(47)=.132$, $p=.90$). A t-test on the illusion effects measured for grasping in the open loop and closed loop conditions was also significant ($t(94)=2.1$, $p=.041$), with illusion effects being larger for grasping in the open loop condition. Furthermore, the illusion effects in the closed loop and open loop ManEst conditions were not significantly different from one another ($t(94)=.72$, $p=.47$). This is unsurprising, as participants should not benefit much from vision of hand and stimuli in the closed loop ManEst condition, as they never view their hands approaching the object.

3.3. Discussion

We can now answer our primary question—whether a difference in illusion effects between grasping and ManEst depends on the presence or absence of visual feedback. As shown in Fig. 3, the illusion effects on grasping and ManEst are identical in the open loop conditions (Experiment 2), but differ in closed loop condition (Experiment 1, replicating Dewar & Carey, 2006). This shows that without visual feedback, bimanual grasping is susceptible to the Müller-Lyer illusion to the same degree as ManEst, and that visual feedback is the critical factor. The results of Dewar and Carey (2006) should therefore not be counted as evidence for the existence of a veridical, undeceived size representation guiding grasping.

Although we have now answered our primary question, we still wanted to assess the generality of our results by comparing them to unimanual grasping. We were also left with some general concerns about the use of bimanual designs. These questions are discussed in the following sections.

3.3.1. How general are our results: comparison with unimanual grasping

To assess the generality of our findings, we were interested whether there may be differences between bimanual and unimanual grasping. We therefore compared our results to the results of Franz et al. (2009), who had investigated right-handed grasping of the Müller-Lyer illusion. Stimuli were very similar, allowing us to directly compare the results.

The closed loop condition of Franz et al. (2009) is similar to our closed loop condition, although we would expect that with unimanual grasping, visual feedback should be exploited better than with bimanual grasping. Therefore, the illusion effects should be smaller in Franz et al. (2009) than in the current study. This is indeed the case: Franz et al. (2009) found a corrected illusion effect of $.9 \pm .36$ mm ($N=56$), whereas we found corrected illusion effects of $2.1 \pm .39$ mm in the closed loop-near condition and $3.7 \pm .64$ mm in the closed loop-far condition. These are, as expected, significantly larger ($t(102)=2.41$, $p=.02$ and $t(102)=3.92$, $p<.001$ for near and far, respectively). The open loop-move condition of Franz et al. (2009) is similar to our open loop condition, with the only difference that it was performed unimanually in that study. Their open loop-move condition yielded a corrected illusion effect of $4.9 \pm .76$ mm ($N=48$, cf. Fig. 7 of Franz et al., 2009), while we found corrected illusion effects of $3.5 \pm .48$ mm in the open loop-near condition and of 5.4 ± 1.02 mm in the open loop-far condition, which are not significantly different from the results of Franz et al. (2009; $t(94)=1.55$, $p=.12$ and $t(94)=.42$, $p=.67$ for near and far, respectively). In summary, our bimanual results are fully consistent with the unimanual results of Franz et al. (2009).

3.3.2. Interpreting bimanual designs: is there an influence of the other hand?

Bimanual designs pose a new problem to the interpretation of the results: because both hands are employed, we need to clarify whether the actions of both hands somehow interact (a problem which does not exist in unimanual designs and was not appreciated by Dewar & Carey, 2006).

Therefore, we evaluated whether the non-relevant figure (i.e., the figure responded to by the opposite hand) had an effect on the response to the target figure. For example, when two figures of different sizes are presented to the left and right hand, the smaller figure could reduce the response directed toward the larger object, and the larger figure could increase the response directed toward the smaller object, a sort of averaging of the responses. This would result in a smaller difference between the responses than would be present if the figures were acted upon unimanually.

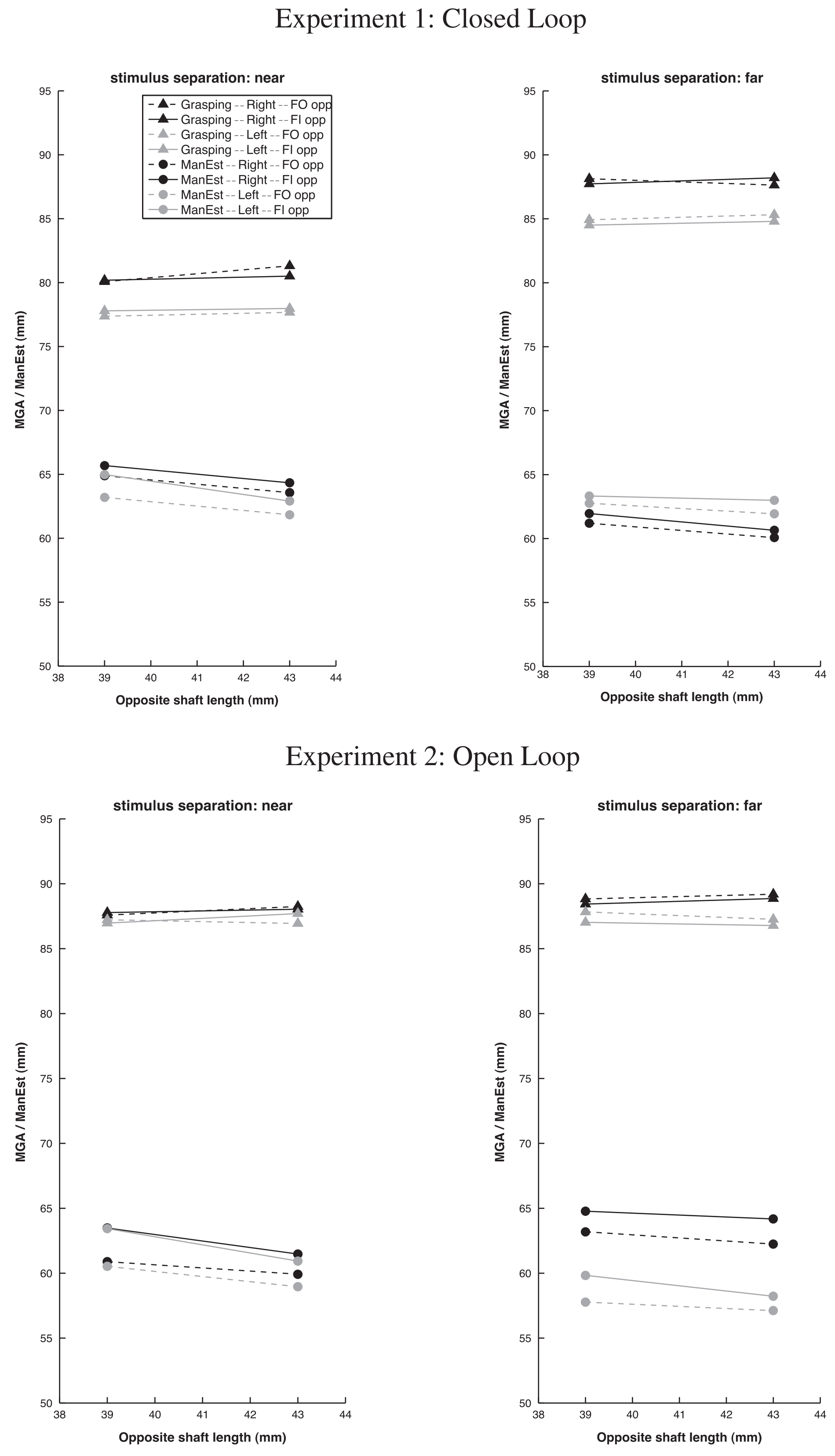


Fig. 4. This figure is analogous to Fig. 2, except MGA and ManEst values are now plotted against the *non-relevant* figure (in terms of both length and configuration). A contrasting effect for both real and illusory size differences can be observed for ManEst but not grasping. Lines in this condition follow a negative slope, and values were overall greater when the non-relevant figure was Fin In rather than Fin Out.

Alternatively, contrasting could drive the responses further apart, such that the response directed toward the larger object would now be even larger, and the response directed toward the smaller object even smaller.

To determine if either of these possibilities holds for our experiments, we analyzed our data based on the stimuli presented to the *opposite hand*. Fig. 4 shows MGA and ManEst as a function of the length and illusory configuration of the non-relevant figure. If there is no effect of the non-relevant figure, all lines should be flat (indicating no effect of the non-relevant physical figure size) and directly on top of one another (indicating no effect of the non-relevant illusion configuration). If the *physical size* of the non-relevant figure has an effect, a positive slope would indicate averaging (because a larger non-relevant figure leads to a larger response), and a negative slope contrasting. If the *illusory configuration* of the non-relevant figure induces averaging (contrasting), then the line corresponding to the non-relevant Fin Out figure should be higher (lower) than the line corresponding to the non-relevant Fin In figures because a larger perceived non-relevant figure leads to a larger (smaller) response.

Fig. 4 shows that for grasping, the non-relevant figure has little or no effect on MGA: the lines lie directly on top of one another and are flat. For ManEst, however, the results look rather different. There is a negative slope, and the line corresponding to a non-relevant Fin In figure is higher than that corresponding to the Fin Out figure. This is the pattern associated with contrasting of both physical and illusory size. These observations are confirmed by an ANOVA on the factors fin direction (Fin In/Fin Out), length (39 mm/43 mm), and vision (open loop/closed loop), performed separately on the data for grasping and ManEst. For grasping, neither fin direction nor length were significant, although length approached significance ($F(1,94)=2$, $p=.16$ and $F(1,94)=3.9$, $p=.051$, respectively). The trend for grasping was toward averaging of physical size. There was also a main effect of vision ($F(1,94)=13$, $p<.001$), with participants opening their hands wider in the open loop condition. All interactions were not significant (all $p>.47$). For ManEst, fin direction and length were both highly significant ($F(1,94)=37$, $p<.001$ and $F(1,94)=32$, $p<.001$, respectively), with ManEst being larger when the non-relevant figure was smaller in physical size, as well as when the non-relevant figure was Fin In as opposed to Fin Out. This indicates some sort of contrasting is taking place which accentuates the differences between the figures. A significant fin direction × vision interaction was also observed ($F(1,94)=4$, $p=.049$). The non-relevant figure's fin direction had a slightly larger influence in the open loop condition.

These analyses establish an impact of the non-relevant figure on ManEst. Consequently, the corrected illusion effects in ManEst should also depend on the non-relevant figure. To examine this, we reanalyzed the data from Experiments 1 and 2, this time differentiating between trials where the non-relevant figure had the same configuration (Fig. 5a) or the opposite configuration (Fig. 5b) as the target figure. The illusion effects were much larger for ManEst when a heterogeneous (Fin In/Fin Out) configuration was used. The illusion effect on grasping, on the other hand, seems to be somewhat smaller when a heterogeneous display was used. This is consistent with the trend toward averaging observed for grasping. To support these observations, we performed an ANOVA on the factors display configuration (Homogenous/Heterogeneous) and vision condition (Closed Loop/Open Loop) for each task separately. For ManEst, as expected, there was a significant effect of display configuration ($F(1,94)=35$, $p<.001$), but not of viewing condition ($F(1,94)=.48$, $p=.49$). The vision × display interaction was not significant ($F(1,94)=1.2$, $p=.28$). For grasping, a significant effect of display configuration was found, with illusion effects being smaller when heterogeneous display configurations were used ($F(1,94)=4.9$, $p=.03$). The effect of vision condition narrowly missed significance ($F(1,94)=3.9$, $p=.051$), but the trend is consistent with our original finding that illusion effects are larger for grasping under open loop conditions. The vision × display interaction was not significant ($F(1,94)=.16$, $p=.69$).

The finding that the corrected illusion effect for ManEst was greater for displays with two different illusory figures parallels the result we found for the influence of the non-relevant figure on the raw ManEst estimate: bimanual ManEst leads to contrasting, or accentuation of differences in length between the two figures. How should this result be interpreted?

We see two possibilities. The first is that, as Dewar and Carey (2006) suggested, a direct comparison of the two halves of the illusion created a stronger perceptual illusion effect, which in turn led to the apparent contrasting effects in ManEst. This is the property of superadditivity of some illusions as discussed in the

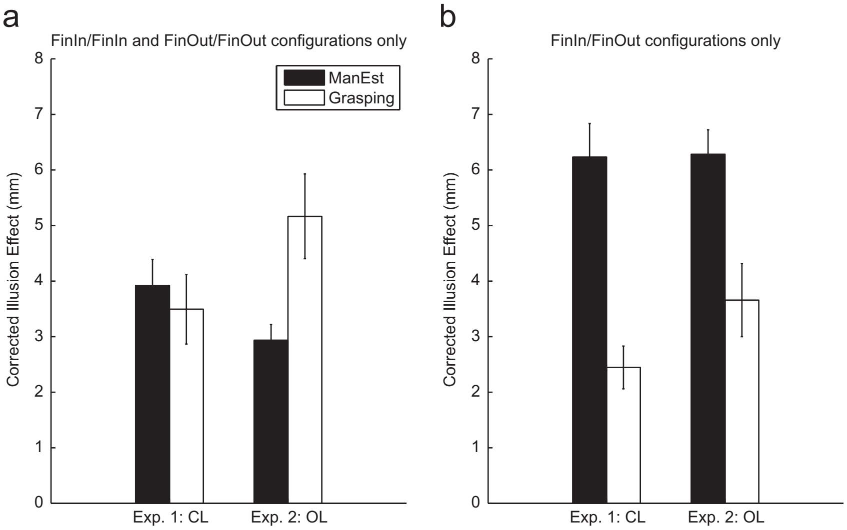


Fig. 5. Similar to Fig. 3, this figure summarizes the illusion effects in the closed loop and open loop conditions for both grasping and ManEst. In this case, however, the analysis is divided based on the configurations used in the display. (a) Only data from homogenous configurations (Fin In/Fin In or Fin Out/Fin Out) are included in the analysis. (b) Only data from the heterogeneous configurations (Fin In/Fin Out) are included in the analysis. We can see that in both cases, the illusion effect for grasping is greater in the open loop (OL) condition. On the other hand, the display configuration has a substantial impact on the illusion effect observed for ManEst. Error bars represent ± 1SEM.

introduction. Under this interpretation, however, the opposing results for grasping and ManEst leave open the possibility that illusions are indeed perceived differently than they are grasped, but that this is only manifested in the illusion's superadditivity (or lack thereof), rather than in the illusion strength of a single component.

The second possibility is that this contrasting effect is a ManEst-specific strategy of accentuating differences. We find this to be the more likely alternative for two reasons: first, differences in general are accentuated in ManEst, as both the physical size and the illusory configuration of the non-relevant figure influenced the estimates of the opposite hand. If the effect was due to the superadditivity of the Müller-Lyer illusion, we would not expect the actual size to have an effect. Secondly, Gilster and Kuhtz-Buschbeck (2010) found that the Müller-Lyer illusion is not superadditive for direct vs. separate comparisons. Our stimuli and procedure nevertheless differ from theirs on several levels, which makes us cautious in generalizing their findings to our experiments. For example, our stimuli were thicker and more block-like, as they were also used in a grasping task, in contrast to their more traditional, thin and stick-like figures. One could also argue that the direct comparison performed in their adjustment task is fundamentally different from a direct comparison achieved through bimanual ManEst (e.g., in terms of attention distribution). For these reasons, although we tend toward the interpretation that the contrasting we found is a ManEst-specific strategy, we recognize that further research must be done in order to determine whether illusory superadditivity may also have played a role.

4. General discussion

We investigated the effects of the Müller-Lyer illusion on bimanual grasping with full vision of hand and stimulus and without vision from the commencement of the movement. We found that the illusion has a smaller effect on grasping under closed loop but not open loop visual conditions. This supports our hypothesis that the difference Dewar and Carey (2006) found in the illusion effects for ManEst and grasping were mainly due to the availability of visual feedback.

Open-loop grasping has been consistently advocated as the best condition for testing dissociations between perception and action (e.g., Haffenden & Goodale, 1998; Post & Welch, 1996; Westwood et al., 2001), because it allows for vision during movement planning while eliminating the possibility of online correction during the movement itself. As this type of task has consistently been thought of as the cleanest way to test the proposed dissociation between dorsal and ventral engagement in perception and grasping, our results show that bimanual grasping of the Müller-Lyer illusion cannot provide evidence for a separate, undeceived size representation as suggested by the perception and action model of visual processing (Goodale & Milner, 1992; Milner & Goodale, 1995).

We also found many other interesting results: (a) that our widely placed stimuli induced a greater illusion effect than our closely placed stimuli; (b) that there was no difference in the illusion effect measured for the right and left hands; (c) that closed loop, unimanual grasping shows a smaller effect of the illusion than closed loop, bimanual grasping; and (d) that the non-relevant figure of the display had an effect on ManEst but not on MGA. We will now discuss the implications of these findings.

4.1. How does visual feedback reduce illusion effects in grasping?

We found that grasping exhibited a smaller illusion effect under closed loop as opposed to open loop visual conditions. This finding is consistent with previous studies that compared open and closed loop grasping and found closed loop grasping to show a smaller illusion effect (e.g., Franz et al., 2009; Heath et al., 2005, 2006; Westwood et al., 2001), as well as a meta-analysis which found that experiments on the effect of the Müller-Lyer illusion on grasping using closed loop conditions had overall smaller illusion effects than those using open loop conditions (Bruno & Franz, 2009). The question remains, however, of why closed loop grasping is consistently more refractory to illusions than open loop grasping. We see three possibilities, all related to the availability of visual feedback in the closed loop condition: online corrections, learning effects, and unique size representations.

4.1.1. Online corrections

Online monitoring of the fingers and grip aperture relative to the stimulus could inform real-time corrections which would reduce the illusion effect. In particular, disparity matching and occlusion have been shown to play a key role in the accuracy of reaching (Bingham, Bradley, Baily, & Vinner, 2001). Grip aperture has long been known to be adaptable in-flight to gross changes in the stimulus (Castiello, Bennett, & Stelmach, 1993; Paulignan, Jeannerod, MacKenzie, & Marteniuk, 1991), and recent data has shown that movements are even able to adapt to more subtle changes in form (Eloka & Franz, 2011) and perceived distance (Bruggeman, Fantoni, Caudek, & Domini, 2010), as well. However, although this indicates that grasping is very adaptable and may quickly make use of the visual information available to it, the case of illusions is somewhat different. In the previously mentioned studies, reaching or grasping was updated based on newly available visual information. In the case of illusions, however, grasping reliant on (deceived) visual information should produce a consistent discrepancy between the intended and actual position of the fingers with respect to the stimulus. In order to correctly contact the stimulus, one possibility, however inefficient, is that this error be repeatedly corrected on each trial based on visual feedback as the fingers approach the object. More advantageous, however, would be for the motor system to learn from its mistakes and recalibrate its visuo-motor mapping in order to avoid having to correct for this error on future reaches.

4.1.2. Learning effects

The capacity of the motor system to adapt itself to new visuomotor linkages is well-known (e.g., Helmholtz, 1867). Artificial manipulations of size and haptic feedback couplings have been shown to affect motor behavior over time (Coats, Bingham, & Mon-Williams, 2008; Mon-Williams, Coats, & Bingham, 2004). Even visual feedback uniquely showing the accuracy of the end point of a movement has been shown to improve reaching accuracy (Bingham, 2005). Beyond this capacity for recalibration, however, there are also several indications in previous research on illusions of the existence of learning effects. Here we focus on grasping, but a similar learning effect has been proposed as an explanation for the smaller effect of visual illusions on saccadic eye movements (Bruno, Knox, & de Grave, 2010).

First, when the existence of dynamic illusion effects under open and closed loop conditions was investigated for the Ebbinghaus illusion, Franz et al. (2005) discovered that illusion effects remained constant throughout the movement whether vision was present or not. If grasping were continually corrected on an online basis, we would expect that, in the closed loop condition, illusion effects would be larger at the beginning of the movement than at the end. That this dynamic effect is not observed, although illusion effects are overall smaller in the closed loop condition, indicates that some sort of learning across trials might take place.

Second, support for learning can also come from studies using different visual feedback schedules. Heath et al. (2006) studied the effect of the Müller-Lyer illusion on grasping under a randomized vs. blocked visual feedback schedule. Consistent with our results, they found that the illusion effect on grasping under closed loop conditions was much smaller than under open loop conditions with a blocked visual feedback schedule. When open loop and closed loop trials were randomized, however, there was no difference in the illusion effect, with grip apertures in both open and closed loop conditions being susceptible to the illusion. If we assume that grasping only shows a smaller effect of the illusion under closed loop conditions due to a learned recalibration of the grasp to a size other than the one perceived, it may simply be the case that the amount of feedback available in the intermixed condition is insufficient and calibration breaks down. Such an effect has previously been found for other modalities; haptic feedback has been shown to be effective in recalibrating grasping of visually and haptically mismatched stimuli only under blocked conditions (Coats et al., 2008; Mon-Williams et al., 2004) and not when the distorted haptic feedback was randomized and available only on 50% of trials (Lee, Crabtree, Norman, & Bingham, 2008). More research seems necessary in order to determine whether recalibration based on visual feedback follows the same pattern, and whether this can indeed explain Heath et al.'s (2006) results.

4.1.3. *What about the planning and control model?*

We have argued that the reduction of the illusion effects on grasping under closed loop conditions can best be explained by online corrections or learning effects. Now one might ask whether this constitutes evidence for Glover and Dixon's planning and control model (PCM, Glover & Dixon, 2001, 2002; Glover, 2004). We will show that this is not the case.

Like many other models of human motor control, the PCM allows for online corrections and learning effects, the two possible explanations we have suggested for our data. The new, additional aspect of the PCM is the notion that the motor system has access to two separate visual representations: one representation is deceived by illusions and affects early phases of the movement (''planning''), and the other is undeceived and affects late phases (''control''). The undeceived control representation is assumed to reduce illusion effects beyond what is achieved through online corrections and learning effects alone. In contrast, more traditional motor control models would not assume such an undeceived representation. For example, to implement a traditional online correction mechanism, it would be enough to assume a simple feedback loop based on the intended and actual position of the hand.

Do our data constitute evidence for these two separate representations as suggested by the PCM? If the PCM is valid, the undeceived control representation should lead to a reduction of the illusion, even if there is no visual feedback available and traditional online correction of the illusion is therefore no longer possible (e.g., Glover & Dixon, 2002, p. 271). This prediction, that grasping behavior should be corrected online in the absence of visual feedback, is the only prediction of the PCM that differs from classic motor control models.

However, our data do not agree with this prediction. MGA is considered by PCM to be a late measure and driven mostly by the undeceived control representation (Glover, 2004, Table 2). It should thus hardly be deceived by illusions, even without visual feedback. However, MGA is deceived if visual feedback is not available. It is even deceived to the same degree as ManEst, which is supposed to be driven by the deceived planning representation (Glover, 2004, Table 2). The fact that we found essentially identical illusion effects in MGA and ManEst under open loop conditions therefore contradicts the idea that in addition to online corrections and learning effects there is another corrective mechanism based on the undeceived control representation.

Now, in an attempt to reconcile PCM's idea of two separate representations with our data, one might argue that perhaps MGA was simply miscategorized by Glover (2004), and that it is in fact an early parameter, guided by the planning representation, while still maintaining the rest of the PCM framework. However, this interpretation is also not supported by our data. Under this scenario, the illusion's effect on MGA should not be reduced in the closed loop condition, as the undeceived control representation should not yet have exerted its influence. But, it is reduced. This reduction of the illusion effect can only be explained if we assume that visual feedback plays a role—which is part of the control processes in the PCM, which brings us back to suggesting that MGA is a late parameter. Therefore, no matter whether we interpret MGA as late or early parameter in the PCM, our data are not consistent with PCM's idea of two separate representations.

It should be noted, however, that our study was not designed to test the PCM. A full test would require elaborate monitoring of the full trajectories in grasping and ManEst (as was done in a detailed study by Franz et al., 2005, where they also did not find evidence for the PCM). Therefore, further research might provide new, unexpected evidence for the PCM and might resolve the contradictions of our data with the PCM discussed above.

4.2. *Do bimanual designs do more harm than good?*

One of our reservations about bimanual designs, and in particular Dewar and Carey's (2006) use of one as a way to balance attentional demands, was that it had never been established that bimanual grasping or ManEst behave in a way comparable to direct perceptual comparisons, or that their task demands are comparable to each other. It is entirely possible that participants divide their attention and grasp or estimate each figure in an individual manner, as they still are not required to make any comparative judgment between the two figures. Alternatively, they could also compare their two estimates not only to the stimuli but to each other. For grasping, dependency of the MGA on a non-relevant object has been shown to depend not merely on the presence of two contrasting stimuli, but rather whether these stimuli are perceived as being part of the same object (''functionally unified''), in which case grip apertures showed evidence of averaging (Jackson et al., 2002; also consistent with the trend in our results). Lacking this ''functional unity'', MGAs have been shown to be independent for bimanual grasping of objects differing in size (Jackson, Jackson, & Kritikos, 1999; Jackson et al., 2002; Dohle, Ostermann, Hefter, & Freund, 2000). This shows that it often requires more than just simultaneity for any sort of direct comparison to take place. Before interpreting a bimanual measure, investigators should thus first establish that the bimanual action does in fact induce a direct comparison.

Furthermore, we found a dependency between the two hands for bimanual ManEst, whereby differences between the two hands are accentuated. This is a clear disadvantage. Consider the fundamental goal of studies comparing illusion effects on grasping and perception: to determine the underlying internal size representation used for grasping and for perceptual judgments, and whether these differ. For grasping, the most obvious and widely-used method to determine the internal size representation is to use MGA, which is known to vary linearly with object size (Jeannerod, 1981, 1984). For perception, a myriad of possible methods are available (e.g., Coren & Girgus, 1972), but ManEst has emerged as an oft-favored alterative (e.g., Daprati &

Gentilucci, 1997; Haffenden & Goodale, 1998), likely due to its overt similarity to grasping (that is, both grasping and ManEst use measures of the distance between the index finger and thumb). In both cases, however, MGA and ManEst can be considered tools used to determine our *actual* variable of interest, namely, the internal size representation.

But, is ManEst really the best measure of internal size representation, or is one of the other perceptual alternatives better suited? In the current experiments, we have determined that for ManEst, the estimation of one hand is dependent on the estimation of the other. An accentuation of differences seems to occur for both real and illusory size contrasts. Previous research has concluded that this accentuation of contrasts does not occur for the Müller-Lyer illusion with a more traditional adjustment method, however (Gilster & Kuhtz-Buschbeck, 2010). The accentuation of contrasts, like the differential sensitivity of ManEst to actual size, is thus likely a property of the tool used to measure perception, not of perception itself, and consequently may give rise to artefacts when using bimanual ManEst.

4.3. Left-handed grasping responds to illusions as right-handed grasping

We found no difference in illusion effects for the right and left hands, both for closed loop and open loop visual conditions. This is noteworthy, as Gonzalez, Ganel, and Goodale (2006) had previously argued that uniquely right-handed grasping shows a smaller effect in response to visual illusions, and that left-handed grasping is controlled by the ventral stream even in left-handed people, a rather controversial and highly disputed claim (Derakhshan, 2006; Gonzalez, Goodale, & Ganel, 2006). Although one might be tempted to conclude that our case represents a simple failure to replicate their results, this is only one of several recent studies where such an effect was not found. For example, Dewar and Carey (2006) also did not find a difference in illusion size between the right and left hands.

Alternative methodologies have also been unable to uncover any evidence for differential processing of visual information for left-handed grasping. Janczyk, Franz, and Kunde (2010) tested whether Garner interference would be present for left-handed grasping—as had been found for perceptual judgements but not right-handed grasping (Ganel & Goodale, 2003)—and found none. In light of these rather consistent findings to the contrary, we should ask what may have caused the anomalous results of Gonzalez, Ganel et al. (2006), rather than conclude that visual information is processed in a fundamentally different way for right-handed and left-handed grasping.

5. Conclusions

We investigated the role of visual feedback on perception and action in a bimanual design. We were able to replicate the result of Dewar and Carey (2006) that grasping showed a smaller effect of the illusion under closed loop conditions than ManEst. We expanded upon this by showing that the illusion effect increased for grasping but not ManEst when visual feedback was not available for the duration of the trial (open loop conditions). This means that the bimanual grasping experiments of Dewar and Carey (2006) did not provide evidence for a separate, undeceived size estimation available to grasping. We also found that bimanual closed loop grasping produced larger illusion effects than unimanual closed loop grasping, which could be attributed to a less effective use of visual feedback when one has two hands to attend to. We furthermore investigated what we saw as an open question in our bimanual design (and that of Dewar & Carey, 2006), namely whether any inter-hand dependencies exist for bimanual grasping or ManEst. We discovered that bimanual ManEst is indeed not independent of the non-relevant figure, in a way that is not easily explained by traditional perceptual effects.

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Study 2

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Letter to the Editor

Inferences about time course of Weber's Law violate statistical principles

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ABSTRACT

Recently, Holmes et al. (2011b) suggested that grasping is only subject to Weber's Law at early but not late points of a grasping movement. They therefore conclude that distinct visual computations and information may guide early and late portions of grasping. Here, we argue that their results can be explained by an interesting statistical artifact, and cannot be considered indicative of the presence or absence of Weber's Law during early portions of grasping. Our argument has implications for other studies using similar methodology (e.g., Heath et al., 2011, Holmes et al., 2011a, 2012), and also for the analysis of temporal data (often called time series) in general.

Holmes et al. (2011b) investigated the aperture between index finger and thumb during grasping, which has a well known profile: The fingers open swiftly to reach a maximum (the maximum grip aperture, MGA), before closing around the object. MGA scales linearly with object size, but its standard deviation (SD) does not depend on object size—a finding that led Ganel, Chajut, and Algom (2008a) to argue that size-coding for grasping does not follow Weber's Law, thereby violating fundamental psychophysical principles.[1] Holmes et al. (2011b) asked whether this is also true for earlier portions of the grasping movement, and therefore investigated the timecourse of the grip aperture's standard deviation (ApSD). They found that early during a movement, ApSD did depend on object size (Fig. 1a) and therefore argued that Weber's Law holds for early portions of the movement.

However, we show that ApSD profiles such as those obtained by Holmes et al. (2011b) are to be expected even in the extreme case that the entire grasping trajectory does not depend on Weber's Law. This is a statistical consequence of how the SD of any temporal function behaves in the presence of temporal noise. The contribution of this statistical artifact can even be predicted by a simple, general formula (Eq. (4) in Appendix A). Applied to grasping, our formula shows that in the simplest case (with no other sources of noise and relatively small temporal noise), ApSD will be proportional to the velocity with which the hand opens and closes (aperture velocity, ApVel)

$$\text{ApSD} = k\text{ApVel}$$

with k being the proportionality factor (see Appendix A for more details). This artifact alone can predict the data found by Holmes et al. (2011b): Because ApVel is zero at the time of MGA, but large and dependent on object size at early time points, ApSD will necessarily depend on object size at early time points—even if Weber's Law does not guide the programming of the grasping movement whatsoever.

While our formula is general and valid for any temporal function, independent of its shape, we think it is useful to consider its effects in the context of a concrete example. We will therefore demonstrate our reasoning with profiles typical of grip apertures, thereby showing the specific problems of the Holmes et al. (2011b) analysis and conclusions. We will start with the simplest and most mathematically tractable case, where the statistical mechanisms of interest are easiest to understand. For this, we will simplify the aperture profile to a sine curve and assume only temporal noise. As discussed in Appendix A, the relationship will get weaker if temporal noise is increased or other sources of noise are added. The possible effects of these additional factors will be evaluated in Appendix B.

Fig. 1b shows a portion of a sine curve which is a simple approximation of a typical aperture profile over time.[2] Assume now we have an almost perfect participant. She estimates the size of the

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[1] This reasoning of Ganel, Chajut, & Algom (2008a) is contentious, but cannot be discussed here. See also Ganel et al. (2008b) and Smeets and Brenner (2008).

[2] There are three reasons to choose a sine curve for our simulations: (a) the sine curve is generated by a unitary process (often conceptualized as a point on the circumference of a wheel rotating with constant angular velocity), allowing us to simulate a grasping movement controlled by a unitary, non-Weberian process; (b) it fits observed grasping profiles reasonably well (e.g., Jeannerod, 1984; Smeets and Brenner, 1999); (c) there is an analytical solution for its first derivative (part of our prediction for the ApSD), namely the cosine. Note, however, that our ability to predict the pattern of ApSD does not depend on this specific choice of the function, as explained in Appendix A.

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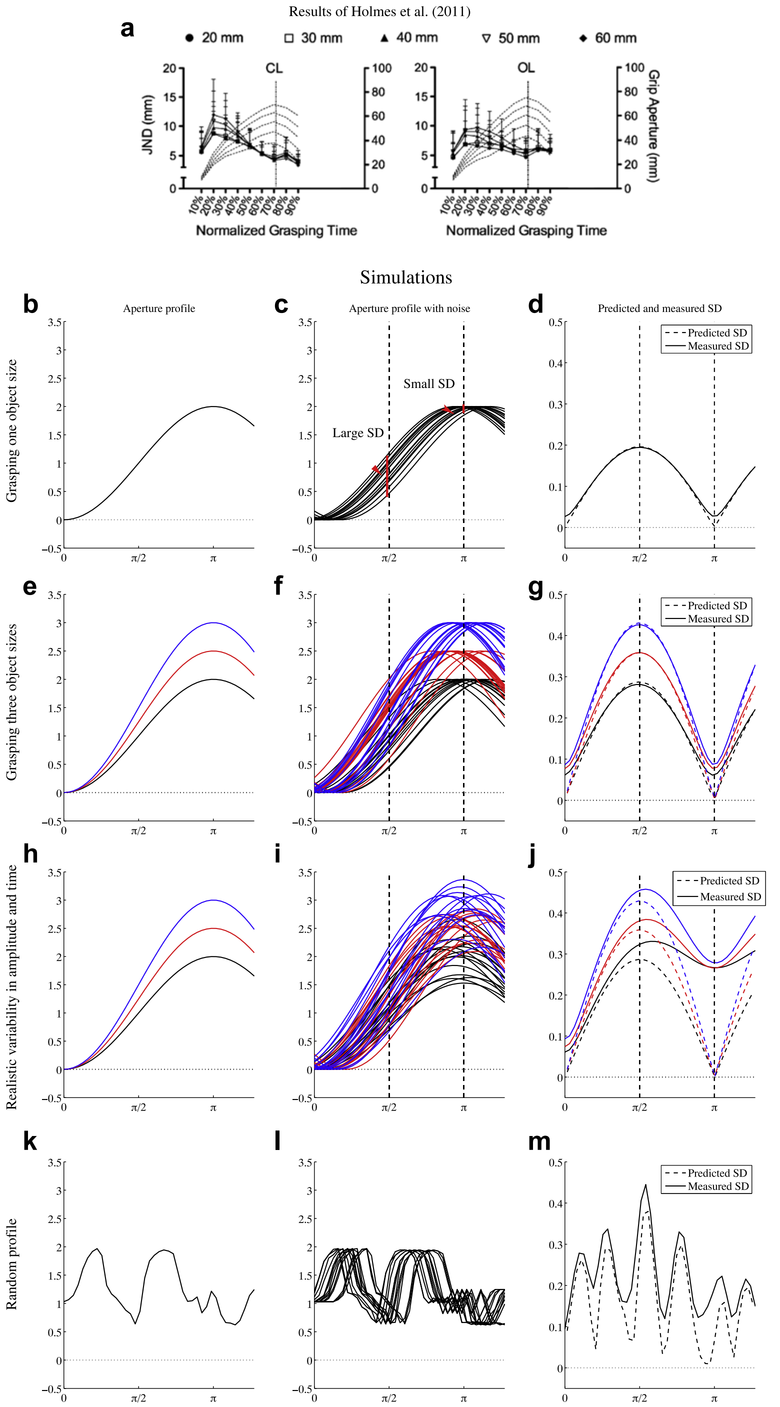

Fig. 1. (a) Results of Holmes et al. (2011b) in two different visual conditions (CL = closed loop grasping; OL = open loop grasping). (Our figure shows only the relevant part of their Fig. 2; reprinted from Vision Research, 51, Holmes, S.A., Mulla, A., Binsted, G., & Heath, M., Visually and memory–guided grasping: Aperture shaping exhibits a time-dependent scaling to Weber's Law, 1941–1948, 2011, with permission from Elsevier.) Shown are ApSD (solid lines; called JND (just noticeable difference) by Holmes et al. (2011b)) and grip aperture (dotted lines) as functions of percent MT. In both conditions, ApSD is dependent on object size (ranging from 20 mm to 60 mm, as indicated by the symbols above the plots) only at early time points (⩽40%MT). This dependency of ApSD on object size is interpreted as an adherence to Weber's Law uniquely at early time points. (**b–m**) Simulated trajectories and SDs for: (**b–d**) grasping one object with temporal noise only, (**e–g**) three objects of different sizes with temporal noise only, or (**h–j**) three objects of different sizes with realistic noise in both time and amplitude of the movement. In all simulations, our Eq. (4) predicts the observed pattern of ApSD very well (see dashed lines in the rightmost column). Different sizes were simulated by selecting different amplitudes of the sine function (1, 1.25, 1.5). Realistic, gaussian variability in amplitude was simulated by choosing a SD of the sine wave amplitude of 0.13 for all three sizes. The proportion of amplitude SD to mean amplitude for our simulated sizes was 0.13, 0.104, and 0.087, respectively. This corresponds well to the values reported by Heath et al. (2011b), who found a proportion of the SD of MGA to MGA of 0.121, 0.101, and 0.088 for their sizes 20 mm, 30 mm, and 40 mm, respectively. Our temporal noise (of SD 0.3) corresponds to a SD of 7.5% of total movement time, consistent with the values reported by Jeannerod (1984), who found an average individual SD of tMGA of 7.9% of total movement time. In both cases—with temporal noise alone (e–g), or temporal noise and constant amplitude variability (h–j)—we observe the pattern that ApSD is dependent on size only at early time points (as reported by Holmes et al. (2011b)), although no part of our simulation conforms to Weber's Law, as all added variability is the same for all object sizes. Panels **k–m** depict an unrelated, complicated looking function, where the relationship between function velocity and SD nevertheless still holds when temporal noise is present (here having a SD of .15). In all simulations shown in this figure, we simulated 1500 trials, 15 of which are shown in the middle column. Temporal noise was introduced by a constant shift in *x*-direction, affecting the full aperture profile.

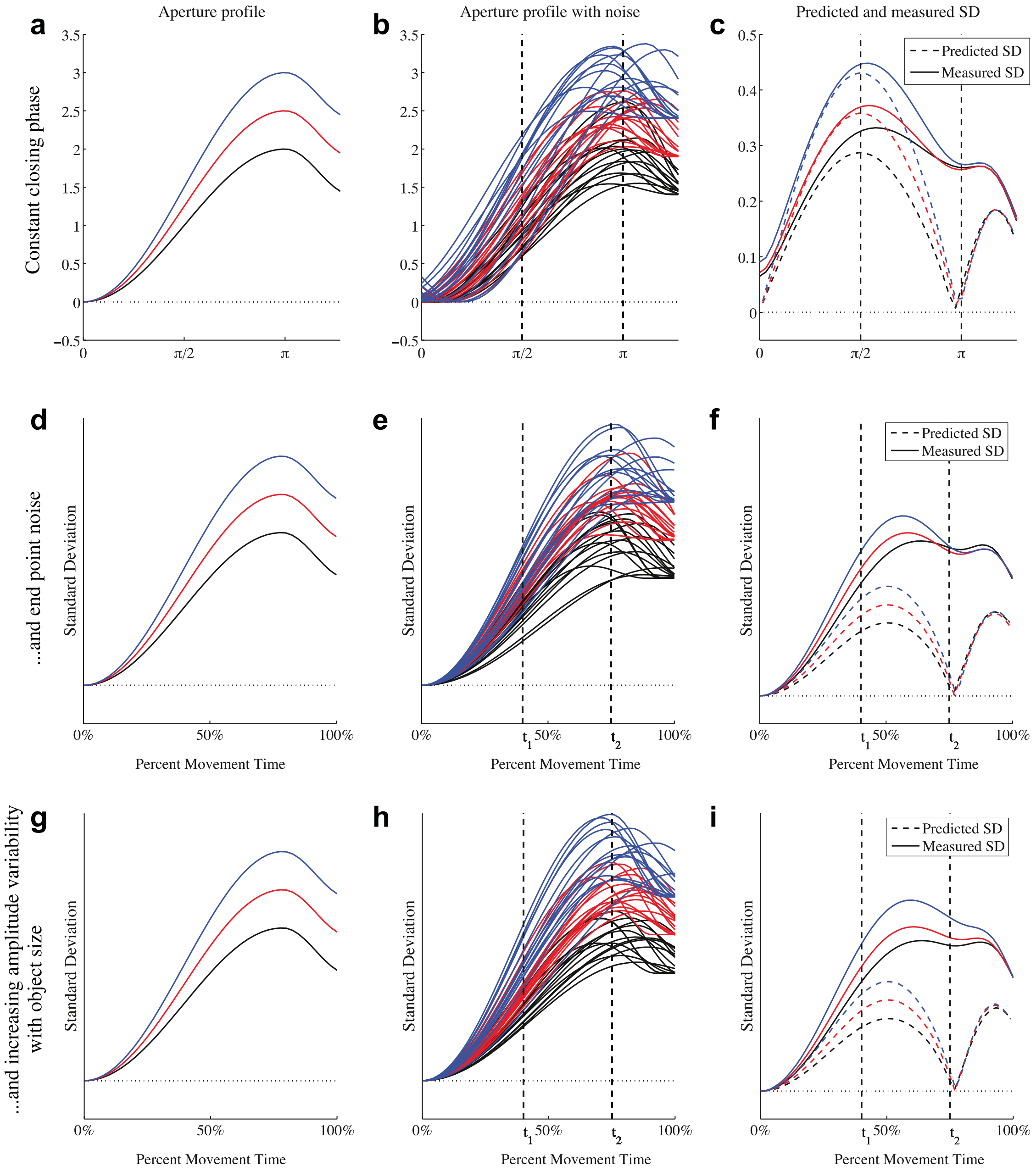

Fig. 2. These simulations address some aspects of the simulations in Fig. 1 which differ from real grasping data. (**a–c**) We replaced the post-maximum portion of the sine curve with a sine of constant amplitude (0.3) and higher frequency (3) for all simulated sizes. In panels where amplitude variability was included (b and c), the amplitude of this second sine curve compensated such that all simulated trajectories for a given size will end with the same y-value. The function then remains constant after this y-value is reached. This represents the final closure of the fingers around the object, after which point the aperture cannot be reduced further. With a constant closing phase, temporal noise no longer causes the predicted or measured ApSD of this portion of the trajectory to depend on object size. (**d–f**) Instead of a phase shift, we included only variability in time of movement offset. The amount of end point noise (SD 0.37) was chosen such that the SD of tMGA remained near the average value of 7.9% MT found by Jeannerod (1984), but was the same for all simulated object sizes. Amplitude variability was included as in simulations (a–c). Despite changing the source of temporal noise, an early but not late dependency of ApSD on object size can still be observed. (**g–i**) Amplitude variability is simulated to increase with object size (SD of 0.13, 0.14, and 0.15) in order to mimic the finding by Holmes et al. (2012) and Ganel, Chajut & Algom (2008a) that the SD of MGA can be dependent on object size under certain grasping and viewing conditions (grasping of 2-D objects and memory-guided grasping, respectively). End point variability is included as in the previous simulation. In this case, ApSD depends on object size throughout the entire trajectory.

object perfectly and grasps repeatedly with identical profiles. The only source of variability is assumed to be temporal noise that shifts the profile slightly in time (Fig. 1c). Calculating the mean profile and its SD (as was done by Holmes et al. (2011b)) shows that ApSD is large at times where the ApVel of the underlying function is large (e.g., at $t = \pi/2$ in Fig. 1d) and small at times where the ApVel is small (e.g., at $t = \pi$ in Fig. 1d) and conforms well with our prediction from Eq. (4) (dashed line in Fig. 1d).

Now consider this almost perfect participant grasping objects of different sizes. Because the overall movement time is relatively stable, this must lead to steeper slopes in the aperture profile for larger objects (as also reported by Holmes et al., 2011b; Fig. 1e). Larger ApSD values are found at the time of these steeper slopes, as predicted by our formula. In Fig. 1g, the pattern observed by Holmes et al. (2011b) is already evident, but it has nothing to do with Weber's Law (because the hypothetical participant is assumed to know the size perfectly, meaning that the only variability in these data is constant temporal noise and there is no variability that could scale according to Weber's Law). But if such a hypothetical, non-Weberian participant will already produce a pattern like that observed by Holmes et al. (2011b), then their observed pattern cannot be counted as informative with regards to Weber's Law.

What about a more realistic participant that shows not only temporal noise, but also some uncertainty in the size estimate and therefore in MGA? In Fig. 1h–j, we simulated this uncertainty, but again in a clearly non-Weberian way. That is, the MGA now also has some variability, but this variability is constant and does not scale with object size. In addition, we again assume temporal noise as in the previous simulations and took care to use as realistic values as possible. Again, we can see in Fig. 1j that our simulation produces results resembling those found by Holmes et al. (2011b), although none of our simulation parameters follow Weber's Law, as added variability was the same for all object sizes.

In conclusion, the finding of Holmes et al. (2011b) that ApSD is dependent on object size at early but not late time points can be explained exclusively by the fact that ApVel of the aperture-profile is dependent on object size at early time points. Any degree of temporal misalignment of the trajectories would mathematically require us to expect their pattern of results—even in the case of uniform or zero variability in the function itself. Without accounting for this effect, Holmes et al.'s (2011b) results cannot be interpreted in terms of motor-estimated size, nor as support for a differential effect of Weber's Law at early portions of a grasping movement.

Finally, we would also like to reiterate that the problem is a very general one, and will always occur when looking at the variability of any temporal data: The variability will always depend on the first derivative (velocity) of the underlying function if temporal noise is present. It is worth pointing out that Holmes et al. (2011b) also recognized the relationship between ApVel and ApSD in their data (their Fig. 4), but interpreted it as theroretically meaningful, in that greater forces must be produced for greater objects, and the production of greater forces is more variable than the production of smaller forces. However, we show that this effect is completely independent of the quantity being measured. To demonstrate this, consider Fig. 1k: We chose some random, complicated looking temporal function (which could, for example, be an EEG pattern), performed the same simulations on it as in the previous examples (i.e., added temporal noise, Fig. 1l) and determined the SD as well as the first derivative (Fig. 1m). Again, the observed pattern of the SD follows closely the first derivative, as predicted by Eq. (4). This relationship will only get washed out (i.e., low pass filtered) if the temporal noise increases, as discussed in Appendix A. We hope this letter will draw attention to this phenomenon within the vision science community.

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Appendix A. Mathematical derivation

Why is there such a close and predictable relationship between the SD of the aperture and the velocity of the underlying aperture profile? We show that this has very general and simple reasons. Let $f(t)$ be an arbitrary, differentiable function. This function is measured multiple times at an arbitrary, fixed point t_0, but with some uncertainty Δ in t_0, such that the measurements can be described as

$$M = f(t_0 + \Delta) \tag{1}$$

where M and Δ are random variables with Δ having an expected value of zero. A Taylor-expansion gives

$$M = f(t_0 + \Delta) = f(t_0) + \dot{f}(t_0)\Delta + \epsilon \tag{2}$$

with $\dot{f}$ being the first derivative of f and ϵ the error of the approximation (depending on the contribution of higher order derivatives of $f(t)$ and higher order powers of Δ). We know that for the SD σ of any random variable X the relationship holds:

$$\sigma(a + bX) = |b|\sigma(X) \tag{3}$$

(with a and b being fixed values). Applying this to the linear term of our Taylor-expansion gives

$$\sigma(M) = \sigma(f(t_0) + \dot{f}(t_0)\Delta) = |\dot{f}(t_0)|\sigma(\Delta) \tag{4}$$

This is the crucial relationship. Applied to the grasping data, it means that the SD of aperture measurements $\sigma(M)$ depends on the amount of temporal noise $\sigma(\Delta)$ multiplied by the absolute value of the local velocity $|\dot{f}(t_0)|$ of the underlying aperture profile. The approximation will be better if the amount of noise is small relative to the contribution of higher order derivatives, with increased noise acting like a low pass filter, blurring the relationship. Our simulations show that for typical aperture profiles and temporal noise values, the blurring is not strong enough to hide the relationship. For real world data, we must also take into account that there are other sources of noise in the data (besides temporal noise). Again, our simulations show that these other sources are not strong enough to hide the relationship.

Appendix B. Special cases and concerns

Here we would like to discuss in detail some more specific concerns which were brought up in the review process.

(1) *In your simulations, SD appears to depend on object size in the post-MGA movement phase. In empirical investigations, however (e.g., Heath et al., 2011; Holmes et al. 2011a,b), a dependency of SD on object size is not found after the MGA. How do you explain this discrepancy?*

That we have a relationship between SD and object size in the post-MGA, hand closing phase in Fig. 1 comes from us using a sine curve: in a sine curve, velocity remains dependent on size even after the maximum. We therefore find that temporal noise creates a dependence of SD on size for this portion of the curve as well. In grasping data, however, the velocity of this phase of the movement typically does not depend on object size (as reported by Holmes et al. (2011b)). If ApVel is not dependent on object size for this portion of the movement, we would not predict a dependency of ApSD on object size due to temporal noise for this phase, either.

To exemplify this, we ran the same simulation as in Fig. 1h–j, but replaced the post-maximum portion of the sine curve with a sine curve of constant amplitude for all simulated sizes. The velocity of the post-maximum trajectory thus no longer depends on the original amplitude, and in Fig. 2a–c we can see that there is accordingly no longer a dependency of SD on object size for this portion of the trajectory, for either the predicted or measured SDs. As this modified curve is more representative of real grasping data, we use it for all other simulations in Appendix B.

(2) *To simulate temporal noise, you add a phase shift. This does not seem like a very realistic representation of noise in the data.*

To explain the phenomenon of interest, we chose the most mathematically simple form of temporal noise, a phase shift, but it is indeed likely not representative of actual noise in the data. It furthermore leads to imperfections such as the appearance that the trajectory begins with a closing movement in some cases.

To show that this simplification is not problematic for our reasoning, we simulated a case where noise comes only from determining the end point of the movement: a very realistic source of noise, as movement offset is typically approximated by a separate but related marker, such as wrist velocity or the touch time of one finger. We added a constant end point variability to each object size such that the SD of the time of MGA (tMGA) remained about the level measured by Jeannerod (1984) of 7.9% and normalized by percent MT. Amplitude variability was constant for all object sizes, as in previous simulations. In Fig. 2d–f, we can see that this alternative form of temporal noise does not affect our observation that the measured SD is dependent on object size at early time points (e.g., t_1) but not late time points (e.g., t_2). Also, the pattern corresponds well to our prediction.[3]

> (3) *In your simulations, there is no dependency of SD on object size at the MGA. However, some empirical studies have found that, under certain conditions (grasping from memory, Ganel, Chajut, & Algom, 2008a; grasping 2-D objects, Holmes et al., 2012), a dependency of SD on object size can be found at the time of the MGA as well. How do you reconcile these findings?*

In our simulations, we assumed an equal SD of MGA for all object sizes, as this is the most difficult case for our argument (i.e., we show that ApSD depends on object size at early time points *despite* not depending on object size at MGA) and also because this is what has consistently been found for natural, full-vision grasping (Ganel, Chajut, & Algom, 2008a; Heath et al., 2011; Holmes et al., 2011b). We then showed that even in this case of constant variability at the MGA, temporal noise requires us to expect a dependency of SD on object size early in the movement due to the dependency of velocity on object size at these points. Velocity is not dependent on object size at the point of the MGA (as it is always 0), and therefore the artifact does not affect ApSD at the MGA.

However, our argument certainly also allows for the contribution of other sources of noise. It is possible that by altering the viewing or grasping conditions, a situation is created where the SD of the MGA is dependent on object size, for reasons unrelated to temporal noise. A simulation of such a hypothetical case is shown in Fig. 2g–i, where simulated amplitude variability increases with object size, and temporal (end point) noise is added as in the previous simulation. We can see that the measured SD is now simply dependent on object size throughout the entire movement, although temporal noise does cause a stronger dependency at pre-MGA movement times.

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[3] Note that temporal noise is now no longer constant, as in previous simulations, but instead increases linearly with time. To account for this, we adapted $\sigma(\Delta)$ of our prediction (Eq. (4)) for each time point, such that $\sigma(\Delta)$ increases linearly with time (with 0% temporal noise at $t = 0$ and 100% temporal noise at $t = 100\%$).

Study 3

Foster, R.M. & Franz, V.H. (2014). Superadditivity of the Ebbinghaus and Müller–Lyer illusions depends on the method of comparison used. *Perception, 43*, 783–795.

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Superadditivity of the Ebbinghaus and Müller-Lyer illusions depends on the method of comparison used

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Abstract. Illusions are useful tools for understanding fundamental visual processing. The method used to measure illusion strength is important but often neglected. We identified two methods of comparing bipart illusion elements (eg of the Müller-Lyer or Ebbinghaus illusions). For simultaneous adjustment an increase in size of one figure causes a decrease in the other. For independent adjustment one figure remains fixed while the other is adjusted to match it. These direct comparison illusion effects are contrasted to separate comparison illusion effects, where a neutral stimulus is matched to each illusory figure. If the illusion is stronger for direct comparisons, it is superadditive. The superadditivity of the Ebbinghaus illusion has been investigated using only simultaneous adjustment (Franz, Gegenfurtner, Bülthoff, & Fahle, 2000, *Psychological Science* **11** 20–25), and the Müller-Lyer illusion using only independent adjustment (Gilster & Kuhtz-Buschbeck, 2010, *Journal of Vision* **10**(1):11, 1–13). Superadditivity was found for the Ebbinghaus but not the Müller-Lyer illusion, but this may have been due to the comparison method or differences between the illusions. Here we test both illusions with both methods of adjustment. Our results suggest that both illusions are superadditive for simultaneous adjustment, but for independent adjustment only under limited circumstances. Implications for research on illusions and perception and action are discussed.

Keywords: illusions, Ebbinghaus, Müller-Lyer, methods, attention

1 Introduction

When dealing with illusions, it is becoming ever more evident that it is not only what the participant is looking at but also how he or she is looking at it that affects the strength of the illusion. That is, in addition to the physical parameters of the stimuli presented, both the participant's interaction with the stimulus, as well as the method of gauging their response, can have a crucial impact on the illusion effect measured (eg Coren & Girgus, 1972a; Franz, 2003). Differences in the perceptual strength of an illusion elicited in such cases are often interpreted as a sort of attentional effect; for example, it has been found that directing attention to the shaft rather than the fins of the Müller-Lyer illusion will reduce its effect (eg Coren & Girgus, 1972b; Gardner & Long, 1961), and ignoring either the outward or inward facing fins in a figure containing both will produce an illusion in the expected direction (eg Coren & Porac, 1983; Goryo, Robinson, & Wilson, 1984). Increasing the stimulus separation between the two illusory figures has also been found to increase the illusion effect (eg Foster, Kleinholdermann, Leifheit, & Franz, 2012; Girgus & Coren, 1982; Pressey & Di Lollo, 1978).

The relatively recent question of whether motor actions are resistant to illusions has also brought to light other influences of task demands on vision illusions. In particular, Franz, Gegenfurtner, Bülthoff, and Fahle (2000) proposed that a mismatch of task demands in grasping and perceptual tasks could explain why some studies find a smaller illusion effect for grasping than for perceptual tasks. Specifically, they examined the study of Aglioti, DeSouza, and Goodale (1995), which found a larger influence of the Ebbinghaus illusion on a perceptual comparison task than on grasping. Aglioti et al.'s perceptual task involved finding a participant's perceptual match—where two stimuli appear to be the same size, although their physical size may differ—by asking him or her to compare the inner circle of one illusory figure (eg small circle surround) directly with the inner circle of the opposite illusory figure (eg large circle surround). They then considered the illusion effect to be the difference in physical size between these perceptually matched figures. For the grasping task, however, participants grasped the illusory disks individually, and the illusion effect was considered to be the difference in maximum grip aperture between disks of the same size placed in the opposite illusory contexts. Using this method, they found a smaller illusion effect for the grasping task than for the perceptual task (see figure 5 of Aglioti et al., 1995).

Franz et al. (2000), however, proposed that the difference in illusion effect may be due not to the different response modality used but rather to different task demands in the two conditions. In particular, they noted that only the perceptual task required the participants to compare one illusory figure with the other; the grasping task required interaction with only one of the two illusory figures. If the difference in task demands affects the degree of illusion effect, it could explain the difference in response conditions found by Aglioti et al. (1995). And, indeed, this is what Franz et al. (2000) found. In Franz et al.'s study participants adjusted the inner circles of the two Ebbinghaus figures until they were perceived to be of the same size. The difference in physical size of these perceptually matched circles was considered to be the illusion effect in the *direct comparison* condition. In the *separate comparison* condition participants adjusted a neutral circle (without surrounding circles) to appear to be the same size as the center circle of each illusory figure individually. The separate comparison illusion effect was considered to be the sum of the individual illusion effects. The illusion effect was found to be larger for direct comparisons rather than separate comparisons, and therefore 'superadditive' (see also Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999).

The finding that the Ebbinghaus illusion effect is stronger when comparing the two figures directly affected subsequent research in the field, with many scientists choosing to balance task demands by presenting only a single illusory figure in both the perceptual and grasping tasks (eg Glover & Dixon, 2002; Haffenden, Schiff, & Goodale, 2001; Westwood, McEachern, & Roy, 2001). However, some researchers (eg Dewar & Carey, 2006; Stöttinger, Aigner, Hanstein, & Perner, 2009) have also attempted to induce a direct comparison in the motor task by using bimanual grasping, and have additionally used illusions other than the Ebbinghaus illusion (the Müller-Lyer and the Diagonal illusion, respectively). This raises the question of whether bimanual grasping balances attention in a manner similar to a direct perceptual comparison (a concern previously raised by Foster et al., 2012, and Stöttinger et al., 2009), but also whether illusions other than the Ebbinghaus illusion are superadditive.

Whether the Müller-Lyer illusion is superadditive has been investigated by Gilster and Kuhtz-Buschbeck (2010). They performed an experiment similar to that of Franz et al. (2000), and asked participants to either adjust a Fin Out Müller-Lyer figure to match a Fin In Müller-Lyer figure (or vice versa; direct comparison), or to adjust a neutral figure (with 90° fins) to match each of the illusory figures in turn (separate comparison). Summing the separate comparison illusion effects and comparing them with the direct comparison illusion effect, they found no evidence for superadditivity of the Müller-Lyer illusion. This would indicate that the Müller-Lyer illusion does not share the property of superadditivity with the Ebbinghaus illusion.

However, there was one further difference between the experiments of Franz et al. (2000) and Gilster and Kuhtz-Buschbeck (2010). In the direct comparison condition of Gilster and Kuhtz-Buschbeck one illusory figure remained stationary, while the second was adjusted to match it; however, the participants in Franz et al.'s experiments adjusted both figures simultaneously—that is, as the size of one inner circle increased, the size of the second decreased. Knowing the important role of attention on the strength of illusions, it is possible that this method of *simultaneous adjustment* divided attention more completely than the *independent adjustment* direct comparison used by Gilster and Kuhtz-Buschbeck (2010).

If a simultaneous adjustment task were used for the Müller-Lyer illusion, it is thus possible that a superadditive effect could be found for this illusion as well. On the other hand, it is also possible that fundamental differences in the illusions cause there to be a superadditive effect for the Ebbinghaus but not the Müller-Lyer illusion. The current experiments attempt to distinguish between these possibilities.

We therefore decided to test both the Müller-Lyer and Ebbinghaus illusions using both forms of direct comparison (simultaneous and independent adjustment), contrasting the illusion magnitude to that found by means of separate comparisons. The first two experiments employed the Müller-Lyer illusion and tested both simultaneous (experiment 1) and independent (experiment 2) direct comparison, respectively. The final two experiments used the Ebbinghaus illusion and also tested both simultaneous (experiment 3) and independent adjustment (experiment 4). We were able to replicate the results of both Gilster and Kuhtz-Buschbeck (2010) (experiment 2) and Franz et al. (2000) (experiment 3). The overall pattern suggests that, for both illusions, simultaneous adjustment produces a superadditive illusion effect, while independent adjustment produces superadditivity under only limited experimental conditions.

2 Experiment 1

In this experiment we first tested the superadditivity of the Müller-Lyer illusion using the simultaneous adjustment method of direct comparison. We therefore set out to compare the magnitude of the illusion effect between direct and separate comparison conditions, where the figures were simultaneously adjusted in the direct comparison condition. In order to keep stimulus dimensions as consistent as possible between the direct and separate comparison tasks, we divided the experiment into two parts: in the first part of the experiment the participants adjusted the two illusory figures until they appeared to be perceptually of the same size. We considered these figures to be a perceptually matched pair, and in the second part of the experiment participants then adjusted a neutral stimulus to each illusory figure of the perceptually matched pair in turn. A visual depiction of this method can be found in figure 1. An advantage to using this method is that the same illusory figure stimulus dimensions on average are used in both the direct and separate comparisons. This is important as stimulus dimensions can also affect the strength of the illusion (eg Restle & Decker, 1977). This basic two-part method was used in all experiments.

2.1 *Material and methods*

2.1.1 *Participants.* Eighteen people participated in the experiment (five male; mean age = 24.9 years). For all experiments participants were recruited from the city of Hamburg, and most were students at the University of Hamburg. A different set of participants was recruited for each experiment. They participated in return for either course credit or payment of 8 euro per hour. All participants reported having normal or corrected-to-normal vision and were naive to the hypotheses of the experiment. Prior to starting the experiment, participants in all experiments gave their informed written consent to participate according to the declaration of Helsinki, and were given the opportunity to stop the experiment at any time.

2.1.2 *Apparatus and stimuli.* A black-and-white bipart version of the Müller-Lyer illusion was used (black figures on a white background; see figure 1) and presented on a 55 cm screen diagonal computer monitor (Samsung SyncMaster 2233 Wide LCD Monitor). Luminance of the white background was measured at 180 cd m^{-2}, and of the thickest part of the stimuli at 20 cd m^{-2}. Programming was done in Matlab (MathWorks Inc., Natick, MA). The same set-up was used for all four experiments.

While all our stimulus measurements were calculated in millimeters for our experiments, as this is most common in grasping studies relevant to the superadditivity of illusions, we also report degrees of visual angle as *approximate estimates* for ease of comparison with other studies.

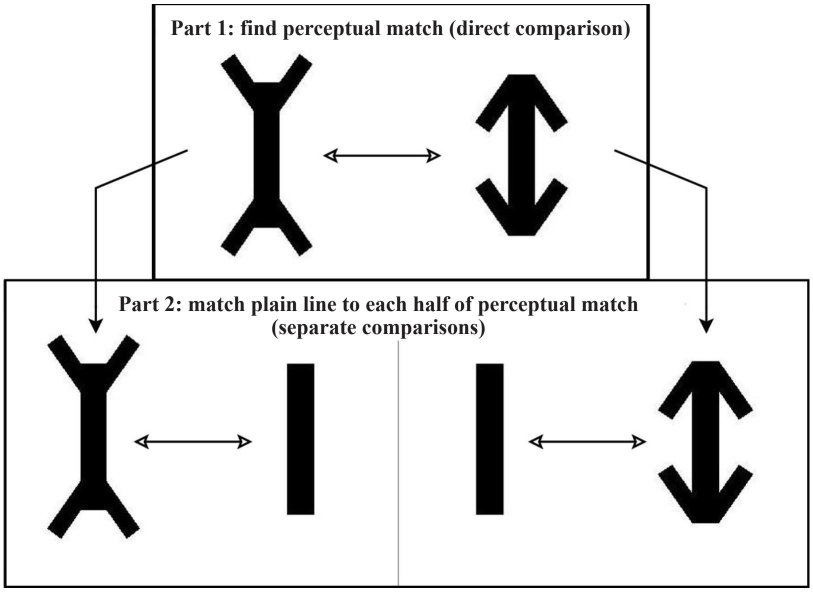

Figure 1. The method used in all experiments, with the Müller-Lyer illusion as an example. In the first part of the experiment a perceptual match of two illusory figures is found (direct comparison). This can be done by means of simultaneous adjustment (reducing the size of one figure increases the size of the other) or by independent adjustment (one figure, the base figure, remains fixed, while the other is adjusted). In the second part of the experiment these perceptual matches are then paired with a neutral figure (in this case a plain shaft), which is then adjusted to match each of the figures that were initially perceived as being of the same size (separate comparisons).

The shaft lengths 39, 43, or 47 mm (5.6 deg, 6.2 deg, 6.7 deg) represent the one possible point of adjustment where both figures would be of the same physical size. The starting offset of the figure lengths was randomly set between –10 and 10 mm (1.4 deg and –1.4 deg; eg if the length was 39 mm, and the offset was 2 mm, one illusory figure would have a starting shaft length of 37 mm, while the other would have a starting shaft length of 41 mm). The shaft of each illusory figure was 8 mm (1.1 deg) wide. The smaller fin angle was always 70°, and the fins could be pointing inward (Fin In) or outward (Fin Out). The longest measurable extent of the fins was 18 mm (2.6 deg), and the width of each of the fins was 5 mm (0.7 deg). The two figures were separated by 80 mm (11.5 deg) and centered horizontally on the computer monitor. A random vertical offset of ±3.5 cm (5 deg) from the center of the screen was determined at the beginning of each new trial for each figure and was consistent for the duration of the trial. This was done to prevent matching of shaft lengths based on position cues.

2.1.3 *Procedure.* The same testing environment and general procedure were used for all experiments. Participants were seated at a desk in front of the monitor in a dark room (approximate viewing distance = 40 cm).

In the first part of the experiment (direct comparison) participants adjusted the shaft lengths of the Müller-Lyer figures using the keyboard until they perceived the two shafts to be of the same length. A change in the length of one figure resulted in an equal and opposite change in the other figure (simultaneous adjustment). The minimum change they could make was ±0.2 mm (0.03 deg) to the length of the shaft. Holding down the key allowed them to make large changes fluidly. They were allowed to take as much time as they wanted and confirmed that the two shafts appeared to be of the same length by pressing the space bar. There were 3 sizes of illusion pairs (39, 43, and 47 mm) presented on either side of the screen (left/right) for 5 repetitions, or 3 × 2 × 5 = 30 trials in the first phase of the experiment. The trial order within both phase 1 and 2 was always randomized in all experiments.

At the end of the first phase of the experiment we determined sets of perceptually matched pairs by averaging their adjustments, collapsing over side (so a total of 10 measurements were averaged for each comparison figure or set). In the second part of the experiment (separate comparison) we presented each element of the perceptually matched pair alongside a *neutral* figure (ie a shaft without fins), which participants adjusted to match the length of the shaft of the illusory figure. The neutral figure was randomly set to a length between 29 and 57 mm (4.2 deg and 8.2 deg).

In the second part of the experiment there were therefore 6 perceptual match elements (2 per size), presented on either side of the screen (left/right), for 5 repetitions each, or $6 \times 2 \times 5 = 60$ trials.

2.1.4 *Data analysis.* Our intent was to compare the magnitude of the illusion effect between the direct and separate comparison conditions. To that end, we first calculated the illusion effects for each condition. For the direct comparison condition the illusion effect was considered to be (Fin In − Fin Out), when considering the adjusted physical sizes of each figure in a perceptually matched pair. For the separate comparison condition the illusion effect was considered to be (Fin In − neutral) + (neutral − Fin Out), again when considering physical sizes of each adjusted figure.

We performed an ANOVA on the illusion effect for the factors comparison type (direct, separate) and size (39 mm, 43 mm, 47 mm). A significance level of $\alpha = 0.05$ was used for all statistical analyses. p-values above 0.001 are given as exact values. A Greenhouse–Geisser correction (Greenhouse & Geisser, 1959) was applied for factors with more than one level in all experiments.

2.2 *Results and discussion*

In the ANOVA on the illusion effect for the factors comparison type and size we found a significant main effect of comparison type ($F_{1,17} = 5.4$, $p = 0.033$), but no effect of size or interaction between size and comparison type (both ps > 0.125). This indicates a superadditive effect for the Müller-Lyer illusion when simultaneous adjustment is used in the direct comparison task. The illusion effects and a depiction of the effect of comparison type can be found in figure 2.

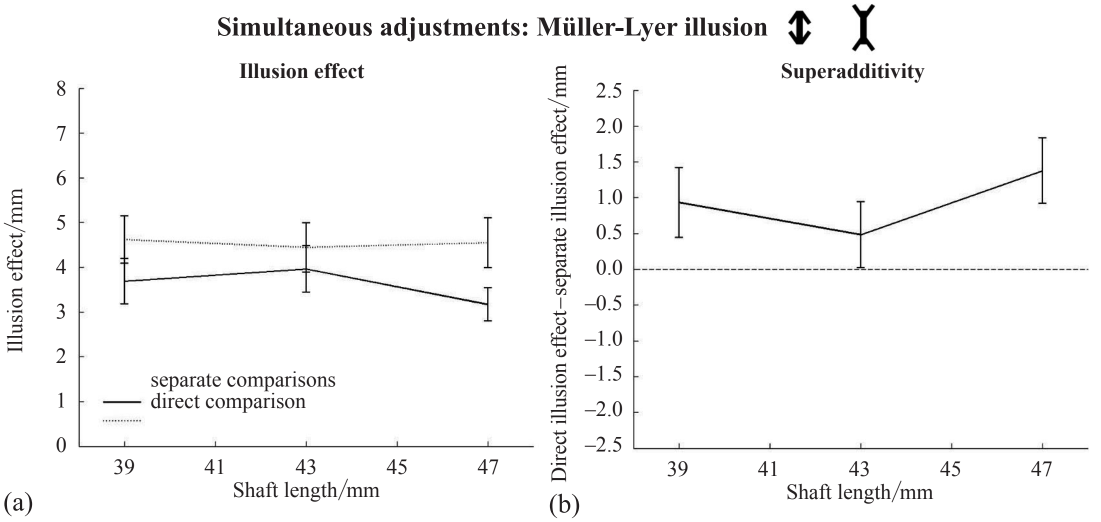

Figure 2. (a) Illusion effects in millimeters for the Müller-Lyer illusion for the simultaneous adjustment method of direct comparison (dotted line; separate comparisons, solid line). The illusion effect is greater when a direct comparison is used, indicating superadditivity. (b) A depiction of the average difference in illusion effect between the direct and separate comparisons. For both figures error bars represent ±1 SEM. In these and all further figures the error bars are informative for the question of whether the values are significantly different from 0 (because they represent the SEM of a difference, which is relevant for a within-subjects ANOVA; Franz & Loftus, 2012).

3 Experiment 2

Having found a superadditive illusion effect for the Müller-Lyer illusion using the method of simultaneous adjustment, we also wanted to see if we could replicate the result of Gilster and Kuhtz-Buschbeck (2010) and find no superadditivity when an independent adjustment task is used. This would indicate that the method of adjustment used affects whether the Müller-Lyer illusion is superadditive.

3.1 *Material and methods*

3.1.1 *Participants.* Nineteen people participated in the experiment (9 male; mean age = 24.3 years).

3.1.2 *Apparatus and stimuli.* For the independent adjustment direct comparison, one illusory figure remained fixed (base figure) while the other could be adjusted. Base figure shaft lengths were either 39, 43, or 47 mm, and the shaft of the adjusted stimulus was randomly set to a starting length of between 29 and 57 mm.

3.1.3 *Procedure.* As in experiment 1, experiment 2 consisted of two stages: the first to find perceptually matched pairs of illusory elements, and the second to find a neutral match to each element of these pairs.

As there were 3 base shaft lengths (39, 43, and 47 mm) and two illusory configurations (Fin In/Fin Out), this resulted in $3 \times 2 = 6$ base figures. These were presented on either side of the screen (left/right) for 5 repetitions, resulting in $6 \times 2 \times 5 = 60$ trials for the first stage of the experiment.

Perceptually matched pairs were found as in experiment 1. The second part of the experiment therefore consisted of 6 base figures and their perceptual matches, presented on each side of the screen for 5 repetitions each, or $6 \times 2 \times 2 \times 5 = 120$ trials. Owing to the length of the experiment, participants were required to take a 5 min break between phase 1 and 2 of the experiment.

3.1.4 *Data analysis.* The illusion effects were calculated as in experiment 1. We performed an ANOVA on the illusion effect for the factors comparison type (direct, separate), size (39, 43, 47 mm), and base configuration (which remained fixed during the direct comparison; Fin In, Fin Out).

3.2 *Results and discussion*

In the ANOVA on the illusion effect for the factors comparison type, size, and base configuration, we found that the effect of comparison type was not significant ($F_{1,18} = 0.54$, $p = 0.47$), replicating the results of Gilster and Kuhtz-Buschbeck (2010) and indicating that there is no superadditive effect for the Müller-Lyer illusion when this form of direct comparison is used. The only significant effect was an interaction between size and base configuration ($F_{1.80,32.36} = 11.23$, $p < 0.001$), whereby for the Fin In base illusion effects tended to increase with size, while for the Fin Out base they tended to decrease with size. All other main effects and interactions were not significant ($p > 0.12$). The illusion effects and the difference between the direct and separate comparision conditions can be seen in figure 3.

4 Experiment 3

Experiments 3 and 4 tested the simultaneous and independent adjustment methods of direct comparison using the Ebbinghaus illusion. As experiment 3 used the method of simultaneous adjustment, we expected to replicate Franz et al. (2000) and find a greater illusion effect when a direct comparison of the illusory elements was used.

4.1 *Material and methods*

4.1.1 *Participants.* Fourteen people participated in the experiment (four male; mean age = 22.4 years).

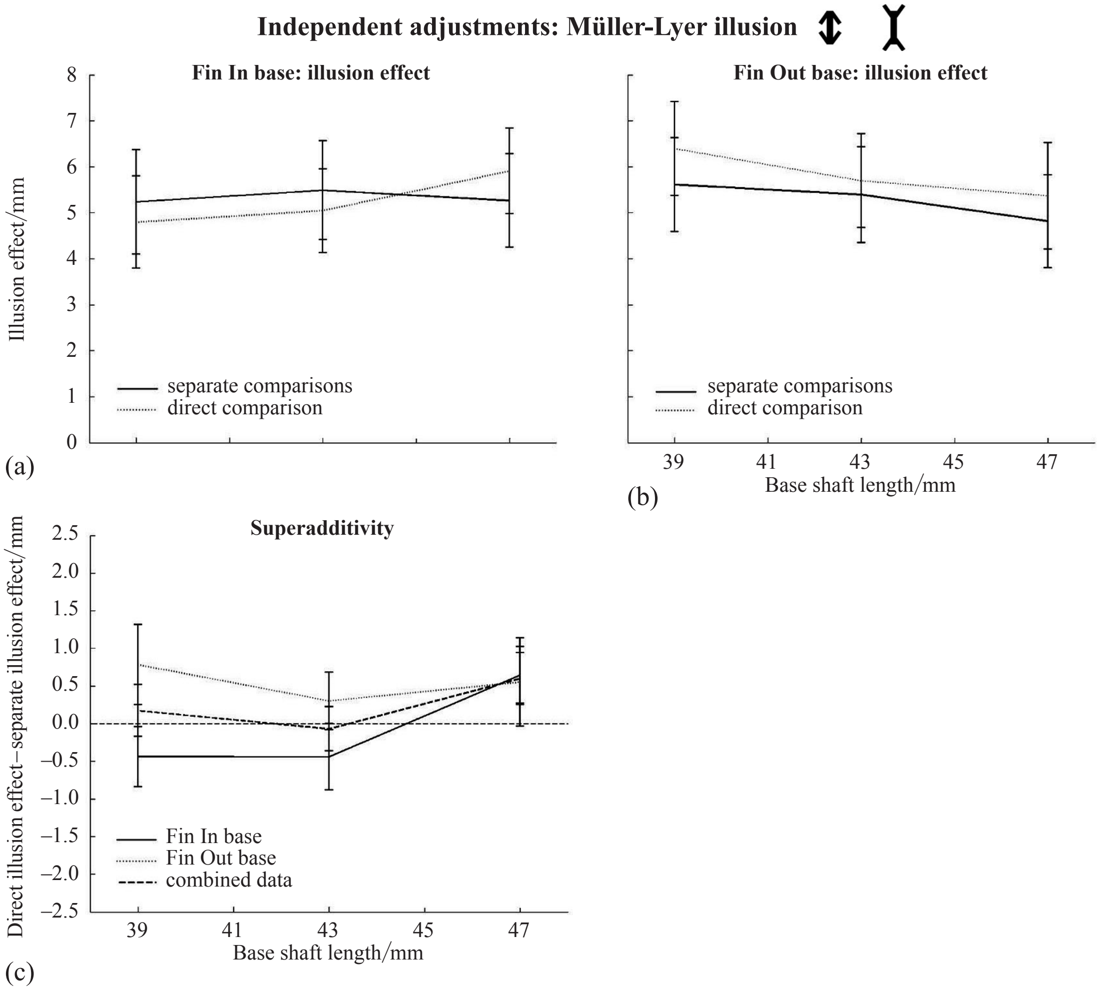

Figure 3. (a, b) Illusion effects for the Müller-Lyer illusion for the independent adjustment method of direct comparison. Pairs where the unmovable base was the Fin In figure are shown in (a), while pairs where the unmovable base was the Fin Out figure are shown in (b). (c) A depiction of the average difference between the direct and separate comparison conditions (superadditivity) for the combined data and distinguishing by base size. The effect of comparison type was not significant ($p = 0.47$). This indicates a lack of superadditivity when this type of direct comparison is used, and replicates the result of Gilster and Kuhtz-Buschbeck (2010). The interaction comparison type × base figure × size was not significant ($p = 0.12$). For all figures error bars represent ±1 SEM.

4.1.2 *Apparatus and stimuli.* Black-and-white exemplars of the bipart version of the Ebbinghaus illusion were presented on the same computer monitor as in previous experiments. Anti-aliasing was applied to improve the appearance of the circles in the Ebbinghaus illusion. The lines comprising the circles were approximately 1 mm thick (0.1 deg).

For the inner circles of the Ebbinghaus illusion, the four radii used when both figures were the same size were 14, 15.5, 17, and 18.5 mm (2 deg, 2.2 deg, 2.4 deg, 2.6 deg). An initial offset to the radii was randomly set between –4 and 4 mm (–0.6 deg and 0.6 deg). For the second phase of the experiment the neutral circle was randomly set to a radius between 11 and 21.5 mm (1.6 deg and 3.1 deg). The five large context circles had a radius of 29 mm (4.2 deg), and there was a distance of 31 mm (4.4 deg) between the midpoint of the inner circle and the innermost edge of the context circles. The twelve small context circles had a radius of 5 mm (0.7 deg), and there was a distance of 24 mm (3.4 deg) between the midpoint of the inner circle and the innermost edge of the context circles. These dimensions were taken from Franz, Bülthoff, and Fahle (2003) and represent a subset of their stimuli and those used by Franz et al. (2000). The midpoints of either the two inner circles or the inner circle and the isolated circle (for the separate comparisons) were separated by 140 mm (20.1 deg). The stimuli were always centered horizontally on the monitor such that the midpoints of the inner circles of both figures were equidistant from the edge of the monitor. The display was also centered vertically on the monitor.

4.1.3 *Procedure.* As in the previous experiments experiment 3 consisted of the same two stages of direct and separate comparisons. In the first part of the experiment a perceptual match was determined by means of simultaneous adjustment of the two illusory figures. We used 4 sizes (14, 15.5, 17, and 18.5 mm) presented on either side (left/right) for 5 repetitions, making $4 \times 2 \times 5 = 40$ trials in the first part of the experiment. In the second stage of the experiment we thus had four perceptually matched pairs, so 4 (pairs) × 2 (figures per pair) × 2 (sides) × 5 (repetitions) = 80 trials in the second part of the experiment. Participants were again required to take a 5 min break between parts 1 and 2 of the experiment.

4.1.4 *Data analysis.* The illusion effects were calculated as in experiments 1 and 2. For the Ebbinghaus illusion this means the illusion effect was considered to be large circle surround − small circle surround for each perceptually matched pair in the direct comparison condition, where each is considered to be the adjusted physical size of the respective figure. For the separate comparisons the illusion effect was therefore (large circle surround − neutral) + (neutral − small circle surround). An ANOVA was carried out on the illusion effect for the factors of comparison type (direct, separate) and size (radius of 14, 15.5, 17, and 18.5 mm).

4.2 *Results and discussion*

In the ANOVA on the illusion effect for the factors comparison type and size we found a significant main effect of comparison type ($F_{1,13} = 7$, $p = 0.02$), which meant that we were able to replicate Franz et al.'s (2000) finding of superadditivity of the Ebbinghaus illusion when the method of simultaneous adjustment was used. The effect of size was also significant ($F_{3,25.10} = 18.48$, $p < 0.001$), with the illusion effect increasing with size. The interaction of comparison type and size was not significant ($p = 0.195$). The illusion effects and a depiction of the effect of comparison type can be found in figure 4.

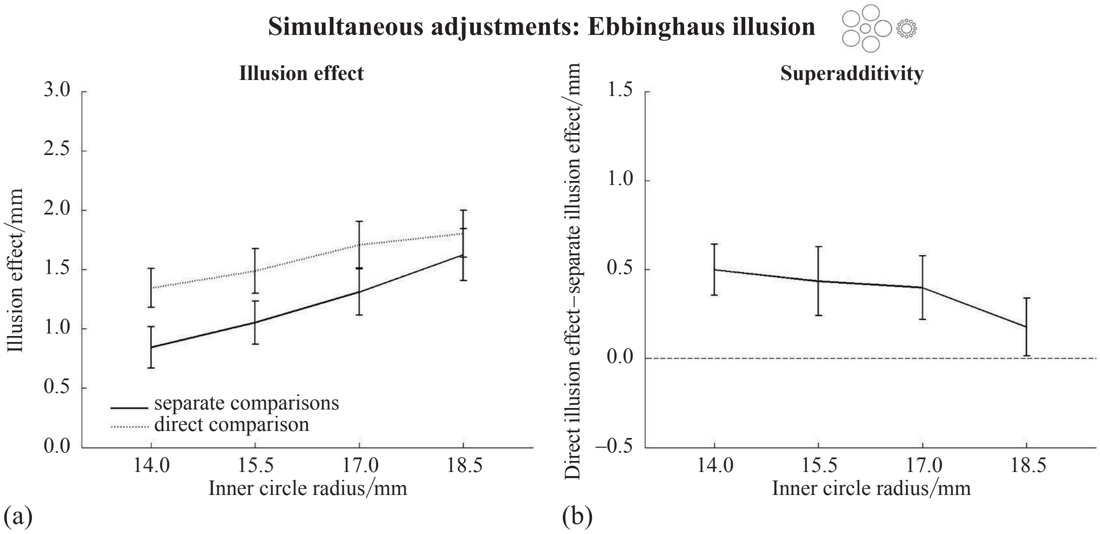

Figure 4. (a) Illusion effects for the Ebbinghaus illusion for the simultaneous adjustment method of direction comparison (dotted line; separate comparisons, solid line). The illusion effect is greater for direct comparisons, indicating superadditivity. This replicates the result of Franz et al. (2000). (b) A depiction of the average difference in illusion effect between the direct and separate comparisons. For both figures error bars represent ±1 SEM.

5 Experiment 4

Experiment 4 used the method of independent adjustment to test for superadditivity in the Ebbinghaus illusion.

5.1 *Material and methods*

5.1.1 *Participants.* Eighteen people participated in the experiment (six male; mean age = 27.3 years).

5.1.2 *Apparatus and stimuli.* For the independent adjustment direct comparison one illusory figure remained fixed (base figure) while the other could be adjusted. The base figure center circle radii were 14, 15.5, 17, or 18.5 mm, and the radius of the adjusted stimulus was randomly set at the beginning of the trial between 11 and 21.5 mm.

5.1.3 *Procedure.* A perceptual match was again determined for each illusory base figure. We used four base radii (14, 15.5, 17, and 18.5 mm), surrounded by one of two illusory configurations (large/small context circles). This resulted in $4 \times 2 = 8$ base figures. As they were presented on either side of the screen (left/right), and there were 5 repetitions, this resulted in $8 \times 2 \times 5 = 80$ trials in the first phase of the experiment.

As in previous experiments, in the second phase each figure of the perceptual match was paired with a neutral circle, which was then adjusted until it appeared to be the same size as the inner circle of the illusory stimulus. In this case the second phase consisted of 8 comparison figures and their perceptual matches, presented on each side of the screen for 5 repetitions each, or $8 \times 2 \times 2 \times 5 = 160$ trials. A pause of 5 min was included between phase 1 and 2 of the experiment.

5.1.4 *Data analysis.* The illusion effects were calculated as in experiment 3. We again performed an ANOVA on the illusion effect for the factors of comparison type (direct, separate), size (radius of 14, 15.5, 17, 18.5 mm), and base configuration (figure that remained fixed during the direct comparison; large, small context circles).

5.2 *Results and discussion*

In the ANOVA on the illusion effect for the factors comparison type, size, and base configuration the effect of comparison type was significant ($F_{1,17} = 4.5$, $p = 0.048$), but there were several interactions which complicate the interpretation of this result. Namely, both the comparison type × base configuration and comparison type × base configuration × size interactions were significant ($F_{1,17} = 6.7$, $p = 0.019$ and $F_{2.3,39.11} = 4.9$, $p = 0.009$, respectively). Upon examining the data, this effect seems to be caused by an appearance of superadditivity only when the small context circle base was used, and then for only small sizes (as seen in figure 5). Apart from this unexpected interaction, we also found a main effect of size ($F_{1.73,29.37} = 18$, $p < 0.001$)—similar to what we found in experiment 3, the illusion effect increased with size for the Ebbinghaus illusion. Furthermore, there was a main effect of base configuration ($F_{1,17} = 48$, $p < 0.001$), whereby illusion effects were overall greater if the small context circle illusion was used as a base. Finally, we also found a base configuration × size interaction ($F_{2.35,39.93} = 3.2$, $p = 0.046$).

6 General discussion

Overall, this set of experiments suggests that both the Ebbinghaus and the Müller-Lyer illusions are superadditive when the figures are simultaneously adjusted in the direct comparison condition, but when independently adjusted (with one illusory figure remaining fixed as the base) only the Ebbinghaus illusion shows signs of superadditivity under limited experimental conditions. In the following we consider possible mechanisms behind this effect.

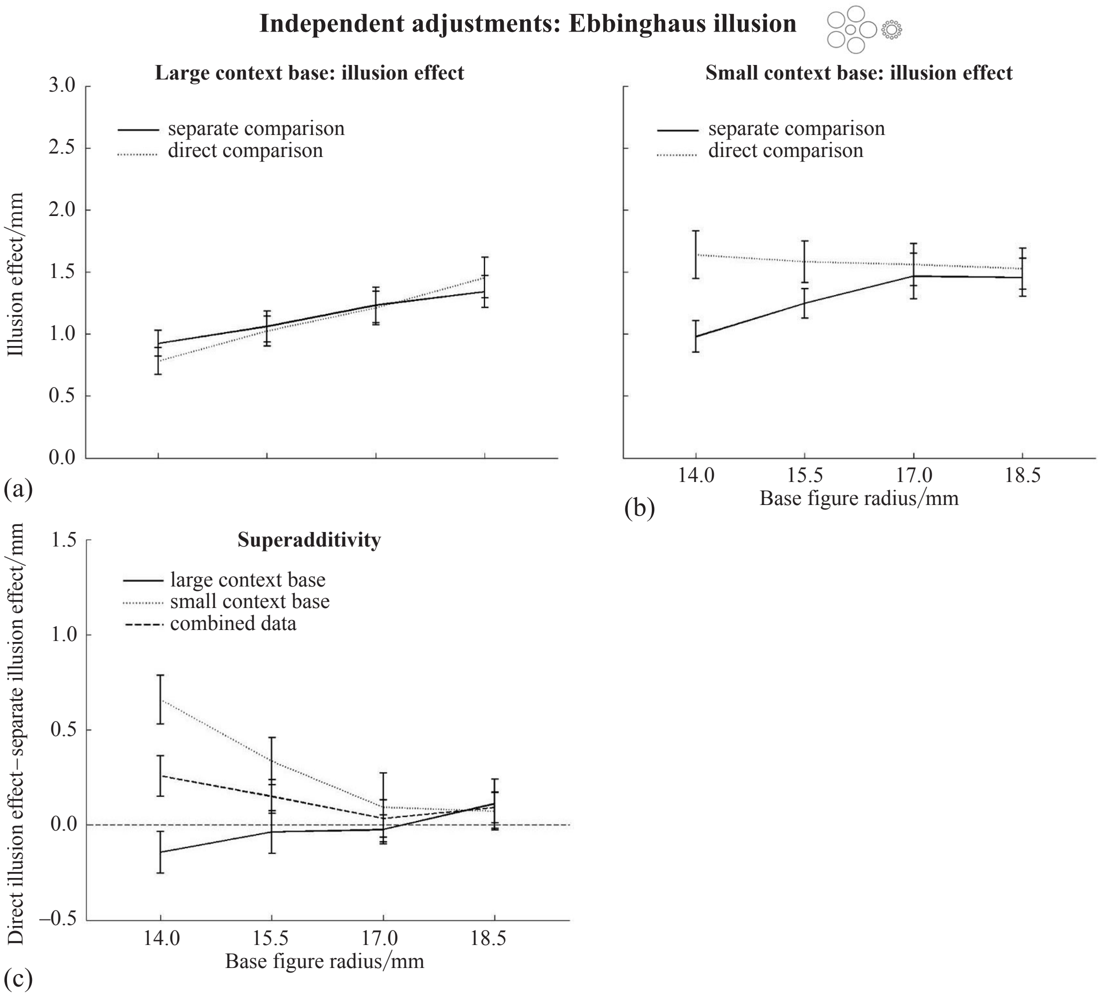

Figure 5. (a, b) Illusion effects for the Ebbinghaus illusion for the independent adjustment method of direct comparison. Pairs where the immovable base figure had large context circles are in shown in (a), while pairs where the immovable base figure had small context circles are shown in (b). (c) A depiction of the average difference between the direct and separate comparison conditions (superadditivity) for the combined data and distinguishing by base size. The effect of comparison type was narrowly significant ($p = 0.048$), but was complicated by the interaction of comparison type × base figure × size ($p = 0.009$), whereby superadditivity seems to occur only when small sizes of the small context circle base were used. For all figures error bars represent ±1 SEM.

6.1 *Use of an internal standard?*

As stated in the introduction, we expected there was an attentional difference between the simultaneous and independent adjustment tasks, whereby attention must be split more fully for simultaneous adjustments in order to update the size estimate of each of the figures. But to what extent was the comparison figure in the independent adjustment task being used at all? There are similarities between our independent adjustment task and what signal detection theory calls a reminder task (eg Macmillan & Creelman, 2004). In a reminder task two stimuli are presented one after the other, and the participant must make a comparison judgment between them. However, in this case the first stimulus is always a reference stimulus, or standard, and never varies. In such a reminder task there are some grounds to believe that observers ignore this presented standard in favor of an internal standard (Lapid, Ulrich, & Rammsayer, 2008; Morgan, Watamaniuk, & McKee, 2000). Assuming that participants are relying on a remembered version of the base stimulus in the independent adjustment task (or, indeed, in the separate comparison task), what effects might we expect?

Unfortunately, what changes occur to visual stimuli, and in particular visual illusions, as they are held in memory has not been extensively researched. Studies investigating the use of an internal standard typically focus on just noticeable difference, or the variability of judgments, rather than whether it introduces a bias in the point of subjective equality (eg Lapid et al., 2008; Morgan et al., 2000).

However, at least one case exists where the effect of simply being the base or adjusted figure of an illusion is examined: Gilster and Kuhtz-Buschbeck (2010) had participants match the same Müller-Lyer configuration to itself (ie Fin In to Fin In, Fin Out to Fin Out, or neutral to neutral), and participants consistently set the adjusted stimulus to be larger than the base stimulus (see their table A1). We will show that our results, too, are generally compatible with the base figure in the independent adjustment being estimated larger than the adjusted figure.

Let us consider the independent adjustment condition with the Ebbinghaus illusion, where the small context circle figure is the base. Given the effect found by Gilster and Kuhtz-Buschbeck (2010), we would expect the inner circle of the base figure to be perceived as larger, as it is held in memory. For this direct comparison the illusion effect would therefore be increased. Our first prediction would therefore be that we find an overall greater illusion effect for the direct comparison when we have a small context circle rather than a large context circle base. And in fact, this is what we found (cf figures 5a and 5b).

For the associated separate comparison condition both illusory figures act as a base in turn, and those illusion effects are summed. Once again, this would increase the perceived size of the center circle of the base figure. However, since this increases the illusion effect for the small context figure, and decreases it for the large context figure, these effects will cancel out when they are summed, with the separate comparison illusion effect being equivalent to what we would find for isolated viewing (assuming the most basic case, that there is an equivalent effect on both figures). Finally, we compare the direct and separate comparison conditions. Since the effect is neutralized in the separate comparisons condition, an increased direct comparison illusion effect also translates into superadditivity: for the small context base condition, where the direct comparison illusion effect is increased relative to isolated viewing, we would thus expect to find a superadditive effect. This again corresponds well to our findings, although for only small stimulus sizes (cf figure 5c).

An overestimated internal standard would therefore help explain the impact of base figure in our independent adjustment condition. It would not, however, explain the interaction of base figure with size on superadditivity found for the Ebbinghaus illusion.

6.2 *The influence of attention*

Another possibility is that the increased attentional load required for the simultaneous adjustment direct comparison itself increases the strength of the illusion. While this idea has not yet been heavily researched, at least one study shows that increasing demands on working memory leads to a stronger effect of the Ebbinghaus illusion (de Fockert & Wu, 2009). In this experiment they measured the effect of the Ebbinghaus illusion via the method of constant stimuli while participants maintained either a short or long string of digits in working memory. They found that the illusion effect was greater when participants had to remember the longer string of digits, by 0.1 deg (their step size). Considering their target circle subtended 2.4 deg, this translates to an additional 4.2% illusion effect caused by increased attentional load. In contrast, when our illusion effects are viewed in terms of percentages, we find an additional 2.3% illusion effect on average for the Ebbinghaus illusion. The effect is thought to arise from a reduced ability to ignore distractors (de Fockert, Rees, Frith, & Lavie, 2001). It is possible that having to store continuously updated stimulus sizes in our simultaneous adjustment condition resulted in a similar increased demand on working memory.

This in turn could lead to a reduced ability to ignore distractors (the fins or surround circles) and an increased illusion effect for this type of direct comparison. That our increase was relatively smaller could be due to our task being less taxing on attentional load than that of de Fockert and Wu (2009).

A final consideration would be that in the simultaneous adjustment there is a contrast between the context elements as well. For the Ebbinghaus illusion, in particular, if the large context elements are perceived as even larger, and the small context elements as even smaller, this could increase the effect of the illusion (Girgus, Coren, & Agdern, 1972; Roberts, Harris, & Yates, 2005). If this contrast of the context elements does not take place in the independent adjustment direct comparsion—perhaps, again, due to the base figure being held more in memory—it should be no suprise that this illusion effect is equivalent to the separate comparisons condition. However, this explanation does not account for the interactions we found for the independent adjustment condition.

6.3 *Implications for experiments on perception and action*

In the introduction we stated that one motivation for these experiments was the use of bimanual grasping in order to induce a perception-like direct comparison between the two illusory elements. Our experiments show that simply interacting with both illusory elements of a display within a single task or trial is not sufficient to guarantee superadditivity. It is difficult to say with certainty what type of perceptual direct comparison would be equivalent to bimanual grasping. Attempts to establish this may also be hard to interpret, as such distinctions can be difficult to disentangle from the argument that divergent behavior in motor tasks can be attributed to dorsal stream control. Therefore, it seems safest and least controversial to match perception and action tasks by using displays with a single illusory figure.

7 Conclusions

While the finer outcomes of our line of experiments may be difficult to interpret, the results nevertheless clearly show that manipulating even subtle task demands can change the perceptual effect of an illusion. They also appear to represent another incidence of the effect of attention on illusions. Furthermore, our results have practical implications: they should be taken into consideration by researchers using illusions as a tool to investigate other aspects of cognition, especially regarding the matching of task demands.

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