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Elizabeth S. Counterman

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ABSTRACT

Investigation of the Goodale and Milner (1992) model of dorsal "vision for action" and ventral "vision for perception" streams of cortical visual processing has yielded controversial results. Some studies using three-dimensional versions of pictorial illusions in neurologically intact individuals have found that grip scaling (largely controlled by the dorsal stream) remains accurate despite robust perceptual illusion effects (e.g. Aglioti, DeSouza, and Goodale, 1995). However, others have found that the visuomotor system is as susceptible to visual illusions as the visuoperceptual system (Franz, 2001). Goodale (2008) has suggested that the less automatic an action, the more likely that the visuoperceptual system will be called upon, making such actions more susceptible to visual illusions.

The current set of experiments explored the effects of grasp awkwardness and eccentric fixation on visuomotor and visuoperceptual susceptibility to pictorial illusions; an effort to explain a recent study's visuomotor illusion findings (Radoeva, Cohen, Corballis, Lukovits, and Koleva, 2005). The first experiment investigated the effect of practice over the course of three days with a potentially awkward measuring device on grip scaling when strongly right-handed participants grasped bars embedded in Müller-Lyer arrowhead illusions with their right and left hands. Results demonstrated that grasps and estimations are less susceptible to the illusion after practice, but further experiments are needed to determine whether the visuomotor and visuoperceptual practice effects were the result of separate mechanisms. The second experiment demonstrated that after correction for scaling, manual estimation and adjustment estimation provide

similar assessments of perceptual sensitivity to the Müller-Lyer illusion, and it provided preliminary evidence for an effect of eccentric fixation on the relative magnitudes of visuomotor and visuoperceptual susceptibility to the illusion.

Influences of Awkwardness and Eccentric Fixation on

Visuomotor Susceptibility to Pictorial Illusions

by

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with Honor

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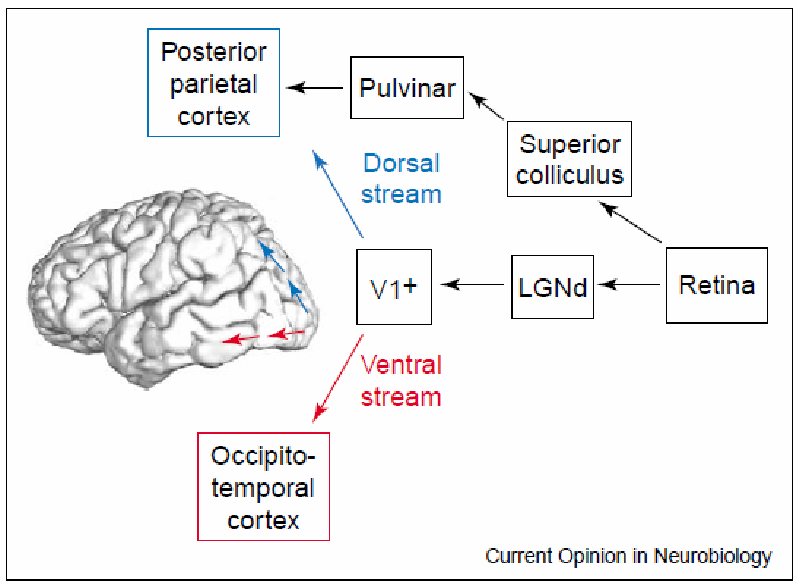
INTRODUCTION

Over 15 years ago, Goodale and Milner (1992) proposed a model for the functional differences between the ventral and dorsal streams of cortical visual processing (Figure 1). They proposed that the ventral "vision for perception" stream, which projects to the inferotemporal cortex, is responsible for generating detailed perceptions, while the dorsal "vision for action" stream, which projects to the posterior parietal region, provides the precise metric information needed for acting upon nearby objects (e.g. Milner and Goodale, 1995, 2008; Goodale, 2008).

The action-perception model proposes that visual *perception* of objects operates largely within allocentric (i.e. object-centered) coordinates and makes size and distance judgments of a focal object that are relative to other objects in the visual field. It is thought that the vision for perception system sacrifices precise metric calculations in favor of relational information, largely because calculation of the exact dimensions of all objects in the visual field would require a prohibitive amount of mental resources. Instead, the vision for perception system encodes information about objects' sizes and spatial positions relative to nearby objects, in order to create a mental representation that can accommodate changing viewpoints. (e.g. Milner and Goodale, 1995; Aglioti, DeSouza, and Goodale, 1995; Milner and Goodale, 2008)

Conversely, the visual control of skilled *actions,* like grasping objects, requires accurate egocentric (i.e. in relation to the observer) information about size and position. Such calculations must be carried out at the instant the action is to be performed, because the egocentric coordinates of an object rarely remain

Figure 1. Schematic representation of the dorsal and ventral streams of visual processing in the brain. The ventral stream projects to the occipito-temporal cortex, while the dorsal stream projects to the posterior parietal cortex. (Goodale and Westwood, 2004)


Posterior
parietal
cortex
Pulvinar
Superior
colliculus
Dorsal
stream
V1+
LGNd
Retina
Ventral
stream
Occipito-
temporal
cortex
Current Opinion in Neurobiology

constant over time as the observer and/or target object move in space. (e.g. Milner and Goodale, 1995; Aglioti, DeSouza, and Goodale, 1995; Milner and Goodale, 2008)

Importantly, Milner and Goodale (2008) argued that "both streams process information about the structure of objects and about their spatial locations, and both are subject to the modulatory influences of attention" (p. 774). However, the two streams gather and process information differently, efficiently serving two distinct output systems. The ventral stream serves the visuoperceptual system, and the dorsal stream aids in the visuomotor system's control of skilled actions (Milner and Goodale, 2008).

Numerous neuroimaging studies and analyses of patients with localized brain damage have provided some of the strongest support for the Goodale perception and action model (e.g., Radoeva, Cohen, Corballis, Lukovits, and Koleva, 2005; Goodale and Westwood, 2004). A particularly well-known patient, DF, has severe damage to her lateral occipital complex (LOC) in the ventral stream and suffers from visual form agnosia, an inability to identify the sizes, shapes, and orientations of objects. She is nevertheless able to accurately aim and scale grasping movements and shows relatively normal activation in the anterior intraparietal sulcus (AIP), an important part of the dorsal stream (Goodale and Westwood, 2004; Goodale, 2008). Conversely, other studies have investigated the effect of dorsal stream damage in patients with optic ataxia. Patients with this disorder have difficulty aiming and scaling grasping movements but are frequently able to verbally describe object orientation and relative position

(Goodale and Westwood, 2004). This double dissociation in patients with specific brain damage provides evidence of the independence of the ventral stream's control of vision for perception from the dorsal stream's control of vision for action.

In 2007, Cavina-Pratesi, Goodale, and Culham used functional magnetic resonance imaging (fMRI) of intact-brain participants to examine cortical activation patterns in response to grasping and perceptual discrimination tasks, using three-dimensional objects. They found that areas in the dorsal and ventral streams were differentially activated by the two task types, with dorsal activation corresponding to grasping tasks and ventral activation corresponding to perceptual tasks. The researchers interpreted these results as providing strong evidence for the functional dissociation of the dorsal vision for action and ventral vision for perception streams in the brain (Cavina-Pratesi et al., 2007).

Illusion Research

A large body of research has explored the existence of two separate visual systems in neurologically intact individuals, much of it using three-dimensional versions of pictorial illusions like the Ebbinghaus, Müller-Lyer, and Ponzo illusions (see Appendix A). This research has yielded a vast array of contradictory results, and two main models (in addition to the Goodale and Milner "action-perception" model) attempt to explain the roles of the dorsal and ventral visual streams in perception and action in intact-brain participants. These models are the "common representation" model (e.g. Franz, Gegenfurtner, Bülthoff, and

Fahle, 2000; Franz, 2001; Bruno and Franz, 2009; and Franz, Hesse, and Kollath, 2009) and the "planning-control" model (Glover, 2002).

Action-perception model. By definition, size-related visual illusions trick the perceptual system into incorrect size determinations, but the existence of a separate, metrically accurate "vision for action" system as proposed by the action-perception model suggests that only perception, and not action, should be susceptible to such illusions. A number of studies have found results that support this prediction. For example, Aglioti et al. (1995) found that when participants grasped a three-dimensional disc embedded in the center of a 'Titchener circles' illusion, their maximum grip apertures (MGA) were accurately scaled to the circle's true size despite perceptual illusions revealed by manual size estimations. Maximum grip aperture, the maximum amount the hand opens during a grasp, is linearly related to the size of the target object under normal grasping conditions (Jeannerod, 1984).

A more recent study (Ganel, Tanzer, and Goodale, 2008) found evidence of a dissociation between action and perception by measuring MGA while participants grasped objects embedded in a Ponzo size-contrast illusion, in which the larger object was perceived as the shorter one and vice versa. The researchers found that "the real and apparent differences in the size of the objects had opposite effects on action (grasping) and perception (manual estimation)" (Ganel et al., 2008), in that grip was calibrated to the true size differences between the two objects, rather than the illusory sizes.

Another recent study, this one by Stöttinger, Soder, Pfusterschmied, Wagner, and Perner (2009), used a parallelogram size contrast illusion to investigate differences between grasping and estimation when the stimulus, but not hand, was visible throughout the course of the movement. The researchers found that at no point in the course of the grasping movement was the size of the grip aperture influenced by the illusory context, even though participants were strongly influenced perceptually by the illusion (as indicated by a significant effect of the illusion on manual size estimations with the thumb and index finger).

Common representation model. In contrast, some studies have found that the visuomotor system is in fact susceptible to visual illusions in grasping tasks, and in some situations is as strongly affected as the visuoperceptual system (Franz et al., 2000; Franz, 2001). Franz et al. (2000) have interpreted these results as evidence against the Goodale and Milner action-perception model; instead, they argued that vision for action and vision for perception draw upon the same internal representation of the visual world.

Franz et al. (2000) contended that some of the original studies (e.g., Aglioti et al., 1995; Haffenden and Goodale, 1998) used inappropriately matched visuomotor and visuoperceptual tasks, in that the perceptual task required the comparison of *two* objects in separate illusory contexts, while the corresponding visuomotor task required only the processing of a *single* target object and its context during a grasp. Franz (2001) argued that if the demands of the visuomotor and visuoperceptual tasks are appropriately matched, the effects of the illusion on grasping and estimation are equivalent in size.

In addition, Franz et al. (2000) argued that before comparing the size of an illusion's effects on grasping and perception, one must correct for the different sensitivities of these measures to actual variation in object size. A meta-analysis by Smeets and Brenner (1999) found that, on average, participants respond to a 1mm increase in physical size with a 0.82mm increase in MGA. Therefore, Franz et al. suggested that the size of an illusory effect on MGA should be corrected by dividing it by the slope of the response function for changes in physical size. Then, the same can be done for perceptual measures.

Franz (2003) found that perceptual measures tend to be more responsive than MGA to physical changes in size, and the perceptual response function therefore tends to have a steeper slope than the MGA response function. For instance, Franz found that the response function for manual estimation (a common perceptual measure in this area of research) generally has a slope around 1.57, while Stöttinger et al. (2009) found a manual estimation slope of 1.03. Both of these, however, are greater than the 0.82 average slope of the MGA response function. If the motor and perceptual measures were not corrected, these differing responses to real changes in size would artificially inflate the size of the perceptual illusion in comparison to the motor illusion.

For example, an early study by Daprati and Gentilucci (1997) found that the Müller-Lyer illusion significantly affected MGA both during grasping and during perception (as evaluated by manual estimation and drawing tasks). The effect of the illusion on grasping was smaller than its effect on perception, but Franz et al. (2000) argued that the direct comparison between the grasping and perceptual tasks was invalid because the illusion magnitudes were not corrected for scaling as described above. Therefore, the present study will employ Franz et al.'s (2000) illusion-correcting technique of dividing by the slopes of the response functions to more accurately compare the sizes of the motor and perceptual illusions.

Proponents of the "common representation" model have argued that the similarly-sized motor and perceptual illusions found in some studies, despite procedural and scaling corrections, suggest that rather than utilizing functionally dissociated vision-for-action and vision-for-perception pathways, humans draw on a single representation of the visual world for both action and perception (e.g. Bruno and Franz, 2009; Franz et al., 2000; Franz, 2001; and Franz, Hesse, and Kollath, 2009). Franz et al. (2009) went on to propose that the amount of visual feedback during grasping is one of the main factors that determine the presence or absence of a motor illusion. When visual feedback is available throughout a grasp, corrections to grip aperture can be made as the hand approaches the target, minimizing any apparent effect of the illusion on the visuomotor system. Therefore, Franz et al. (2009) argued, the increase in motor illusion that occurs when a delay is introduced between stimulus presentation and movement onset is due not to a shift from online dorsal control to perception-based ventral control of the movement, but rather to the lack of visual feedback for online corrections.

Planning-control model. Alternatively, Glover (2002) proposed that the widely varying effects of visual illusions on grasping can best be explained by a planning-control model, in which there is a dissociation between perception and *online control* of actions, rather than actions as a whole. He suggested that one visual representation governs the planning of actions, which can be affected by illusions because it must take the context surrounding the target object into account. However, he argued that actions themselves are controlled by a separate, online control system that can correct errors in planning as the hand approaches the target, and is therefore immune to the effects of visual illusions if visual and proprioceptive feedback are available through the course of a movement.

To test this proposal, Glover and Dixon (2002) examined more closely the temporal characteristics of the grasps of objects embedded in visual tilt and Titchener illusions. They found that, in general, an illusion initially had a large effect on grip aperture. However, its effect decreased as the participant's hand approached the target, and there was a negligible effect by the grasp's completion. While interpreting these results as support for his planning-control model, Glover (2002) acknowledged that proponents of the perception-action and common representation models also provided explanations for this "dynamic illusion effect" (p. 4) within their models' frameworks. The perception-action model explains the decrease in illusion size over the course of a grasp as a switch from ventral "perception" to dorsal "action" control, while Franz et al. (2009) also added the idea of online movement correction to their common representation model as discussed above.

Other factors that may influence grasping. Stöttinger et al. (2009) and Bruno, Bernardis, and Gentilucci (2008) have recently enumerated a number of additional factors that may influence grasping and must be carefully examined in order to avoid experimental confounds. Stöttinger et al. (2009) argued that a number of studies that have attempted to clarify the perception-action debate were not in fact experimentally valid tests of the questions at hand. For instance, the researchers claimed that a number of studies that tried to separate perception and action were confounded by the differing degrees of visual feedback available in the two conditions. In some studies, visual feedback of the hand was not available during grasping but was available during estimation (e.g. Franz et al. 2003); this was reversed in some other studies, especially those involving manual estimation in which vision of the hand was not allowed (e.g. Radoeva et al., 2005). Visual feedback was also somewhat restricted in the Radoeva et al. study, because target objects were presented near the outer periphery of the left and right visual fields, thereby limiting the online control of grasping.

In addition, Bruno et al. (2008) did a meta-analysis of a number of studies and found that in many, the effect of an illusion on the aiming of pointing movements decreased over repeated trials. This suggests that learning and attentional processes may play a role in performance, as participants learn to attend selectively to the target with which they are required to interact and to ignore its context. While this meta-analysis looked only at pointing, not grasping, studies, it is likely that learning and attention also play a role in repeated grasping trials.

Finally, Franz (2003) suggested that some of the differences in estimation and grasping illusion effects in earlier studies (e.g. Haffenden and Goodale, 1998) could be due to their use of manual estimation as a perceptual measure. Franz's

2003 study therefore compared manual estimation illusion sizes to those with standard perceptual measures like adjusting the length of a bar to match a stimulus. Franz (2003) found that there were significant differences between manual estimation and an adjustment task with regard to participants' responses to a three-dimensional version of the Ebbinghaus illusion. Without correction for scaling, manual estimation illusions were significantly larger than adjustment illusions and also significantly larger than the corresponding grasping illusions. Franz also found that there were no significant differences in illusion size between grasping and estimation by adjusting a line to match. However, he found that once the illusions were all corrected for scaling to physical differences in size, manual estimation and adjustment were not significantly different from each other, or significantly different from grasping. The current study's second experiment included both manual estimation and an adjustment estimation procedure to investigate further any differences between these two measures.

Radoeva study and its criticisms. In a recent study, Radoeva et al. (2005) found that the magnitude of the perceptual illusion when manually estimating the length of three-dimensional bars embedded in a Müller-Lyer illusion was significantly greater than the magnitude of the illusion's effect on the visuomotor system, as predicted by the perception-action model. However, participants did show small but significant visuomotor illusion effects, which is contradictory to the predictions of Goodale and Milner's perception-action model and has drawn significant attention since the paper's publication. The present set of experiments investigated two possible explanations for this finding.

One of the main criticisms of the Radoeva et al. (2005) study is that the custom-made grip aperture measuring device may have constrained finger movement significantly, and therefore affected the study's results that both action and perception were influenced by the visual illusion (Bruno and Franz, 2009). The device was a goniometer (an angle-measuring device) consisting of two thin rods attached to the thumb and index finger with metal finger-holders. The rods were both attached to a potentiometer, and their movement in relation to each other changed the resistance of the potentiometer. Thus, when a voltage was applied to the potentiometer, the output voltage changed as the thumb and index finger moved relative to each other. By monitoring the changing output voltage, the researchers could record grip aperture over the course of each grasping movement (Figure 2).

Goodale (2008) argued that this device may have restricted movement in a way that would have made it less automatic and more likely to be influenced by perceptual information from the ventral stream. The idea is that the more conscious cognitive control is required to successfully complete an action, the more likely it is that the visuoperceptual system will be called upon. This, therefore, would make such cognitively-controlled actions more susceptible to visual illusions. The kinematics of reaching and grasping movements are most commonly recorded with Optotrak (Northern Digital, Waterloo, ON, Canada) equipment, which tracks the three-dimensional position of infrared light-emitting diodes (LEDs) attached to the fingers and wrist. As demonstrated in Figure 3, configurations of Optotrak LED markers have varied considerably between

Figure 2. The recording device used by Radoeva et al. (2005). “The potentiometer at the pivot point of the two arms changed its resistance as the two arms moved relative to each other. Thus, a certain distance between the participant's thumb and index finger corresponded to a specific voltage.” (p. 1767)

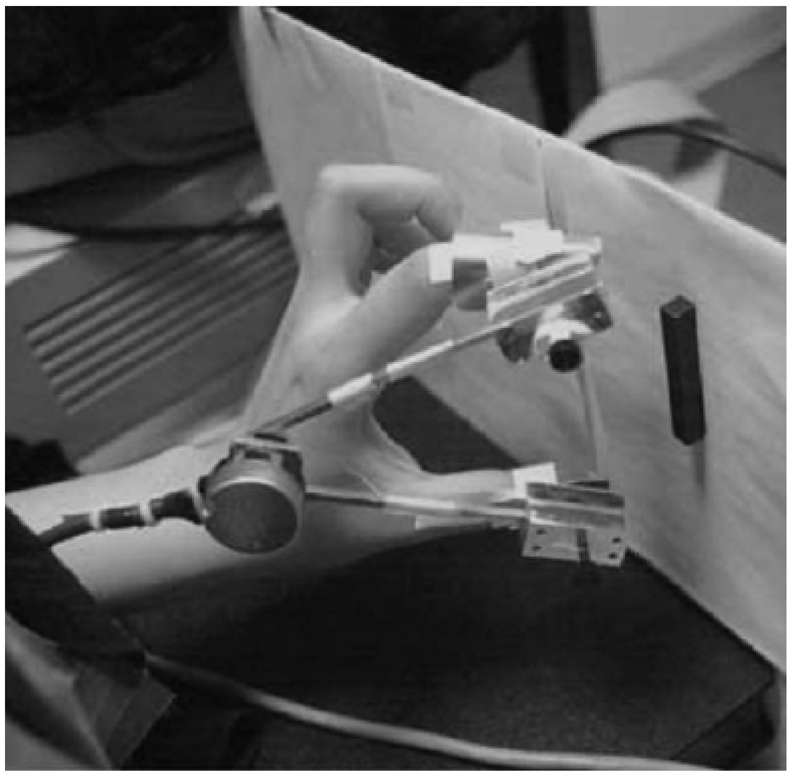
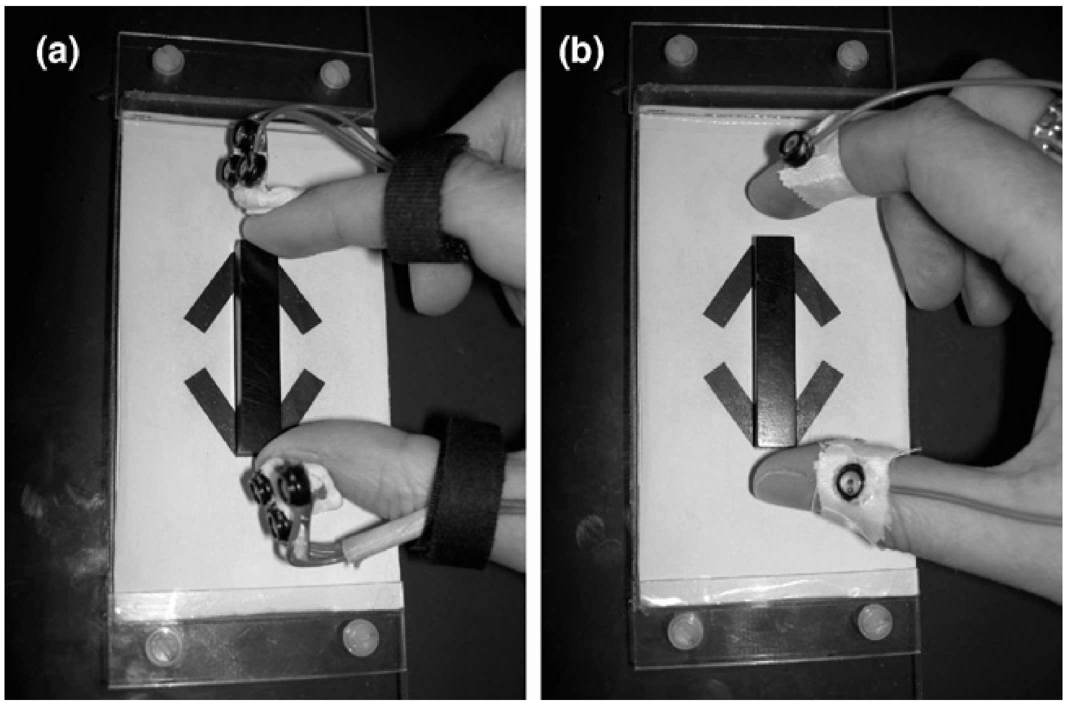


Figure 3. Optotrak (Northern Digital, Waterloo, ON, Canada) devices, with infrared light-emitting diodes attached to various points on the hand. (a) 3-marker method used by some researchers (e.g. Franz et al., 2000; Franz, Hesse, and Kollath, 2009) (b) 1-marker method in which single LEDs are attached to the index finger, thumb, and wrist, generally used in experiments by Goodale and colleagues (e.g. Aglioti et al., 1995; Goodale, 2008). Both images are from Franz, Hesse, and Kollath (2009).


(a)
(b)

experiments, with Franz and colleagues using a three-marker configuration designed to leave the finger pads free (e.g. Franz et al., 2000; Franz et al., 2009), and Goodale and colleagues using a single-marker configuration (e.g. Aglioti et al., 1995; Goodale, 2008). Goodale (2008) argued that the latter apparatus was the least constraining configuration, and that it was therefore significantly less awkward than the Radoeva et al. goniometer and less likely to disrupt online dorsal control of grasping.

Researchers tested the proposed relationship between movement automaticity and susceptibility to visual illusions in a task involving skilled (thumb and index finger) and awkward (thumb and ring finger) grasps when picking up three-dimensional bars embedded in a Ponzo illusion (Gonzalez, Ganel, Whitwell, Morrissey, and Goodale, 2008). Gonzalez et al. found that the awkward grasps were affected by the size illusion, while the skilled grasps were not. In addition, the MGAs for the awkward grasp group were significantly more variable than those for the skilled grasp group. The researchers proposed that these results suggested that the awkwardness of the thumb and ring finger grasp led to the recruitment of the ventral visuoperceptual stream in conjunction with the dorsal stream's control of the grasp.

Gonzalez et al. (2008) went on to test whether the level of automaticity of an action could be increased with practice, and whether this would result in decreased involvement of the perceptual system (ventral stream) as indicated by a reduction of the effect of the Ponzo illusion on grip scaling. Participants performed the same grasping task with the awkward grip using the Ponzo illusion, but this time over the course of three days. A reduction in sensitivity to the illusion was found within each day, and by the third day, the illusion did not have a significant effect on maximum grip aperture. Gonzalez et al. (2008) argued that this reduction in grip aperture sensitivity to a visual illusion with practice using an awkward grasp provides evidence that the more automatic an action is, the more likely that it will be controlled solely by the dorsal visuomotor system, rather than being in part under the cognitive control of the ventral visuoperceptual system. This evidence suggests that if the Radoeva et al. goniometer was in fact an awkward constraint on normal, automatic hand movement, participants would have employed greater cognitive control of their grasping actions, which could have led to a significant visuomotor illusion.

Experiment 1. To address this possibility, Experiment 1 repeated the Radoeva et al. experiment using precision grasping of three-dimensional objects embedded in the Müller-Lyer illusion, preceded by a two-day practice period with the goniometer. If the visuomotor illusion were due to device-induced awkwardness, it was predicted that there would be a non-significant effect of the illusion on grip aperture by the third day of the experiment.

Another important aspect of the Radoeva et al. (2005) study involves the differential size of the illusion effect on both hemispheres. Through their investigation of the performance of patients with unilateral brain damage, it was found that patients with left hemisphere damage who performed estimation and grasping tasks with the left hand (controlled by the undamaged right hemisphere) for stimuli presented in the left visual field showed similarly-sized grasp and estimation illusion effects. However, patients with right hemisphere damage showed a significantly larger estimation illusion effect than grasping effect when performing tasks with the right hand in the right visual field. This greater dissociation between the visuomotor and visuoperceptual performance in the left hemisphere corresponds to neuroimaging evidence that the two streams interact more in the right hemisphere. However, such a hemispheric asymmetry in the dissociation between estimation and grasping illusion susceptibility was not found in the intact-brain participants; an effect attributed to information transfer between the hemispheres via the corpus callosum. (Radoeva et al., 2005)

Gonzalez et al. (2008) also conducted an experiment to test whether practice of an awkward grasp with the left hand would yield a reduction in sensitivity to the Ponzo illusion equivalent to that found with the right hand. Interestingly, they found that while participants became faster and less variable with practice with their left hands, their grip apertures remained significantly affected by the illusion. This corresponds with their previous finding that precision grasping with the left hand in both right- and left-handed participants was susceptible to visual illusions, while grasping with the right hand was not (Gonzalez, Ganel, and Goodale, 2006). Researchers interpreted both pieces of evidence to mean that the left hemisphere contains specialized mechanisms for visuomotor control of “rapid, target-directed” (Gonzalez et al., 2006) motions, and that these mechanisms are not equally represented in the right hemisphere.

A study by Tretriluxana, Gordon, and Winstein (2008) examined the differences in grasp kinematics between the right and left hands when participants grasped cylinders of varying size. The researchers found that while MGA did not differ between the left and right hands of right-handed participants, pre-shaping of the grip aperture in response to object size occurred sooner in the left hand than in the right. In addition, there was a stronger correlation between hand movement velocity and the size of the grip aperture in the right hand, which the researchers interpreted as evidence that in right-handed individuals, "the right hand (dominant) system appears to be more important for the coordinated control of hand reaching and finger grasping" (Tretriluxana et al., 2008, p. 314). These results provide additional evidence of fundamental asymmetries in the control of grasping movements by the left and right hemispheres.

In natural settings, left-handed individuals tend to use their non-dominant (right) hands 52% of the time for grasping, while right-handed individuals use their non-dominant (left) hands only 22% of the time. This suggests that a fundamental hemispheric difference exists in the visuomotor control of grasping that is not tied to the hemispheric differences governing traditional handedness. (Gonzalez et al., 2006) Therefore, in the present study, it was predicted that if the Radoeva et al. visuomotor illusion finding was due to the awkwardness of the grip aperture measuring device, practice grasping with the device would eliminate the visuomotor illusion in the right hand, but that a significant visuomotor illusion would still be observed in the left. It was initially planned for Experiment 1 to include both right- and left-handed participants, in order to investigate the Gonzalez et al. (2006) handedness effect, but only right-handed participants were ultimately used, due to time and left-handed participant availability constraints.

Experiment 2. A second possible cause of the small Radoeva et al. visuomotor illusion is that participants maintained fixation on points 6° to the right or left of the stimuli throughout their grasping movements. This was done to present the illusion in either the right or left visual field and have it processed (at least initially) in either the left or right hemisphere, but it is possible that preventing the participants from fixating on the target, as usually occurs during grasping, may have decreased the ability of the dorsal stream to provide online control of grip scaling without the help of the ventral perceptual stream. Past research has found that participants normally fixate on contact points when grasping, and that even when an object is partially occluded where the digits will make contact, participants still fixate on those occluded positions (de Grave, Hess, Brouwer, and Franz, 2008). In addition, Schlict and Schrater (2007) found that MGA varied linearly with the eccentricity of the target from the point of fixation, suggesting that grasping is systematically affected by the degree of visual uncertainty.

Within the framework of the Goodale and Milner perception-action model, the dorsal stream is thought to calculate target size precisely, using relatively accurate estimations of eye-to-target distance and the size of the target's retinal image (Goodale, Gonzalez, and Króliczak, 2008). During a grasp, the target object is generally fixated upon (Sivak and MacKenzie, 1990), so that its image falls on the retina in a predicable location. When fixation upon the target is prevented, the dorsal stream's precise calculation of its size may therefore be disrupted, which may encourage the involvement of the ventral perceptual stream in grip aperture scaling.

Through the lens of the Franz et al. (2000) common representation model, it could be hypothesized that depriving a participant of central vision of the hand and target at the end of a grasping movement would impair the participant's ability to perform online corrections of grip scaling as the hand nears the target. Previous research has indicated that MGA generally appears at about 90% of the total distance of the grasping movement (Jeannerod, 1994), at which point the hand would generally be entering central vision during a normal, centrally-fixated grasp.

Experiment 2 therefore investigated the possibility that the position of the target 6° from fixation was enough to disrupt the automatic, online dorsal control of grasping and make grip aperture at least mildly susceptible to the illusion. Participants grasped three-dimensional Müller-Lyer illusion targets, some of which were presented at the point of fixation, and some of which were presented 6° of visual angle below it. It was expected that there would be a small visuomotor illusion when grasping an object 6° from fixation, but no visuomotor illusion when grasping an object at the fixation point. This experiment, in conjunction with Experiment 1, aimed to determine why Radoeva et al. (2005) found a small visuomotor illusion when the Goodale and Milner two-visual-systems model suggests that the dorsal stream-controlled "perception for action" system should not be susceptible to visual illusions.

This study's predictions. In summary, the goals and predictions of these two experiments were as follows. The goal of the first experiment was to determine whether the custom-made grip aperture measuring device used by Radoeva et al. (2005) awkwardly constrained movement, and (presumably due to increased involvement of the ventral vision-for-perception stream), caused a small but significant visuomotor illusion. For Experiment 1, it was therefore predicted that there would be significant estimation and grasping illusions in both hands on the first day, but that by the last day there would be significant estimation and grasping illusions in the left hand, and a significant estimation illusion in the right hand, but no significant grasping illusion in the right hand. For Experiment 2, it was predicted that, within the two different perceptual measures, manual estimation would show a larger mean illusion magnitude than adjustment of a bar on a computer screen. In addition, it was predicted that the grasping illusion would be significantly greater when participants fixated eccentrically than when they fixated on the center of the stimulus.

METHOD

Participants

Twelve female Mount Holyoke College students, ages 18 to 22, participated in Experiment 1, and twelve participated in Experiment 2. All participants were right-handed, as assessed by the Edinburgh Handedness Inventory (EHI) (Oldfield, 1971).

All subjects had normal or corrected-to-normal vision, and provided written consent before participating in the study. Participants in Experiment 1 received three research participation credits or entry into a raffle for $50 for their participation, and participants in Experiment 2 received one research participation credit or entry into a raffle for $15. All procedures were approved by the Mount Holyoke College Institutional Review Board.

Apparatus and Stimulus Materials

Each participant was seated at a table with a chin rest directly in front of her and a metal stimulus stand positioned so that the distance from the participant's eyes to the stimuli was approximately 57 cm. The chin rest could be adjusted in height to be comfortable for each participant, but the visual distance was not significantly affected by such adjustments. The overhead lights in the room were turned off, and the sole lighting was provided by two floor lamps placed approximately 1 m apart and centered about 2 m behind the participant. This lighting arrangement was designed to eliminate the appearance of shadows from the stimulus bars, which might otherwise have affected participants' perceptions of stimulus length.

Similar to the stimuli used by Radoeva et al. (2005), this study's Müller-Lyer stimuli were constructed from black wooden bars (6.0 cm x 0.8 cm x 0.8 cm) secured lengthwise over the central shafts of two-dimensional drawings of open and closed versions of the Müller-Lyer illusion (see Figure 4 for sample stimuli). The illusion drawings were black, with 2.7 cm x 0.8 cm arrowheads forming 30° angles with the central three-dimensional shafts. In addition, control stimuli consisted of three-dimensional black bars taped to white paper, 0.8 cm x 0.8 cm in cross-section, with lengths of 4.0 cm, 6.0 cm, and 8.0 cm. All stimuli were mounted and centered on stiff white cards 7.0 cm by 11.0 cm in size.

Participants' movements in the grasping and estimation tasks were measured with respect to the distance between their thumb and index fingers by a modified version (Figure 5) of the Radoeva et al. (2005) goniometer-like device. The device consisted of a potentiometer at the pivot point of two aluminum arms, which were attached to participants' thumbs and index fingers with rubber band loops. The resistance of the potentiometer varied with the angle between the two arms. When 12V of power was supplied, the output voltages corresponded to specific distances between the two fingers. During each trial, voltages were sampled at a rate of 1000 Hz by a LabView program and monitored by a computer, via a National Instruments Data Acquisition Card.

Before and after the two blocks of trials for each hand, the device was calibrated as described in Mahajan (2006) to determine the individual voltage/thumb-forefinger distance relationship for each participant. In the

Figure 4. The Müller-Lyer illusion stimuli. The top figure is the “open” Müller-Lyer figure, and the bottom is the “closed” figure.

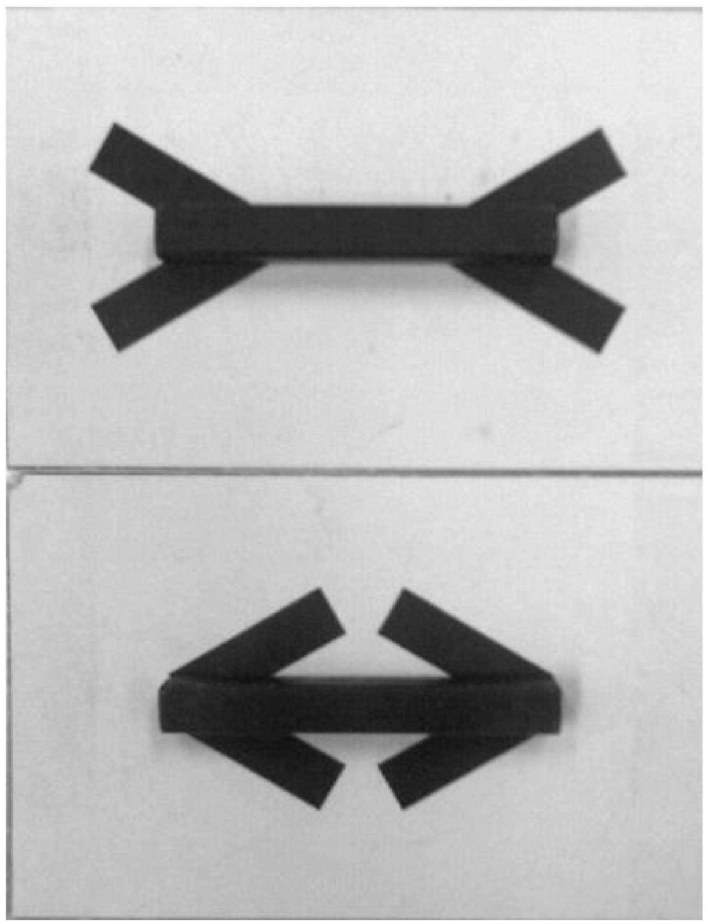
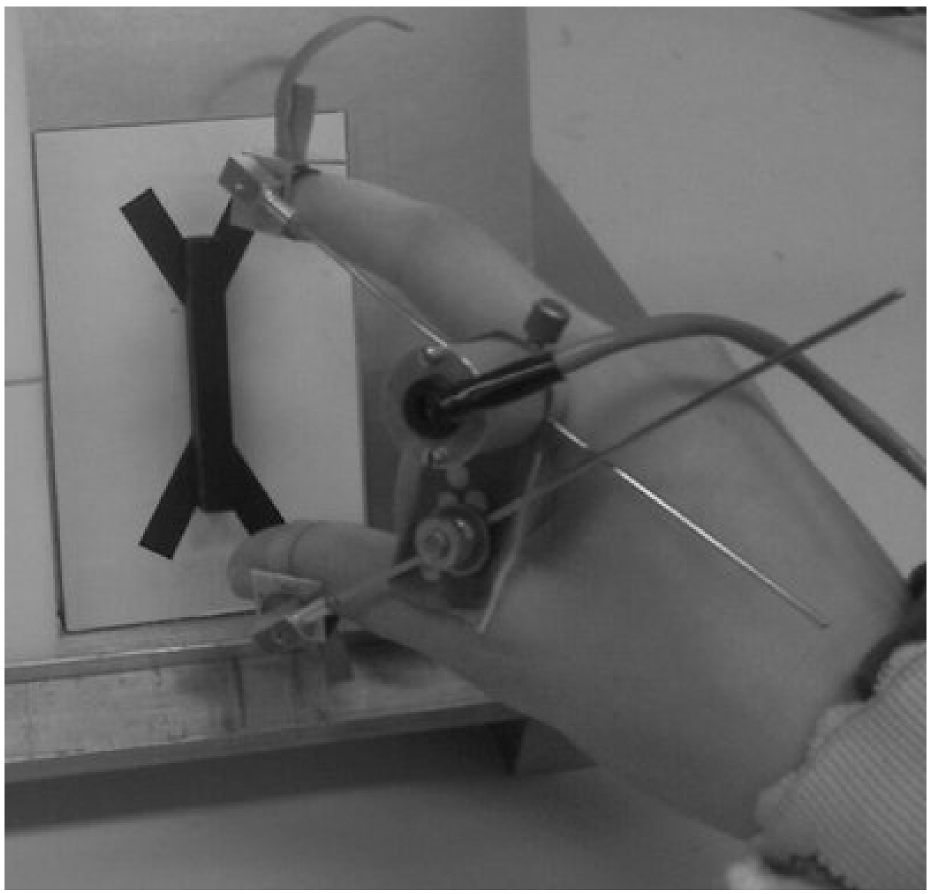


Figure 5. Our modified version of the recording device used by Radoeva et al. (2005). Like the original device, this device consists of a potentiometer, 12V power supply, two aluminum arms (thinner than on the Radoeva et al., 2005 device) and two finger-holders (now rubber bands). The voltage through the potentiometer was monitored by a computer via a National Instruments Data Acquisition Card (NI-DAQ-1200).



calibration procedure, each participant grasped a series of black bars (0.8 cm x 0.8 cm in cross-section), ranging from 2.0 to 10.0 cm in length in 1.0 cm increments. Calibration bars were attached to narrow white strips of plastic, and arranged in ascending order on the stimulus stand (Figure 6). During the calibration procedure, participants grasped each bar lengthwise in ascending order (beginning with the 2.0 cm bar) three times in total. Voltage was sampled for 1000 ms while the participant held each bar, and then graphed as a function of bar length. A third degree polynomial function was fit to each calibration data set in order to convert the voltages recorded during each grasp and estimation trial to accurate distance measurements (Figure 7), as in Radoeva et al. (2005).

Procedure

Experiment 1. The goal of this experiment was to determine whether the custom-made grip aperture measuring device used by Radoeva et al. (2005) awkwardly constrained movement, and (presumably due to increased involvement of the ventral vision-for-perception stream), caused a small but significant visuomotor illusion. To test whether practice grasping with the recording device eliminated any grasping illusion, this experiment took place over the course of three consecutive days, with participants doing visuomotor and visuoperceptual tasks in response to three-dimensional objects embedded in Müller-Lyer illusions each day. It is important to note that this study's grip aperture measuring device (Figure 5) was a modified version of the original 2005 device (Figure 2), and was a bit lighter and had thinner arms than the original, and may therefore have been less constraining than the original device.

Figure 6. Calibration bar setup for experiments 1 and 2. Bars ranged in size from 2.0 cm to 10.0 cm.

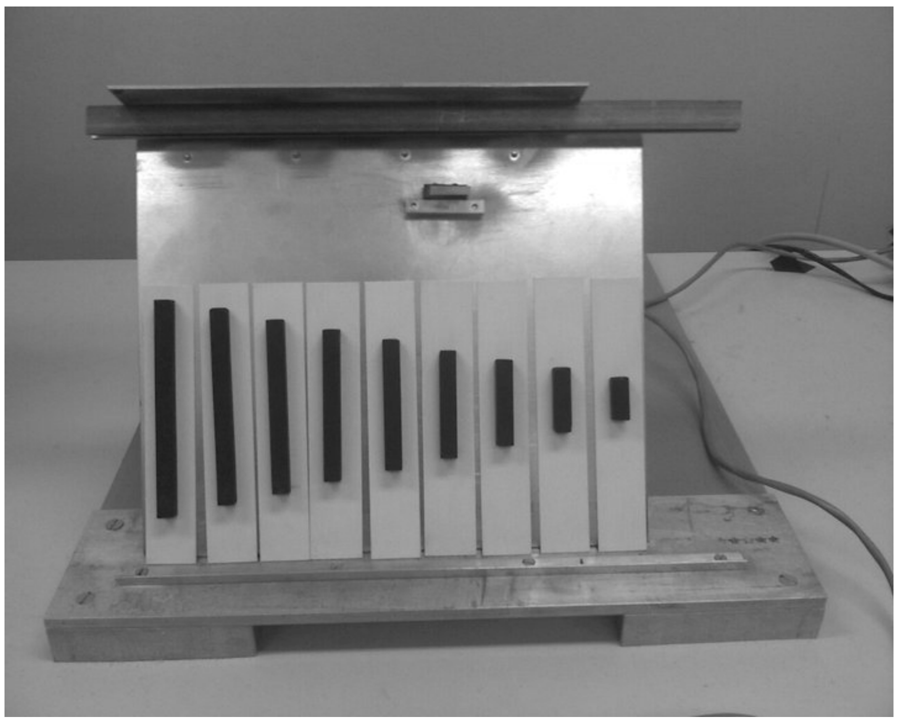
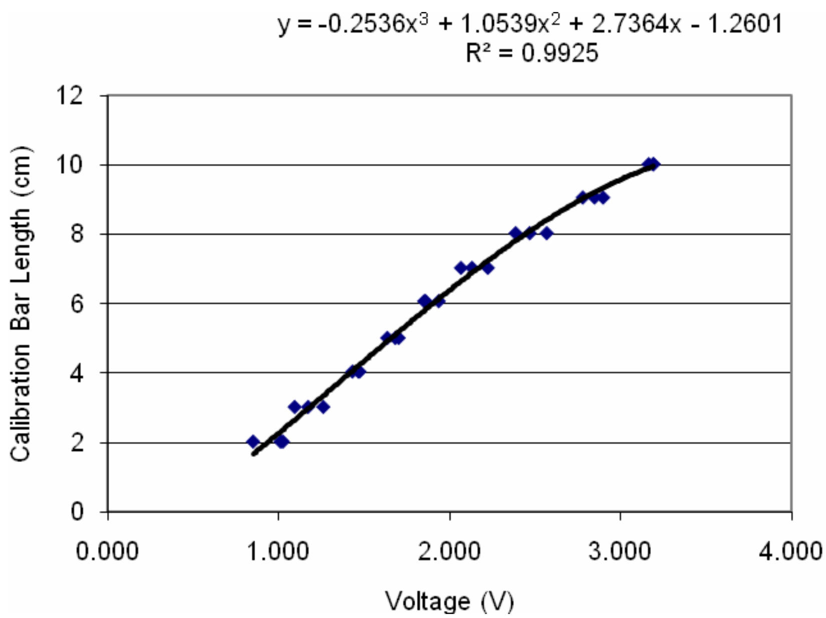


Figure 7. Sample graph of the data for a single calibration. Each length of bar was grasped three times total, and a third degree polynomial was fit to the curve to generate an equation translating voltage to distance for that individual participant.


y = -0.2536x3 + 1.0539x2 + 2.7364x - 1.2601
R² = 0.9925
Calibration Bar Length (cm)
Voltage (V)
0.000
1.000
2.000
3.000
4.000
0
2
4
6
8
10
12

Participants completed a total of 80 trials each day, divided into four blocks of 20. A grasping block and an estimation block were completed with each hand, and the order of these blocks was counterbalanced across participants. Each block consisted of 20 trials in random order; seven with the open Müller-Lyer illusion, seven with the closed Müller-Lyer illusion, and two with each of the three lengths of control bar (4.0, 6.0, and 8.0 cm). Participants performed grasps and estimations of the control stimuli intermixed with the illusion stimuli to provide individual scaling data that reflected participants' responses to physical changes in stimulus size. The following is a sample experimental session: right hand calibration 1, right hand grasping, right hand estimation, right hand calibration 2, left hand calibration 1, left hand estimation, left hand grasping, left hand calibration 2.

Between trials, each participant was instructed to keep her eyes closed, chin on the chin rest, and index finger and thumb together. During the grasping trials, she was additionally instructed to use those two fingers to press down on a metal button embedded in a wooden platform on the table directly on the other side of the chin rest. While the participant's eyes were closed, one of the researchers set up the stimulus on the stand, and slid the white plastic shield on its track to cover the stimulus. The shield had a narrow slit cut from it horizontally, and the participant was instructed to open her eyes and fixate on the small, black central part of the stimulus bar visible through the slit. She was cued to begin each trial by the sliding of the white shield to reveal the entire stimulus bar (Figure 8).

Figure 8. The Experiment 1 setup. The white shield was pulled to the left to reveal, in this case, the “open” stimulus. (The lighting in this picture is not the same as it was during the experiment.)

Grasping procedure. In each grasping trial, the participant then grasped the three-dimensional bar by its long axes, lifted it from the stimulus stand, and placed it on the table in front of her. A millisecond timer began when the stimulus was completely revealed and stopped when the participant lifted her hand off the button to begin reaching for the bar, and therefore measured the amount of time between stimulus presentation and movement onset.

Each participant performed a minimum of two practice grasps of the 6.0 cm control bar before beginning the blocks of experimental trials, and the researchers observed the grasps closely to make sure that they were fluid and did not involve irregular movements like keeping the fingers together until reaching the stimulus or opening and closing the fingers during the movement of the hand toward the stimulus. Additional practice trials were given until the participants felt comfortable with the procedure, but never exceeded four in total.

Estimation procedure. In the estimation trials, each participant approximated the lengths of the three-dimensional stimulus bars, not including the arrow heads, by keeping her hand off to the side (outside her visual field) and opening her thumb and index finger to her best estimation of the bar's length. She was instructed to keep her fingers open to her final estimation until the experimenter indicated that sampling was complete. This estimation procedure was modeled after the manual estimation procedure used in a number of previous studies (e.g. Haffenden & Goodale, 1998; Radoeva et al., 2005).

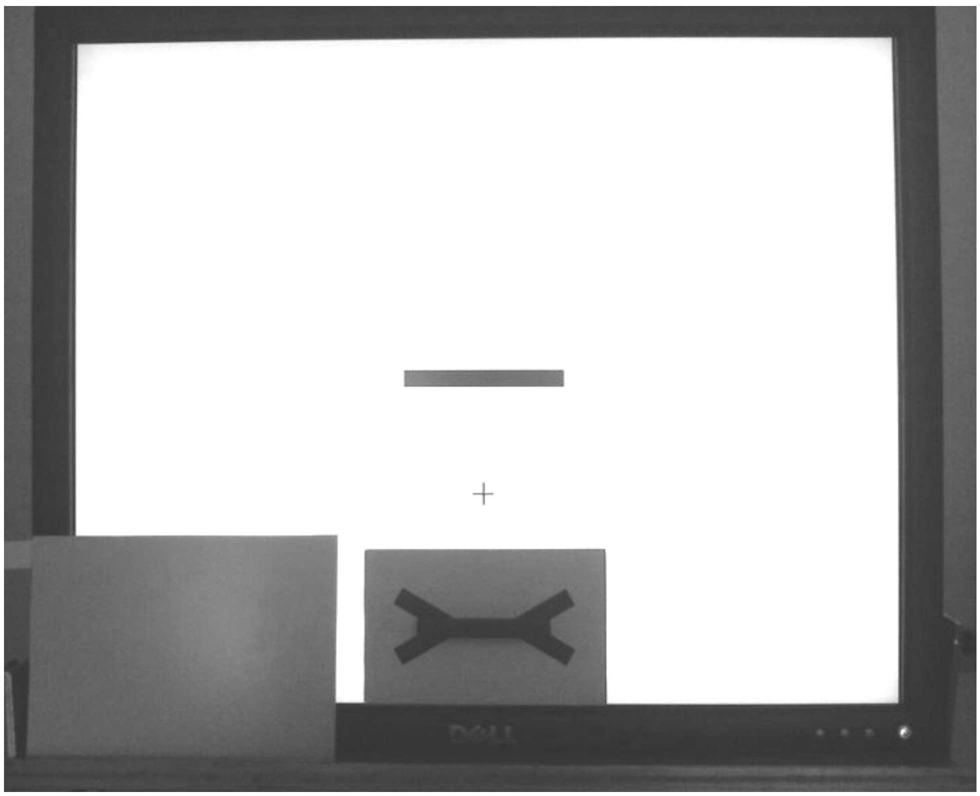
This procedure was repeated for three consecutive days with each participant, with the order of trials and blocks the same each day for a given participant.

Experiment 2. The goal of this experiment was to assess whether the visuomotor illusion was greater in magnitude when the Müller-Lyer stimulus was 6° of visual angle below the fixation point (eccentric condition) than it was when the participant fixated on the stimulus itself (centered condition). In addition, the experiment investigated whether there were any differences in illusion size between finger estimations as described in Experiment 1 and estimation by adjusting the length of a bar on a computer screen to match the stimulus.

The stimulus cards (the same as those used in Experiment 1) were centered on the bottom of a computer screen and oriented horizontally on all trials. The horizontal orientation ensured that both ends of the stimulus bar were equidistant from the fixation point in the eccentric condition, that the bar was presented equally to the right and left visual fields, and that the participant did not disrupt her fixation on the fixation point by reaching in front of it while grasping.

In the centered condition, the adjustment bar was displayed 6° of visual angle above the stimulus, measured from the center of the stimulus to the center of the adjustment bar. In the eccentric condition (Figure 9), the stimulus was placed in the same location, and a fixation cross was displayed 6° of visual angle above the stimulus, with the adjustment bar 6° of visual angle above that. In the centered condition, participants were instructed to fixate on the center of the

Figure 9. Experiment 2 “eccentric fixation” condition setup. Participants fixated on the black fixation cross through the trial’s entire duration. The white shield was pulled to the left to reveal, in this case, the “open” illusion stimulus. On computer adjustment trials, the black bar on the screen above the fixation cross was adjusted to match the illusion stimulus bar in length.



stimulus bar throughout each trial, and in the eccentric condition, participants were instructed to maintain fixation on the fixation cross throughout each trial.

Experiment 2 consisted of a total of 120 trials, divided into six blocks of 20. Using her right hand only, each participant completed a grasping block, finger estimation block, and computer estimation block in both the eccentric and centered conditions. The order of blocks was counterbalanced across participants, and each block consisted of 20 trials as described in Experiment 1. The device was calibrated at the beginning, middle, and end of each experimental session to take into account any shifting of the device on the hand during the experiment. As in Experiment 1, the device was calibrated after every two blocks requiring its use (grasping and finger estimation).

The following is a sample sequence of conditions for an experimental session: calibration 1, then centered finger estimation block, centered grasping block, centered computer estimation block, calibration 2, eccentric grasping block, eccentric computer estimation block, eccentric finger estimation block, and finally calibration 3. As this example demonstrates, the three trials in each eccentricity condition were grouped together, but the order of the eccentricity conditions (centered or eccentric) was varied randomly across participants.

Grasping and finger estimation procedures. The grasping and finger estimation procedures were identical to those used in Experiment 1, except participants did not have to hold a button down before movement onset as they did in the Experiment 1 grasping trials.

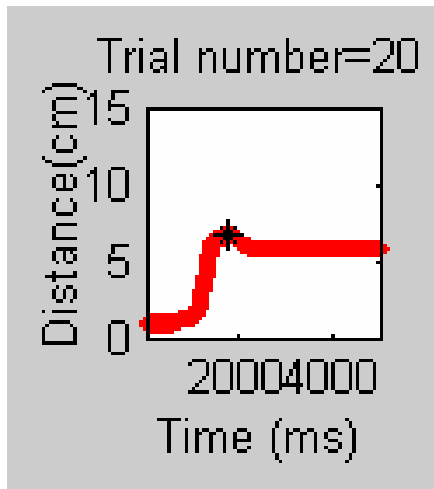
Computer estimation procedure. The initial length of the computer estimation adjustment bar on the screen varied randomly between small, medium, and large lengths on each trial (3.3, 5.1, and 7.3 cm), and the adjustment bar was displayed during all blocks to keep visual conditions constant. In each computer estimation trial, a participant could adjust the bar's length using the '1' and '2' keys on a keyboard, and then enter her final estimation using the 'e' key. The computer estimation program was written in MATLAB, using the Psychophysics Toolbox extensions (Brainard, 1997; Pelli, 1997).

Data recording and analysis

For all but the computer estimation trials, distance between the thumb and index finger was recorded for five seconds beginning slightly before the stimulus was revealed, and the change in voltage over time was later translated to distance and graphed using a custom MATLAB program. For finger estimation trials, the estimated distance was measured as the distance between the fingers at the end of the five-second sampling period. For grasping trials, maximum grip aperture was measured as the maximum distance between the thumb and index finger from the start of the trial to the time the distance plateaued when the bar was held (see Figure 10 for sample grasp plot). For each participant, results from equivalent trials within each block were averaged.

The size of the illusion was calculated as the mean of the MGA or estimation distances in the open illusion minus the mean of the MGA or estimation distances in the closed illusion as in Radoeva et al. (2005). Regression lines were then fit to the scaling data to determine how accurately participants

Figure 10. Graph of the change in distance between the fingertips over time during a grasping trial, produced by the custom MATLAB program. The asterisk indicates the maximum grip aperture for this trial, the measure that was used in assessments of illusion magnitude.


Trial number=20
Distance(cm)
15
10
5
0
20004000
Time (ms)

scaled their grasps and estimations to the control stimuli, and the slopes of the resulting regression fit lines were used as individual scaling factors for each participant. Each participant's uncorrected grasping and estimation illusions were divided by the corresponding scaling factors in order to calculate corrected illusions (as in Franz et al., 2001).

SPSS Statistics 17.0 (SPSS, Inc., Chicago, IL) statistical software was used for all statistical analyses, with an alpha level of .05 on all tests.

RESULTS

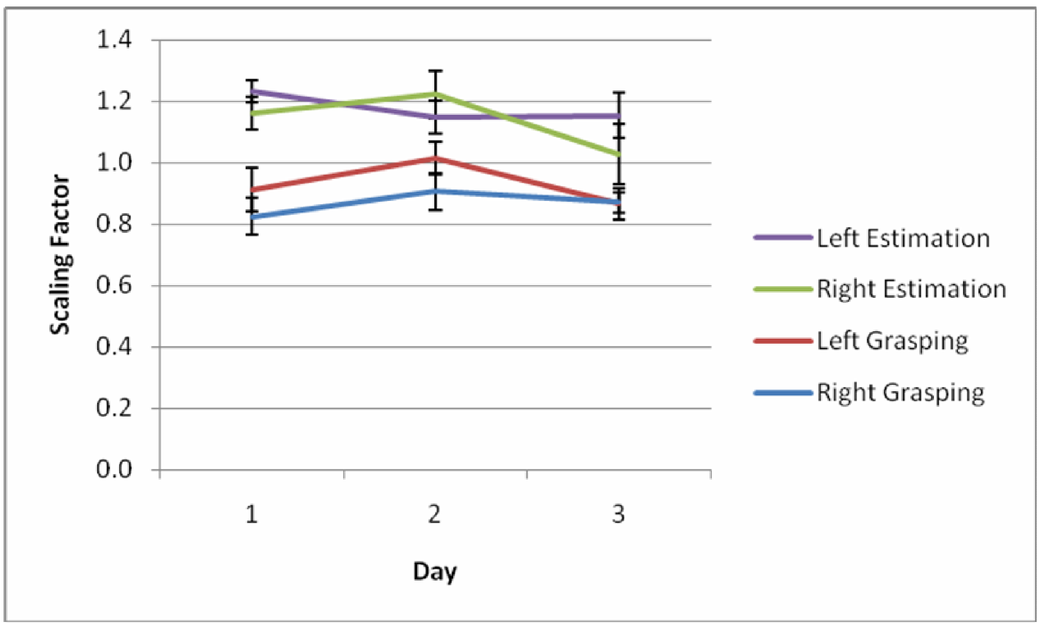
Experiment 1

Data were missing for Participant 12 Day 1 right grasping and Participant 3 Day 2 right estimation, so participants 12 and 13 were initially excluded from all ANOVAs. Then, each missing data point was replaced with fitted values determined by SPSS (SPSS, Inc., Chicago, IL), so that all 12 participants could be included in the analyses.

As described previously, each block contained six grasps or estimations of the three control bars (4, 6, and 8 cm). The responses to these control bars were plotted against their true lengths and regression lines were fit to the data from each block to find scaling factors, in order to reflect participants' responses to true differences in size. Figure 11 depicts the mean scaling factors across participants for the three days in the right grasping, left grasping, right estimation, and left estimation blocks.

A 2 (Hand: Right, Left) x 2 (Task: Grasping, Estimation) x 3 (Day: 1, 2, 3) repeated measures ANOVA of the scaling factor data revealed that there was a significant main effect of task, $F(1) = 24.375$, $p < 0.001$, with scaling factors significantly larger in the estimation blocks ($M = 1.156$, $SE = .037$) than in the grasping blocks ($M = .899$, $SE = .028$). There was no main effect of day, $F(2) = 2.837$, $p = .080$, no main effect of hand, $F(1) = 3.186$, $p = .102$, nor any significant interactions between hand and task $F(1) = .008$, $p = .929$, hand and day, $F(2) = .420$, $p = .663$, day and task, $F(2) = 2.865$, $p = .083$, or day, hand, and task, $F(2) = 1.526$, $p = .244$.

Figure 11. Change in average scaling factor (slope of control bar response function) for each block over 3 days, averaged across all 12 participants (±SE). There was a significant main effect of task, $F(1) = 24.375$, $p < 0.001$, with scaling factors significantly larger in the estimation blocks ($M = 1.156$, $SE = .037$) than in the grasping blocks ($M = .899$, $SE = .028$).



1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Scaling Factor
1
2
3
Day
Left Estimation
Right Estimation
Left Grasping
Right Grasping

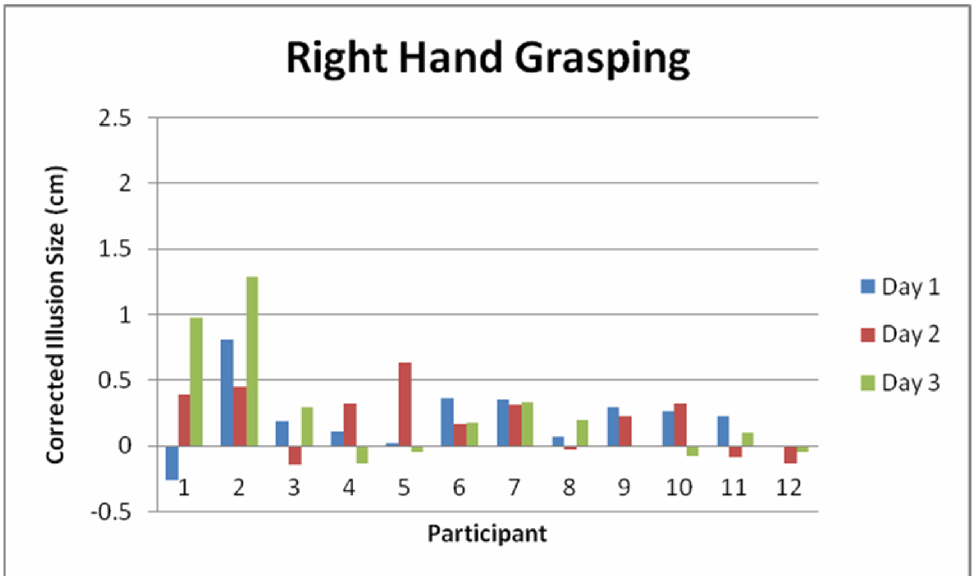
Control bars were interspersed with the illusion stimuli in each block, so each block for each participant had its own scaling factor and illusion size. Because the slopes of the response functions were significantly different for grasping and estimation across participants, and therefore show that participants' grasps and estimates did not respond equally to physical variations in stimulus size, they were used as scaling factors to calculate "corrected" illusion sizes for all blocks. All further analyses were then performed on these corrected illusion data.

Figure 12 (grasping) and Figure 13 (estimation) depict the individual corrected illusion sizes for each participant over all three days of the experiment. The figures show that there was a great deal of variation in how illusion sizes changed over the days for each individual participant and block.

To determine whether the corrected visuomotor and visuoperceptual illusions were significantly different from zero, one-sample *t*-tests (with test value = 0) were performed on the corrected illusion data for each of the four blocks on each day. As shown in Figure 14, on the first day all but the left grasping illusion were significantly different from zero. On the second day, all four blocks (right and left grasping, and right and left estimation) yielded significant corrected illusions. On the third day, a significant illusion was present only in the left estimation block; the right grasping, left grasping, and right estimation illusions were all non-significant.

A 2 (Hand: Right, Left) x 2 (Task: Grasping, Estimation) x 3 (Day: 1, 2, 3) repeated measures ANOVA was used to examine how the corrected visuomotor and visuoperceptual illusions changed with practice over the three days, and

Figure 12. Individual participant corrected illusion sizes in right and left hand grasping blocks over all 3 days.


Right Hand Grasping
Corrected Illusion Size (cm)
2.5
2
1.5
1
0.5
0
-0.5
1
2
3
4
5
6
7
8
9
10
11
12
Participant
Day 1
Day 2
Day 3

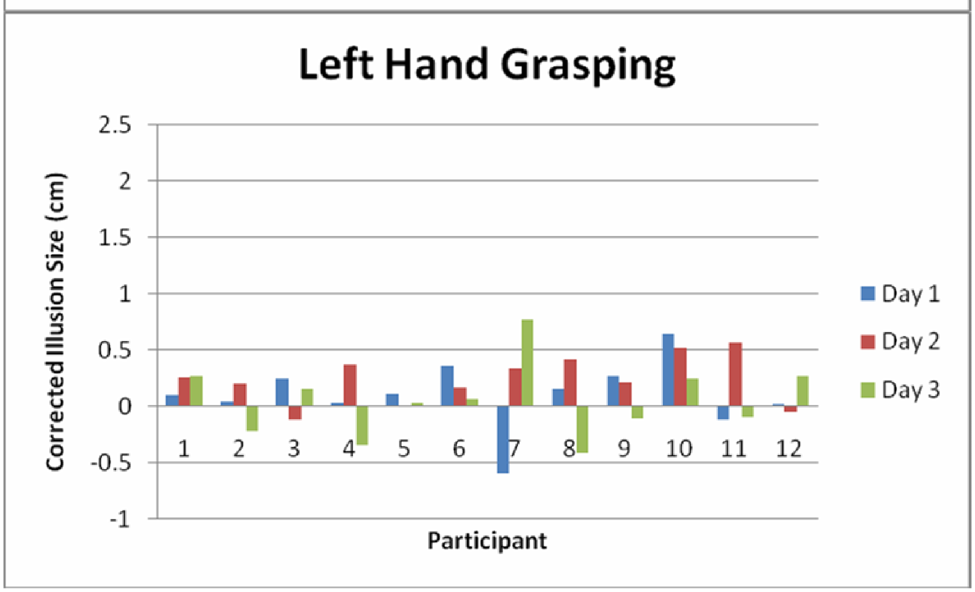
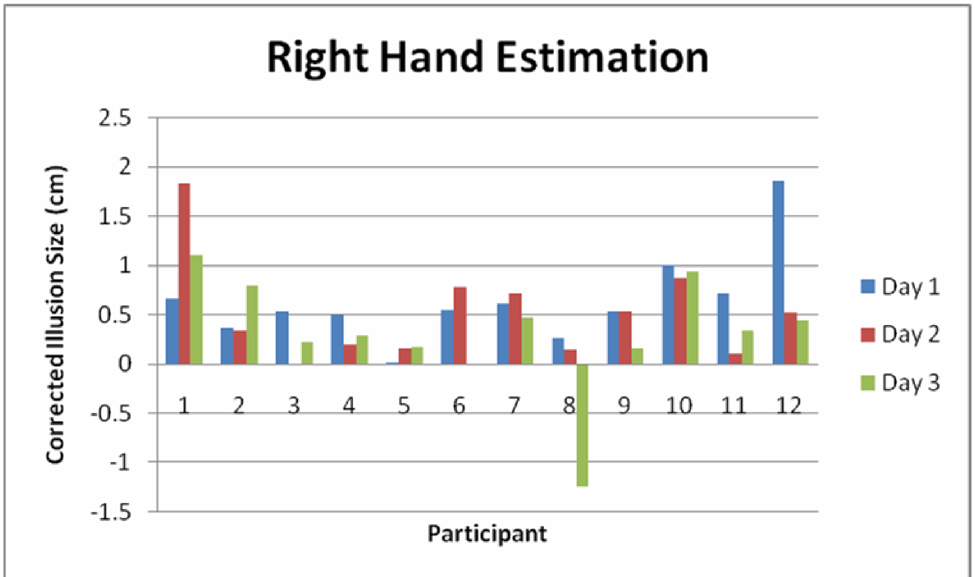

Left Hand Grasping
Corrected Illusion Size (cm)
2.5
2
1.5
1
0.5
0
-0.5
-1
1
2
3
4
5
6
7
8
9
10
11
12
Participant
Day 1
Day 2
Day 3

Figure 13. Individual participant corrected illusion sizes in right and left hand estimation blocks over all 3 days.


Right Hand Estimation
Corrected Illusion Size (cm)
2.5
2
1.5
1
0.5
0
-0.5
-1
-1.5
1 2 3 4 5 6 7 8 9 10 11 12
Participant
Day 1
Day 2
Day 3

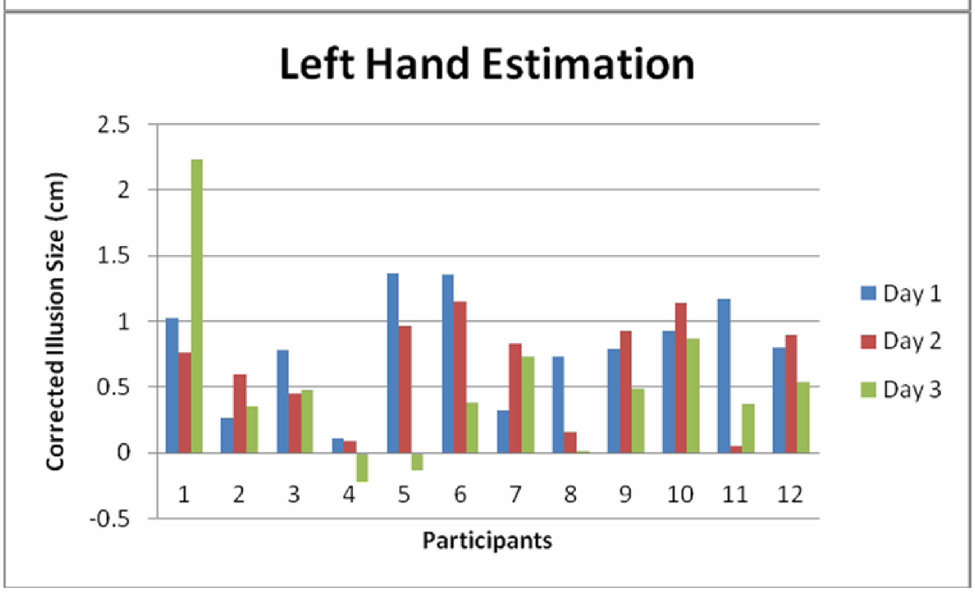
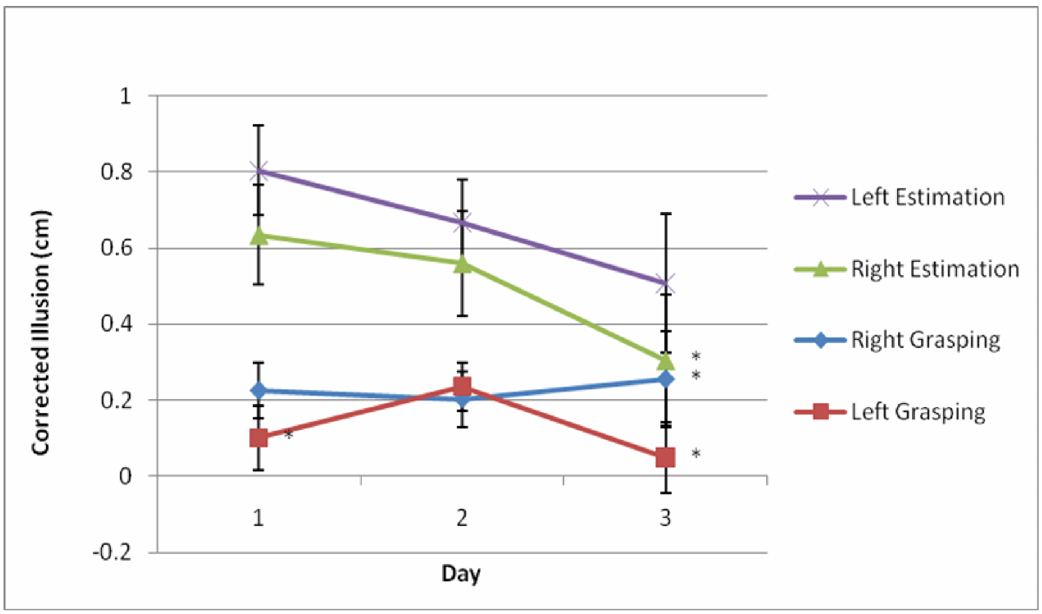

Left Hand Estimation
Corrected Illusion Size (cm)
2.5
2
1.5
1
0.5
0
-0.5
1 2 3 4 5 6 7 8 9 10 11 12
Participants
Day 1
Day 2
Day 3

Figure 14. Change in corrected illusion size over three days in the right and left hands in grasping and estimation tasks (±SE). Asterisks denote data points that are *not* statistically significantly different from zero.



1
0.8
0.6
0.4
0.2
0
-0.2
Corrected Illusion (cm)
1
2
3
Day
*
*
*
*
Left Estimation
Right Estimation
Right Grasping
Left Grasping

whether those changes were significantly different between the left and right hands. With data from two participants excluded due to missing data as previously described, this analysis revealed a significant main effect of task, with the mean estimation illusion (M = .579 cm, SE = .098) significantly larger than the mean grasping illusion (M = .175 cm, SE = .036), $F(1) = 14.096$, $p = .005$. In addition, there was a significant hand by task interaction, $F(1) = 7.142$, $p = .026$, in that the difference between grasping and estimation illusion sizes was significantly greater in the left hand (.529 cm) than the right (.278 cm) (Figure 15).

The missing data were then replaced with fitted values determined by SPSS (SPSS, Inc., Chicago, IL), and the 2 (Hand: Right, Left) x 2 (Task: Grasping, Estimation) x 3 (Day: 1, 2, 3) repeated measures ANOVA was repeated. As before, there was a main effect of task, $F(1) = 21.104$, $p = .001$, with the mean estimation illusion (M = .579 cm, SE = .098) .40 cm larger than the mean grasping illusion (M = .179, SE = .035). As depicted in Figure 16, there was also a hand by task interaction, because the difference between the grasping and estimation illusion sizes was greater in the left hand (.529 cm) than in the right (.272 cm), $F(1) = 5.724$, $p = .036$.

In addition, this data from all 12 participants contained a day by task interaction, $F(2) = 3.463$, $p = .049$, which is shown in Figure 17. The size of the estimation illusion decreased more rapidly over the three days than did the size of the grasping illusion. This is evidenced by a nearly significant main effect of day on the estimation blocks, $F(2) = 3.199$, $p = .060$. On day 3, there was no overall grasping illusion (M = .152 cm, SE = .08), as indicated by a one-sample t-test with

Figure 15. Corrected illusion sizes for the estimation and grasping blocks for each hand (±SE), collapsed across days. These means do not include fitted values for missing data. The hand by task interaction was significant, $F(1) = 7.142$, $p = .026$; the size difference between the grasping and estimation illusions was greater in the left hand (.529 cm) than the right (.278 cm).

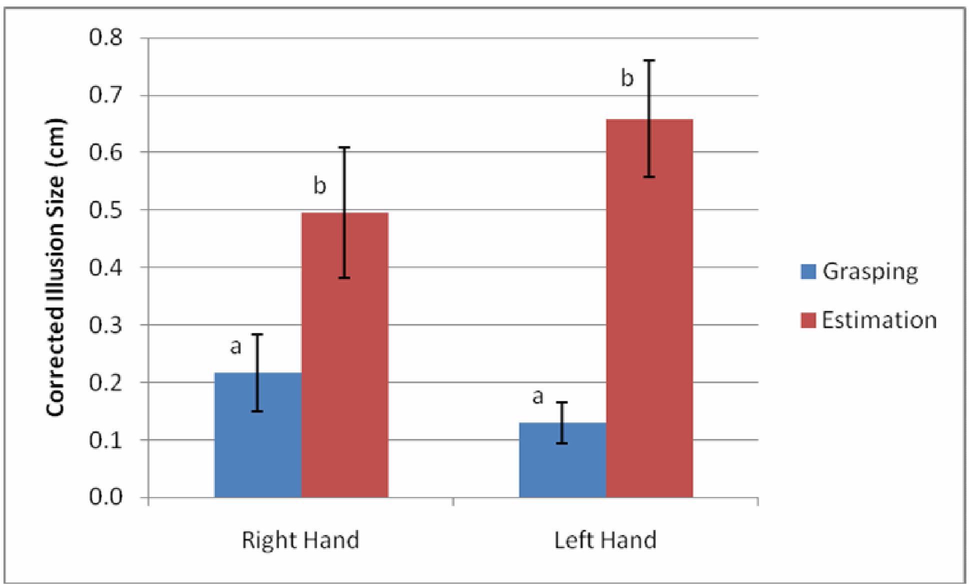

Corrected Illusion Size (cm)
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
a
b
a
b
Right Hand
Left Hand
Grasping
Estimation

Figure 16. Hand by task interaction, with missing data replaced with fitted values (±SE). The hand by task interaction was significant, $F(1) = 5.724$, $p = .036$, in that the size difference between the grasping and estimation illusions was greater in the left hand (.529 cm) than in the right (.272 cm). All means in this figure were significantly different from zero.

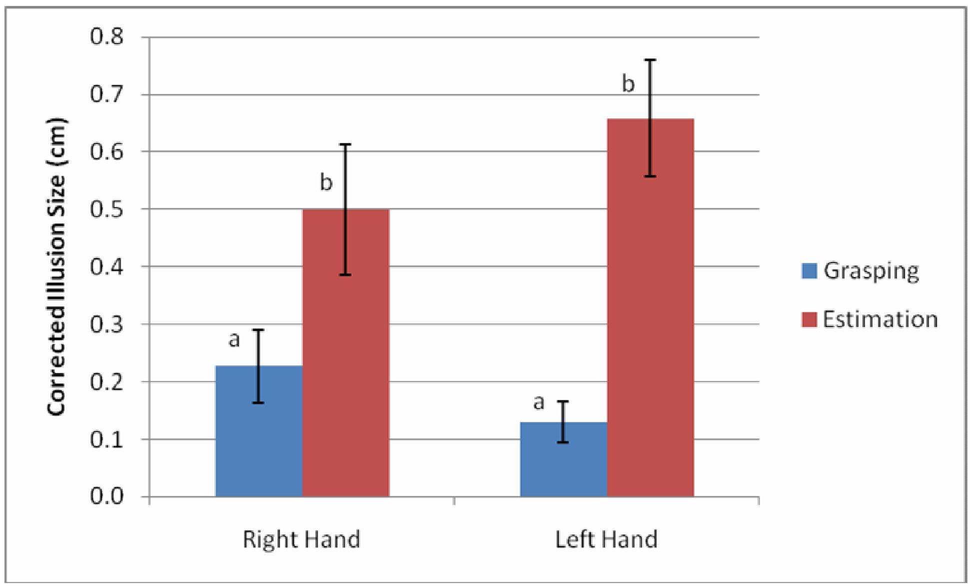
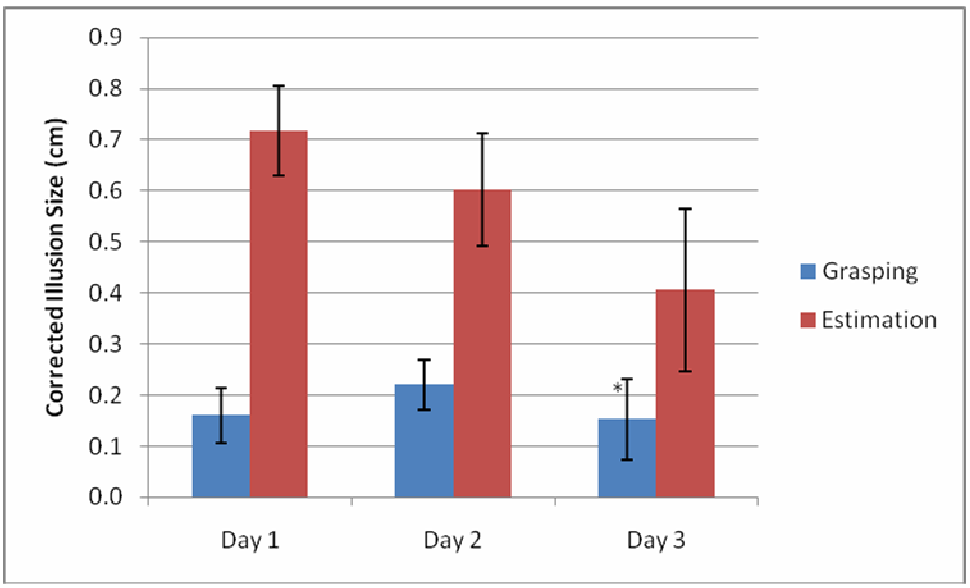

0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Corrected Illusion Size (cm)
a
b
a
b
Right Hand
Left Hand
Grasping
Estimation

Figure 17. Day by task interaction (±SE). The size of the difference between the grasping and estimation illusions decreased over days, because the size of the estimation illusion decreased much more rapidly over the three days than the size of the grasping illusion. The asterisk on Day 3 grasping indicates the only block with no significant difference from zero.


Corrected Illusion Size (cm)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
Day 1
Day 2
Day 3
*
Grasping
Estimation

a test value of zero, $t = 1.903$, $p = .083$. Additionally, a series of paired-sample t-tests confirmed that the estimation and grasping illusion sizes were significantly different on Day 1 ($p < .001$) and Day 2 ($p = .005$), but only marginally significantly different by Day 3 ($p = .051$).

Most previous illusion studies, unless specifically looking at laterality and handedness differences, have tested grasping and estimation only in the right hand in right-handed participants. Therefore, in order to better compare the results of this study to previous results, a 3 (Day: 1, 2, 3) by 2 (Task: Grasping, Estimation) repeated measures ANOVA was run using only the data from the right hand blocks. This analysis revealed a main effect of task, $F(1) = 5.205$, $p = .043$, with the estimation illusions significantly larger than the grasping illusions. However, there was no main effect of day ($p = .446$) or interaction between day and task ($p = .095$).

The amount of time (in milliseconds) between stimulus presentation and initiation of grasping movement was also recorded for each grasping trial, and average response times were therefore calculated for each participant on each day with each hand. A 3 (Day: 1, 2, 3) x 2 (Hand: Right, Left) repeated measures ANOVA showed neither a main effect of day ($F(2) = .784$, $p = .469$) nor a main effect of hand ($F(1) = .144$, $p = .712$) on reaction time, nor a significant interaction between day and hand ($F(2) = 1.646$, $p = .216$).

Experiment 2

The data was corrected for scaling as described in experiment 1, and all analyses were performed on this corrected data. Again, an alpha level of .05 was used for all statistical tests.

First, one-sample *t*-tests (test value = 0) were used to determine whether the corrected visuomotor and visuoperceptual illusions in each eccentricity condition were significantly different from zero. As shown in Figure 18, all but the centered grasping block yielded significant illusions.

A 3 (Task: Grasping, Finger Estimation, Computer Estimation) x 2 (Eccentricity: Eccentric, Centered) repeated measures ANOVA was used to determine whether the relative sizes of the visuomotor and visuoperceptual illusions were different when the participant was instructed to fixate on a point 6° of visual angle from the stimulus than when the participant fixated on the stimulus itself. As depicted in Figure 19, this analysis revealed a main effect of task, $F(2) = 6.837$, $p = .005$, with significant differences between grasping ($M = .220$ cm, $SE = .112$) and finger estimation ($M = .992$ cm, $SE = .176$, $p = .041$), and grasping and computer estimation ($M = .640$ cm, $SE = .096$, $p = .004$), but not between finger estimation and computer estimation ($p = .592$). There was no main effect of eccentricity and no interaction between eccentricity and task.

Figure 18. Mean corrected illusion sizes for all six blocks (±SE). The asterisk indicates that centered grasping was not statistically significantly different from zero, but the other blocks all yielded significant illusion effects.

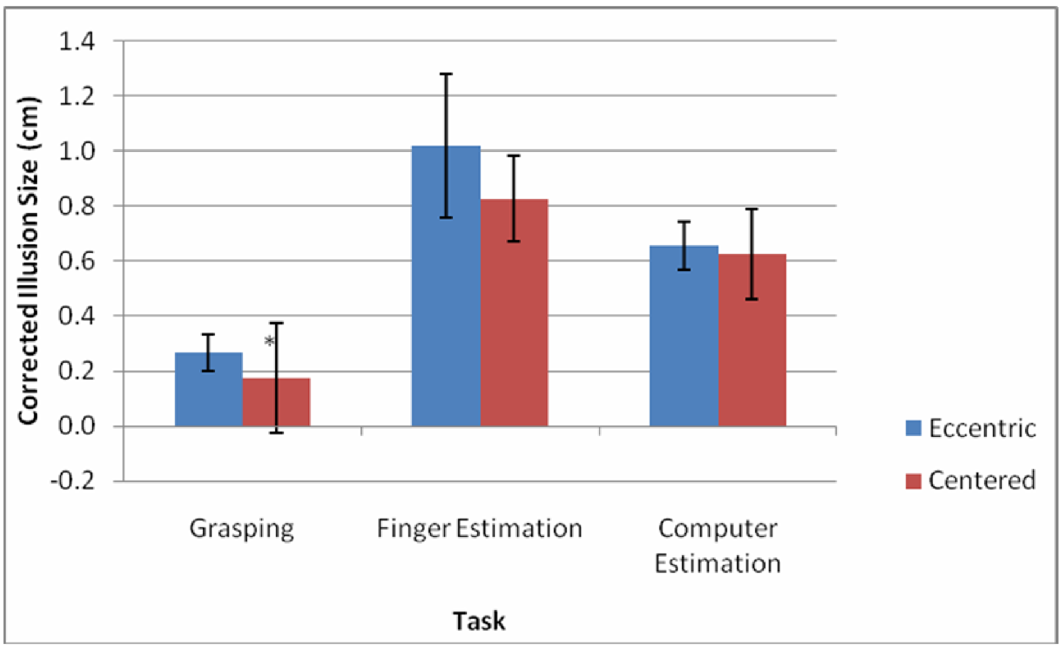
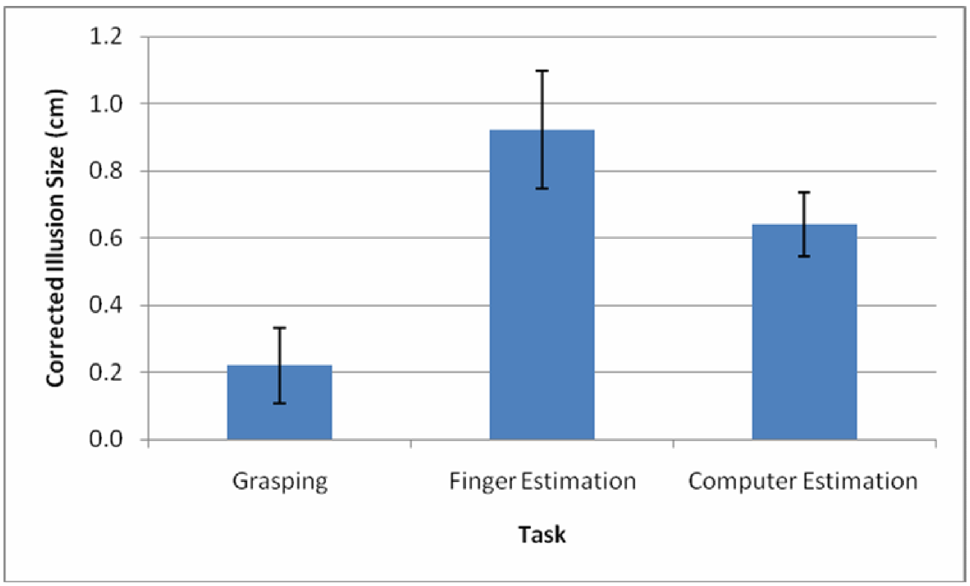

Corrected Illusion Size (cm)
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
*
Grasping
Finger Estimation
Computer Estimation
Task
Eccentric
Centered

Figure 19. Main effect of task (±SE). There were significant differences between grasping (*M* = .220 cm, *SE* = .112) and finger estimation (*M* = .992 cm, *SE* = .176, *p* = .041), and grasping and computer estimation (*M* = .640 cm, *SE* = .096, *p* = .004), but not between finger estimation and computer estimation (*p* = .592).


1.2
1.0
0.8
0.6
0.4
0.2
0.0
Corrected Illusion Size (cm)
Grasping
Finger Estimation
Computer Estimation
Task

DISCUSSION

Experiment 1

Scaling data. The first aspect of Experiment 1 was the analysis of the slopes of the response functions for the control bars, which reflected participants' responses to true variations in object size. A number of studies have found that measures of grasping, like MGA, and measures of perception, like manual size estimation, show different levels of responsiveness to physical changes in object size, which are reflected in different response function slopes (e.g. Franz, 2003; Smeets and Brenner, 1999). Franz et al. (2009) discussed in depth the need to correct grasping and illusion sizes for these different sensitivities, by dividing each by its respective scaling factor. A meta-analysis by Smeets and Brenner (1999) found a mean grasping scaling factor of .82 across a number of studies, and Stöttinger et al. (2009) found a mean manual estimation scaling factor of 1.03. The mean grasping scaling factor in this study was .97, which is a bit higher than Smeets and Brenner's average, suggesting that participants responded to changes in size with slightly larger changes in MGA in the present study than in the studies included in their meta-analysis. However, our mean grasping scaling factor was quite close to the Radoeva et al. (2005) mean of .9 for grasping. The 1.03 mean manual estimation scaling factor reported by Stöttinger et al. was similar to the mean estimation scaling factor in this study (1.157) and the mean estimation factor in the Radoeva et al. (2005) study (1.1 – 1.2). In general, the mean estimation and grasping scaling factors in this study closely replicate the

Radoeva et al. results, a finding that was expected in light of the studies' very similar methods.

The significant difference between the estimation and grasping scaling factors in this study demonstrated the need to correct the illusion sizes by dividing each block's illusion by its individual scaling factor, a procedure suggested by Franz (2003) and described in this study's method section. This correction allowed an accurate comparison of the grasping and estimation illusion sizes.

Illusion data. One of the most salient results of Experiment 1 was the main effect of task on illusion size. Even after the illusion magnitudes were corrected for scaling, the overall estimation was significantly larger than the overall grasping illusion. This is in line with the predictions of the Goodale and Milner (1992) model, which predicts the ventral "perception" stream to be significantly more susceptible to size illusions than the dorsal "action" stream. However, the existence of a small but significant overall visuomotor illusion, as also found by Radoeva et al. (2005), is in itself contradictory to the predictions of the perception-action model and the findings of a number of previous studies (e.g. Aglioti et al., 1995; Haffenden and Goodale, 1998).

Individual analysis of the illusion magnitudes for each of the twelve blocks provided additional detail about which specific conditions yielded significant illusions, and how the illusion sizes changed over the three days in each condition. On the first day in the right hand (the conditions most similar to the Radoeva et al. (2005) experimental conditions), there was a .219 cm grasping illusion, which, although significantly greater than zero, was much smaller in magnitude than the .6 cm Radoeva et al. grasping illusion. There was a .634 cm corrected right hand estimation illusion on the first day, compared to Radoeva et al.'s larger 1.0 cm estimation illusion. While both the grasping and estimation illusions in the right hand on the first day were smaller than the corresponding illusions in the Radoeva et al. study, the magnitude differences between the grasping and estimation illusions were quite similar between the two studies (.4 cm in Radoeva et al. and .381 cm in this study).

These different grasping and estimation illusion sizes in the right hand on the first day are likely due to one of the two main procedural differences between the Radoeva et al. study and the present one; either the actual grip aperture measuring devices used, or the location of gaze fixation in relation to the stimulus. The former remains a possibility, because the Radoeva et al. goniometer was heavier and the bars were more substantial than the goniometer used in the present study, and the latter was investigated in Experiment 2.

Practice effects. One of the main goals of this study was to investigate Goodale's (2009) proposal that the significant Radoeva et al. (2005) visuomotor illusion was due to the measuring device's awkward constraint of the grasping movement, which reduced automaticity and therefore presumably increased the involvement of the ventral vision-for-perception stream. This study therefore tested whether three days of practice with the grasping device would yield, by the third day, a non-significant grasping illusion.

For simplicity of comparison, I began by analyzing only the right hand illusions and their changes over the days of the experiment. On the first two days, the grasping and estimation illusions were all significantly larger than zero, and the estimation illusions were significantly larger than the grasping illusions. The fact that there was a small but significant visuomotor illusion in the first two days (while the perceptual illusion remained robust) may suggest that the ventral stream had some input in the dorsal stream's control of the grasp on the first two days. On the third day, neither grasping nor estimation was significantly larger than zero, and they were not significantly different from each other.

At first glance, these results appear to fulfill the prediction that practice with the grasping device would yield a non-significant grasping illusion by the third day of the experiment. However, it is important to note that there was a non-significant estimation illusion in the right hand on the last day, in addition to the non-significant grasping illusion. This indicates that participants may not have been perceptually susceptible to the illusion by the last day, and mirrors the results obtained by Judd (1902), in which perceptual susceptibility to the Müller-Lyer illusion decreased over repeated trials.

There are two possible rationales for these results that are in line with the Goodale and Milner (1992) vision-for-action and vision-for-perception model. First, it is possible that repeated exposure to the stimulus caused decreased *perceptual* susceptibility by the last day, and that practice with the grasping device separately led to more automatic, dorsal stream control and therefore decreased *action* susceptibility by the last day as well. In this way, the two streams may have been affected separately by practice, in ways that correspond to their putative functions. Second, it could be that three days of practice were not enough to reduce the awkwardness of the grasping device and the ventral stream still provided information for the grasp, but that its input was not obvious because, like the dorsal stream, it was impervious to the illusion by the third day.

Alternatively, these results can be interpreted within the framework of the Franz et al. (2000) common representation model, which proposes that action and perception rely upon a common internal representation of the visual world. The significant grasping and estimation illusions on the first two days could indicate that the two tasks were drawing upon the same, illusion-affected internal representation, and the performance on the third day could reflect an internal representation that was no longer affected by the illusory context due to the repeated exposure to the same stimuli.

The significant main effect of task was not predicted by the common representation model, which proposes that since estimation and grasping both draw upon the same representation, they should be similarly affected by the Müller-Lyer illusion. However, Franz et al. (2009) recently amended the common representation model to include the effect of visual feedback on grip scaling, proposing that grip aperture can be adjusted during flight based upon visual feedback of the hand nearing the target, which effectively reduces the effect of the visual illusion on grip scaling. It is possible that such an adjustment during flight would reduce but not completely eliminate the visuomotor illusion, which could provide one explanation for this study's small but significant visuomotor illusions in the first two days.

Finally, the reduction in the visuomotor illusion by the last day could be attributed to learning and attentional processes, as suggested by Bruno et al.'s (2008) meta-analysis of pointing studies. They proposed that with practice, participants can learn to attend selectively to the three-dimensional target with which they are required to interact, and ignore its illusory context. Such a practice effect could have worked in tandem with the physical practice of grasping while wearing the grip aperture measuring device, and the effects of the two cannot by teased apart by this experiment.

With the data from both hands included, there was a significant day by task interaction, in which the size of the difference between the grasping and estimation illusions decreased over days. The overall grasping means did not decrease as quickly as the means of the estimation illusions did across the three days (with a main effect of day on estimation illusion magnitude that neared significance). This interaction supports the possibility of different mechanisms acting on the estimation and grasping practice effects.

Differences between the two hands. One of the expected effects, based upon past research by Gonzalez et al. (2006), was a difference in visuomotor illusion susceptibility between the right and left hands. The aforementioned study found that right-handed participants showed significantly larger grasping illusion magnitudes with their left hands than with their right hands. The authors interpreted this to mean that the right hemisphere uses perceptual information in the control of movements with the left hand, in contrast to the automatic, illusion-resistant dorsal control of the right hand during grasping.

In addition, in the Radoeva et al. (2005) patients with unilateral brain damage, estimation and grasping illusions were of similar magnitude in the left hand, and there was a greater difference between the visuomotor and visuoperceptual illusions in the right hand. These results correspond with neuroimaging evidence that the two streams are more dissociated in the left hemisphere, which controls the right hand (Radoeva et al., 2005).

Based upon this prior research, it was expected that this study would yield a significant task by hand interaction. It was expected that the *perceptual* illusion would be of similar size in both hands, because the stimulus was presented in the center of the visual field and should have been processed by both hemispheres. However, based upon the greater dissociation between the dorsal and ventral visual streams in the left hemisphere, it was predicted that the difference between the visuomotor and visuoperceptual illusions would be significantly larger in the right hand (controlled by the left hemisphere) than in the left hand (controlled by the right hemisphere).

Experiment 1 did indeed yield a significant task by hand interaction, but it was in the opposite direction than expected. The difference between the grasping and estimation illusion magnitudes was significantly *greater* in the left hand than in the right hand. Although the differences between right and left hand grasping and between right and left hand estimation were not statistically significant, the mean left hand grasping illusion was smaller than the mean right hand grasping illusion, and the mean left hand estimation illusion was larger than the mean right hand estimation illusion. This difference was enough to yield a significant task by hand interaction. It is unclear why the mean grasping illusion was smaller (although not significantly smaller) in the left hand than in the right, when previous research predicted the opposite (Gonzalez et al, 2006). Since all Experiment 1 participants were strongly right-handed, their precision grasps with their left hands should have been more awkward and recruited more ventral perceptual control for that reason. In addition, it was expected that more relational, illusion-susceptible information from the ventral stream would be used in the control of the left hand grasps, simply because the dorsal and ventral streams are not as dissociated in the right hemisphere as they are in the left (Radoeva et al., 2005). Further experiments are required to identify the source of this unexpected finding.

Experiment 2

Perceptual measures. The first part of Experiment 2 addressed a question also investigated by Franz (2003), about whether "traditional perceptual measures (Franz, 2003)" like adjusting a line on a computer screen are systematically different from the manual estimation perceptual measure used in a number of other studies (e.g. Radoeva et al., 2005; Experiment 1 of the present study). Franz (2003) found that there were significant differences between manual estimation and an adjustment task with regard to participants' responses to a three-dimensional version of the Ebbinghaus illusion. In his study, without correction for scaling, manual estimation illusions were significantly larger than adjustment illusions and also significantly larger than the corresponding grasping illusions. He also found that there were no significant differences in illusion size between grasping and line adjustment estimation. However, he found that once the illusions were all corrected for scaling to physical differences in size, manual estimation and adjustment were not significantly different from each other, nor significantly different from grasping.

This study replicated some of Franz's (2003) results, in that after correction for scaling, although the manual estimation illusions were slightly larger in magnitude than the computer adjustment task illusions, the two measures did not yield statistically different results. This seems to suggest that as long as the two different perceptual measures are corrected for scaling, as the grasping and manual estimation measures were in the first experiment, they provide comparable assessments of a visual illusion's effect on perception.

Eccentricity effects. The other main goal of the second experiment was to investigate whether one of the factors that led to the small visuomotor illusion in the Radoeva et al. (2005) study was that the participants estimated and grasped targets that were 6° of visual angle from the fixation point. Since people normally fixate directly on anticipated points of contact while grasping (de Grave, Hess, Brouwer, and Franz, 2008), it was postulated that normal grip scaling and estimation would be affected when central fixation was not allowed. Further, it was hypothesized that the predictions of the perception-action model would hold in the centered stimulus condition (a significant estimation illusion but no significant grasping illusion), but that in the eccentric fixation condition, dorsal control of the grasping movement would be disrupted and the ventral stream would provide additional, illusion-affected size information.

As predicted, the only block that did not show a significant illusion was the centered grasping block (although this result did differ from the significant right hand grasping illusion on the first day of Experiment 1). There were significant illusion effects in eccentric grasping and all estimation blocks. Each of the estimation conditions (eccentric and centered finger estimation, eccentric and centered computer estimation) had a significantly greater illusion magnitude than the two grasping conditions, which was demonstrated by the main effect of task. This result could be explained within the perception-action model; preventing the participants from fixating on the target, as usually occurs during grasping, may have decreased the ability of the dorsal stream to provide online control of grip scaling without the help of the ventral perceptual stream. It is also possible to explain this result within the common representation model, which proposes that both estimation and grasping are affected by the illusion, but that grasp scaling can be corrected in flight when visual feedback is available. It could be that when fixation is eccentric, rather than directly on the target, the online correction of grip aperture is more difficult, and a small but statistically significant visuomotor illusion is observed.

Contrary to predictions, there was no main effect of eccentricity, and no significant difference between the centered and eccentric grasping means. There was, however, a trend toward greater eccentric than centered illusion sizes, so future experiments with larger sample sizes may reveal a statistically significant difference between the two eccentricity conditions.

General Discussion

Both of this study's experiments sought to add to the current understanding of how the dorsal and ventral streams function in creating conscious perceptions of the visual world and in controlling goal-directed actions such as grasping. The results suggest that a number of factors come into play in determining the extent to which grip scaling and estimations are affected by the Müller-Lyer illusion.

Experiment 1 demonstrated that grasps and estimations show decreased illusion susceptibility after practice, but further experiments are needed to determine whether or not the visuomotor and visuoperceptual practice effects were the result of separate mechanisms. In addition, Experiment 1 indicated that there is a difference between the right and left hand in right-handers in the size of the difference between visuomotor and visuoperceptual illusion susceptibility. This difference was, however, opposite that found by a previous study (Gonzalez et al., 2006), and future experiments with more participants (both right- and left-handed) are needed to reconcile this difference, and to explore the role of handedness in the differences between right and left hand performance.

Experiment 2 demonstrated that after correction for scaling, manual estimation and adjustment estimation provide similar assessments of perceptual sensitivity to the Müller-Lyer illusion, at least under this experiment's particular conditions. In addition, it provided preliminary evidence for an effect of eccentric fixation on the relative magnitudes of visuomotor and visuoperceptual susceptibility to the Müller-Lyer illusion. Additional experiments could investigate whether, with a greater number of illusion trials per block, as well as a greater number of participants, this difference between illusion susceptibility in different fixation eccentricity conditions becomes more pronounced.

Appendix: Common Illusion Stimuli Used in Grasping Experiments

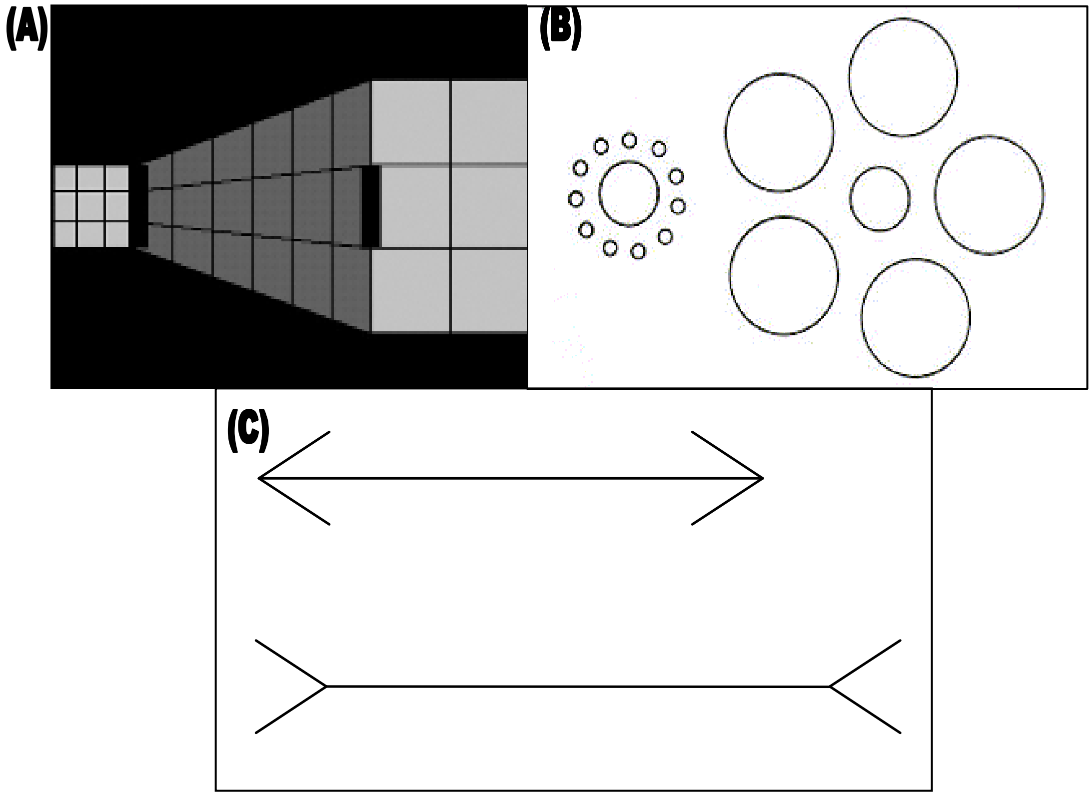


Figure A. Three common illusions used in grasping experiments. (A) "Example of the Ponzo display and stimuli. The two objects that are seen against the 2D illusory background are usually perceived as different in size, although they are identical" (Gonzalez et al., 2008). (B) Standard version of the Titchener circles (or Ebbinghaus) illusion. "The target circles in the centre of the two arrays appear to be different in size even though they are physically identical. For most people, the circle in the annulus of smaller circles appears to be larger than the circle in the annulus of larger circles." (Aglioti et al., 2005) (C) The Müller-Lyer illusion. The two center lines are the same length, but for most people the lower line appears longer.

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