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## A haptic size-contrast illusion affects size perception but not grasping

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**Abstract** Object features (e.g. size, shape and orientation) are relevant for recognition and identification, but also for the control of manual actions. Converging evidence suggests a dissociation between the visual systems that mediate object perception and object-directed action. Here we present evidence suggesting that a similar dissociation might exist in the haptic domain. We demonstrate that a haptic variation of a size-contrast illusion influences the perceived size of a target object, but not the degree to which the hand is opened when that object is the target of a grasping movement. This finding is consistent with the view that object perception is “scene-based” and takes into consideration not only the size of the target object but also the sizes of other nearby objects. In contrast, the control of object-directed action is primarily driven by the absolute size of the target object independent of the relative sizes of other objects in the environment, suggesting a “actor-based” frame of reference. The present findings suggest that dissociations between action and perception are not unique to the visual system, but might instead reflect a general organizational principle of sensory processing.

**Keywords** Action · Perception · Haptics · Prehension · Illusion

### Introduction

Object features like size and shape are relevant for recognition and identification, but also for the control of

skilled manual actions. Converging evidence suggests that these two modes of object processing—“vision-for-perception” and “vision-for-action”—are mediated by separate neural pathways (Milner and Goodale 1995). The strongest evidence in favour of this view comes from neurological patients who have lesions restricted either the ventral or dorsal visual pathways. On the one hand, patient DF, whose lesion is concentrated primarily in visual cortex at the junction of the occipital and temporal lobes, demonstrates no evidence of conscious form perception but can nevertheless adjust her grasping hand to take into account the size, shape and orientation of the target object (Goodale et al. 1994). On the other hand, patient AT, whose lesion is concentrated in bilateral posterior parietal cortex, demonstrates intact object perception but impaired manual prehension. Taken together these cases suggest that the dorsal visual pathway plays a leading role in the visual control of action, whereas the ventral pathway is primarily responsible for conscious visual perception.

More recently, it has been suggested that dissociations between action and perception can be demonstrated in normal-sighted individuals using certain types of visual illusions. Early studies in this area reported that size-contrast illusions influence the perceived size of a target object, but not the peak opening of the hand during manual prehension (Aglioti et al. 1995; Haffenden and Goodale 1998; Hu and Goodale 2000). Although not without controversy (Franz 2001; Franz et al. 2000; Glover 2002; Pavani et al. 1999), the illusion findings are largely consistent with the two-visual-systems hypothesis. The resistance of grasping to size-contrast (and other) illusions has been taken as evidence that the visuomotor system operates in an absolute metrical frame of reference, in which the size of the target object is computed independent of other objects in the visual scene. The perceptual system, however, makes use of relational metrics, taking into consideration the size of the target object but also the sizes of adjacent objects. Consistent with these arguments, Goodale and Humphrey (1998), among others (e.g. Gentilucci et al. 1996), have suggested

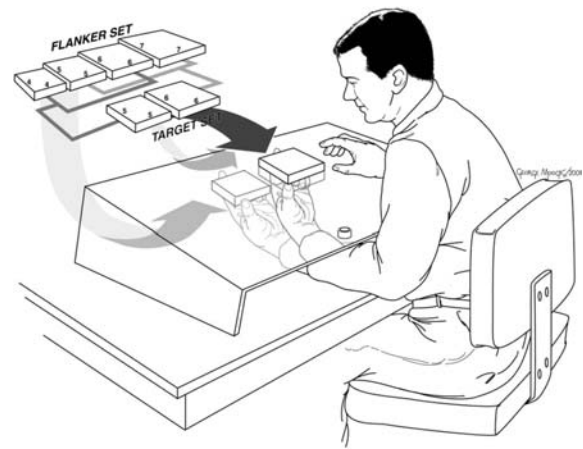
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that “vision-for-action” operates in a viewer-based or egocentric frame of reference, whereas “vision-for-perception” works in a scene-based or allocentric frame of reference.

Little is known about the relationship between object perception and object-directed action outside of the visual domain. Bridgeman et al. (1997) found that an acoustic Roelofs-type illusion produced similar biases in verbal and motor judgments of an auditory target’s location, suggesting that—unlike the visual system—the auditory system maintains only a single representation of space that is shared by cognitive and sensorimotor systems. To our knowledge, however, no studies have investigated the processing of *intrinsic* object features for action and perception in a single, non-visual modality. Some studies have looked at interactions between visual and haptic information in the perception of object features and the control of object-directed actions (e.g. Flanagan and Beltzner 2000; Gentilucci et al. 1998), and found evidence suggesting differences in the way visual and haptic information are integrated for action and perception. For example, Gentilucci et al. (1998) found that manipulating an unseen distractor object with the right hand influenced the size of the grip aperture in the left hand when reaching to grasp a visible object. Similar interference was not observed when the task was to estimate the size of (rather than grasp) the target object, leading the authors to suggest that visual and somatosensory information are more readily integrated for the control of object-directed action than for the perception of object features. But what is the relation between object perception and object-directed action when information from only a single modality is available, such as when one uses the hand to explore an unseen object? Following the arguments outlined earlier about the different frames of reference that are utilized for action and perception in the visual domain, one might predict that the intention to interact with an object will influence the processing of haptic information related to that object.

Here we present evidence from a purely haptic task that suggests a dissociation between perception and action in the processing of object features. In this study we employed a haptic variation of a size-contrast illusion, in which a target object is presented beside a larger, or smaller, or same-sized flanking object (e.g. Hu and Goodale 2000). Participants used their left hand to feel the unseen flanker and target objects, and then used their right hand to either indicate the size of the target object (by adjusting the size of the finger-thumb aperture), or to reach out and pick up a block matching the dimensions of the target object. Consistent with many reports from the literature on visual illusions, we find that perceptual judgments of object size are influenced by the size-contrast display whereas the scaling of the peak grip aperture is not.



**Fig. 1** Experimental apparatus. Two blocks (left side, flanker; right side, target) were felt in sequence using the left hand (1.5 s for each). A third block, matching the size and position of the target object, was mounted on the top of the platform. The right hand was used to estimate the size of the target block, or to reach out and grasp the matching block on the top surface of the platform; the left hand remained on the target during the response. Eyes were shut throughout

## Methods

### Participants

Sixteen right-handed undergraduate students (six male, ten female; mean age 20.8 years) from the University of Western Ontario participated in this investigation, and received a small payment for their service. Participants provided informed consent in accord with institutional guidelines for ethical research practices, consistent with the Declaration of Helsinki. Participants were not provided any specific information about the experimental hypotheses.

### Stimuli

Stimulus arrays consisted of two square objects mounted beside each other on the bottom surface of a platform (Fig. 1). Each array consisted of a flanker object (always presented on the left side) and a target object (always presented on the right side). Two target sizes were used in the experiment (5×5 cm, and 6×6 cm), and the flanker object was smaller (4×4 cm or 5×5 cm), or larger (6×6 cm or 7×7 cm), or the same size (5×5 cm or 6×6 cm) as the target object. Altogether there were six possible target arrays (two target sizes × three relative flanker sizes). Participants never received vision of the target or flanker objects, and were not told how many objects were used in the study. In addition to the target and flanker objects, a third “goal” object was mounted on the top surface of the platform; this object matched exactly the size and position of the target object which was located beneath the platform. The purpose of this block was to provide a tangible target for the grasping phase of the experiment (see below). Again, participants did not receive any visual information about the goal object.

### Tasks

Participants performed two tasks (size estimation and grasping) in separate blocks of trials. The sequence of events was the same for both tasks; the only difference was the type of response that was required in response to an auditory “go” stimulus. Participants kept their eyes closed for the entire experiment, except between blocks of trials. A series of auditory tones was used to control the haptic

exploration phase of each trial. An initial tone signalled the participant to use the index finger and thumb of their left hand to feel the size of the flanker object (in the front-to-back axis) on the left side of the display. A second tone came 1.5 s later, signalling the participant to use their left hand to feel the size of the target object on the right side of the display. A third tone came 1.5 s later, signalling the participant to make a response (size estimation or grasping) with their right hand on the top surface of the platform. During the response phase, participants were instructed to keep the left hand in contact with the target object so that the object's properties would not need to be remembered.

In the size-estimation trials, participants were instructed to indicate the size of the target object by adjusting the separation between the index finger and thumb of their right hand. The right hand was not transported towards the goal object but rather remained positioned above an initial starting location at the front edge of the platform. The opening of the right-hand aperture was aligned with the front-to-back axis, corresponding to the orientation of the left hand beneath the platform. In the grasping trials, participants were instructed to reach out with their right hand and grasp (using the index finger and thumb) the goal object on the top surface of the platform. Instructions were to grasp the object in the front-to-back axis, quickly and accurately.

Grasping (G) and size-estimation (S) trials were carried out in separate blocks of trials (G-S-G-S or S-G-S-G, order counterbalanced across subjects). Target arrays were presented in random order. Each of the six target arrays was presented six times in each response condition, for a total of 72 trials.

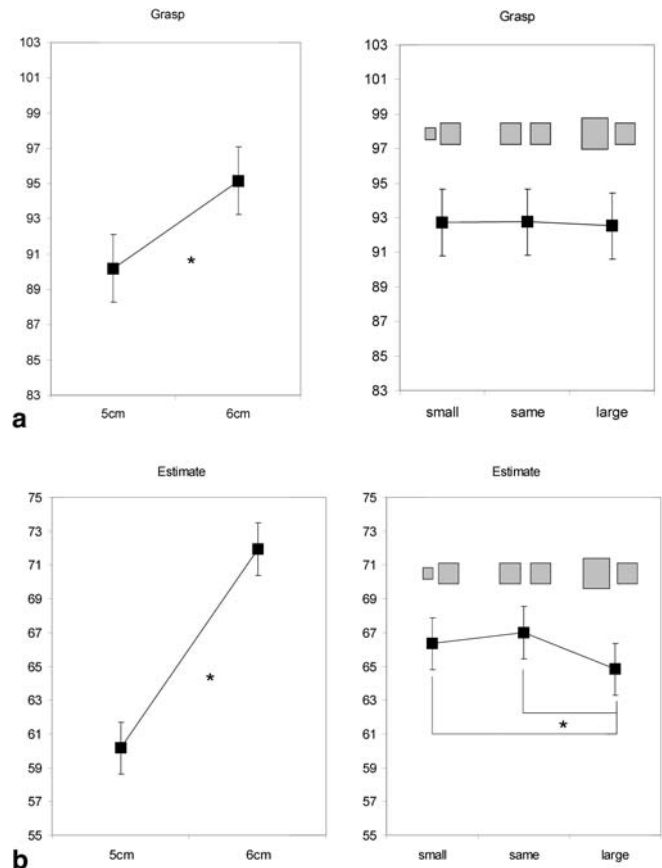
In a separate psychophysical experiment, eight additional participants (four male, four female; mean age 22.6 years) made size-estimation and grasping responses to six target objects ranging in size from 4.4 to 5.4 cm, in 0.2-cm increments. Target objects were presented on the underside of the same platform used in the main experiment. Participants kept their eyes shut for the entire experiment. The left hand was used to feel the size of the target object for 1.5 s, after which an auditory tone signalled the participant to use the right hand to either indicate the size of the target, or to reach out and grasp a matching block on the top surface of the platform. Responses were made in two separate blocks of trials, with order counterbalanced across participants. Object sizes were presented in random order, with four trials per target per response condition.

#### Data analysis

Hand movements were monitored and recorded using an OPTO-TRAK 3020 system (NDI, Waterloo, Ontario, Canada). Infra-red emitting diodes (IREDs) were positioned on the index finger, thumb and wrist of the right hand. IRED positions were sampled at 200 Hz for 3 s following the auditory response cue. Offline, grip aperture time series were generated by computing the resultant distance between the IREDs for the index finger and thumb. For the size-estimation trials, a stable grip aperture value was chosen as the first grip aperture value in a series of five consecutive values that did not vary by more than 2 mm. For the grasping trials, peak grip aperture was chosen as the largest value for the grip aperture time series. Data were analyzed using a 2 task  $\times$  2 target size  $\times$  3 flanker size repeated-measures ANOVA,  $\alpha=0.05$ . Significant interactions were explored using simple-effects analysis,  $\alpha=0.05$ . In the psychophysical experiment, linear regression analysis was used to determine the slope of the relationship between object size and grip aperture for the size-estimation and grasping trials.

## Results

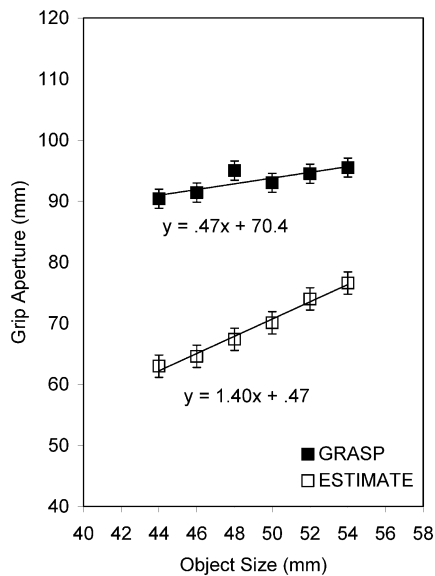
Consistent with previous studies, peak grip aperture for grasping was significantly greater than stable grip aperture for size estimation ( $F_{(1,15)}=64.3$ ,  $P<0.001$ ). This



**Fig. 2.** **a** Target (*left panel*) and flanker effects (*right panel*) for peak grip aperture in grasping responses. Target, but not flanker, effects were significant. **b** Target (*left panel*) and flanker effects (*right panel*) for grip aperture in size-estimation responses. Target and flanker effects were significant. Grip aperture was smaller when the target was felt after a larger flanker. Bars extending from symbols represent within-subjects SEMs. \* $P<0.001$

effect has previously been attributed to the requirement for the grasping hand to be opened wider than the target object in order to enclose it (Jeannerod 1986). Grip aperture values were larger for the 6-cm than for the 5-cm target object ( $F_{(1,15)}=145.2$ ,  $P<0.001$ ), and this effect was greater for size estimation than for grasping (interaction  $F_{(1,15)}=54.3$ ,  $P<0.001$ ), see Fig. 2. This suggests a difference in the psychophysical size-scaling function for size estimation and grasping; this difference can be quantified as the ratio of the target-size effect (i.e., the aperture for the 6-cm target minus the aperture for the 5-cm target) for the two tasks: size estimation 11.8 mm, grasping 5.0 mm, ratio 2.36. In other words, an equivalent change in the size of the target object produces a 2.36-times greater effect on stable grip aperture for size estimation than on peak grip aperture for grasping.

Critically, a task by flanker interaction ( $F_{(2,30)}=3.63$ ,  $P=0.04$ ) indicated that size estimation was affected by the size of the flanker object ( $F_{(2,30)}=8.0$ ,  $P=0.002$ ), but grasping was not ( $F_{(2,30)}<1$ ,  $P>0.05$ ). As seen in Fig. 2, targets were estimated to be smaller when a larger flanker object was felt first; estimated size was similar for the



**Fig. 3** Results of the psychophysical experiment. Regression functions are plotted for peak grip aperture (grasping, *GRASP*) and stable grip aperture (size estimation, *ESTIMATE*) in relation to the size of the target object. Data points are means for eight participants. Bars extending from symbols represent within-subjects SEMs

smaller and same-sized flanker conditions. The direction and magnitude of the observed flanker effects are similar to those reported in other experiments that have used visual size-contrast displays (e.g. Hu and Goodale 2000). A ratio of the flanker-size effect (grip aperture for small flanker–large flanker) for size estimation and grasping was calculated for comparison with the ratio for the target-size effect. This ratio was 7.5:1 (size estimation 1.5 mm, grasping 0.2 mm). In other words, although the flanker effect was quite small for the size-estimation responses, the effect was statistically reliable and much greater than what would be predicted from the psychophysical size-scaling functions for size estimation and grasping. This suggests a non-trivial difference in the use of flanker-size information for size-estimation as compared to grasping.

The results of the psychophysical experiment are presented in Fig. 3. Grip aperture was scaled to the size of the target object in both tasks, but the slope of the scaling function was 2.98-times greater for size estimation (1.40) than for grasping (0.47). This ratio provides a more stable estimate of the different size-scaling functions for size estimation and grasping than the ratio of target-size effects in the main experiment. Nevertheless, the two obtained ratios are quite similar (2.36 for the main experiment, and 2.98 for the psychophysical experiment), and also much smaller than the ratio for the flanker-size effect obtained in the main experiment (7.5). These observations suggest that the different flanker effect for size estimation and grasping cannot be attributed, at least exclusively, to a fundamental difference in the sensitivity of these responses to size information.

## Discussion

We used a haptic task to explore the relationship between conscious size perception and the control of manual prehension. We provide evidence that suggests a dissociation between perception and action in haptic object processing; object-size estimations fell prey to a size-contrast illusion, whereas object-directed grasping movements did not. In other words, haptic size perception took into consideration not only the size of the target object but also the size of the nearby flanker object, whereas the control of prehension was sensitive only to the size of the target object. Although the flanker-size effect was quite small for the size-estimation task, we believe the effect is not trivial for three reasons. First, the effect is similar in magnitude to that observed in experiments that have used visual size-contrast illusions (e.g. Hu and Goodale 2000). Second, the effect is more than twice as large as that predicted from the different size-scaling functions for size-estimation and grasping. Third, and most important, the flanker-size effect was statistically reliable and therefore in need of explanation.

As discussed earlier, dissociations between the effect of *visual* illusions on object-directed action and object perception have been attributed to differences in the metrics and frames of reference used by the visuomotor and perceptual systems (e.g. Goodale and Haffenden 1998). Specifically, the visuomotor system is thought to make use of absolute metrical information and egocentric frames of reference—consistent with the requirement for movement accuracy—whereas object perception makes use of relative metrics and scene-based frames of reference—consistent with the role of perception in representing and interpreting the surrounding environment. Although there are some important differences between the visual size-contrast displays that have been used in previous studies and the haptic size-contrast display used in the present investigation, we suggest that similar arguments can be made in both cases.

Visual size-contrast displays involve the simultaneous presentation of target and flanker objects, such that direct comparisons between the two are possible. In the haptic task used in the present investigation, it was necessary to separate in time the presentation of haptic information about the flanker and target objects; participants always felt the flanker object first, followed by the target object. In other words, any comparison of the flanker and target objects in the haptic task would have necessarily required memory for the features of the flanker object. Nevertheless, such a comparison was presumably made in the size-estimation task, as evidenced by the small but reliable flanker-size effect. The fact that this comparison would have required memory for the size of the flanker object is somewhat immaterial; the key point is that the comparison was made at all.

Our results suggest that the size of the flanker object was not taken into consideration in the haptic grasping task, because in this case the size of the peak grip aperture was sensitive only to the size of the target object. A



question for future research is whether this effect is due to the limited memory capacity of the sensorimotor system (e.g. Hu and Goodale 2000; Westwood et al. 2000)—which could make temporally-extended comparisons impossible—or whether instead this effect is due to the nature of the metrical computations carried out by the sensorimotor system (i.e. absolute versus relative size). In any case, our results indicate that object perception and object-directed action engage different haptic processing, because similar sensory input was available in both tasks; the only difference was the nature of the required response.

### Size versus position

Smeets and colleagues (e.g. Smeets and Brenner 2001; Smeets et al. 2002) have suggested that reported dissociations between action and perception in the visual domain could be due to the use of different information in the two types of tasks. In other words, there might be no need to suggest that action and perception systems compute the same object feature (e.g. size) in different ways. For example, perceptual size judgments might access a representation of object size *per se*, whereas the control of the grasp might access a representation of the positions of the object's edges. Representations of size and position need not be mutually dependent; size-contrast illusions could influence the representation of object size, but not the representation of edge location. Although it is not clear that this proposal is different in any fundamental way from other arguments about absolute and relative object metrics, it is useful to consider the present results from this perspective.

In the present experiment, the left hand was used to acquire haptic information about the flanker and target objects, and the right hand was used to respond. Importantly, the left hand remained in contact with the target object while the right hand was used to make the response. In the grasping task, participants could have guided the finger and thumb of the right hand to the absolute spatial positions of the finger and thumb of the left hand immediately beneath the platform surface. Perhaps the size-contrast illusion does not affect the representation of finger position, but only the representation of the size of the target object. In the size-estimation task absolute spatial information about finger position would likely be of little use for controlling the right-hand response, because the right hand was not transported towards the target object. Size-estimation might necessarily access a representation of the size of the target object—a representation based on the relative separation of the digits on the left hand, rather than the absolute positions of each digit. The sensitivity of size estimation to flanker size might then be attributed to a direct effect of the size-contrast illusion on the representation of object size *per se*. We are currently exploring this intriguing possibility by manipulating the potential to

use absolute spatial information about digit position for grasping and size-estimation responses.

### Different size-scaling functions for grasping and size estimation

It is interesting to note the different target-size scaling functions for the size-estimation and grasping responses, seen most clearly in Fig. 3 from the psychophysical experiment. Specifically, the slope of this function was quite shallow for the grasping task (0.47 mm increase in peak grip aperture for every 1 mm increase in object size), whereas the slope was much steeper for the size-estimation task (1.40 mm increase in finger aperture for every 1 mm increase in object size). There is also a large difference in the intercept for the grasping (70.4 mm) and size-estimation (0.47 mm) scaling functions. A similar pattern of slope and intercept values has been reported in the visual domain (Hu and Goodale 2000; Westwood et al. 2000).

The goal of grasping—to enclose the target object with the hand—is accomplished most effectively by first opening the grip wider than necessary, and then closing the aperture as the hand homes in on the object's location (e.g. Jeannerod 1986). This “grasp overshooting” strategy guards against inadvertent underspecification of the grip size, which would otherwise need to be corrected through a time- and energy-consuming reversal of the hand closure pattern. A corollary of the overshooting strategy is that the peak grip aperture need not be modulated in a 1:1 relationship with the actual size of the object; after all, the peak aperture is already programmed to be much greater than the object. As Glover and Dixon (2002) and others (e.g. Jeannerod 1986) have demonstrated, the slope of the function relating target size and grip aperture increases monotonically as the grasping movement unfolds, suggesting that information about the size of the object is relied upon most strongly for controlling the final stages of prehension. Our future work will investigate this temporal relationship in haptic grasping.

Unlike grasping, the goal of the size-estimation task is to provide an accurate indication of the perceived size of the target object. As such, one would predict a slope value of approximately one for the object size/grip aperture function in this task. The observed slope of 1.4 therefore suggests the possibility of a distortion in the haptic perception of object size—an overestimation of the object's size that is quite separate from the perceptual illusion induced by the size-contrast display. Alternatively, the unexpectedly high slope could be related to the mechanism by which sensory information from the one hand is transformed into motor commands for the other. These possibilities merit further inquiry.

## Interference in perception and action systems

Gentilucci and colleagues have demonstrated that irrelevant haptic information can influence the control of visually-guided grasping movements—peak grip aperture was larger when the (non-responding) right hand manipulated an unseen distractor that was relatively larger than the visible target of the grasping movement (Gentilucci et al. 1998). This result was interpreted as evidence for interference in the sensorimotor system between conflicting sources of target information. It seems unlikely, however, that a similar interference model can account for the results of the present experiment.

In the first place, participants in the present experiment received no visual information about any of the objects in the experiment for the duration of the protocol. More importantly, however, participants were never given discordant information about the size of the target object; i.e. the target object felt under the platform was always the same size as the goal object, and this was explained clearly to each participant prior to the experiment. Of course, the concordance between the sizes of the target and goal objects was detectable only in the grasping task (and indeed only after the response was complete), since the participant did not interact with the goal object in the size-estimation task. In short, there was never the possibility for interference between different sources of target information during the grasping or size-estimation responses. However, because haptic information about the flanker object was likely to be available in memory, one could construe that object as a possible source of interference during responding. According to Gentilucci et al. (1998), interference should manifest in an increase in the size of the grip aperture when the distractor is larger than the target; this is precisely opposite to what was observed here in the size-estimation task. Moreover, Gentilucci and colleagues found evidence for interference only in their grasping task, whereas the flanker object had no effect on grasping in the present experiment.

In light of the preceding arguments, it seems unlikely that the flanker effects observed in the present experiment are due to an interference mechanism of the sort proposed by Gentilucci and colleagues. In any case, the possibility for interference in the sensorimotor and perceptual systems could be explored more directly in future experiments of this type by introducing conflicting haptic information about the target object during the response.

## Neural substrates

At this time, it would be premature to make any strong statement about the possible neural mechanisms that might underlie the differential processing of haptic information for object-directed action and object perception. Whereas there is a good deal of direct and indirect evidence for the role of the dorsal and ventral visual pathways in vision-for-action and vision-for-perception (Milner and Goodale 1995), there is much less informa-

tion available about the neural substrates underlying haptic processing. Nevertheless, some speculation about the possible organization of the haptic processing system seems warranted.

In a recent functional magnetic-resonance imaging (fMRI) study, James et al. (2002) demonstrated decreased functional activation in the ventral visual pathway [lateral occipital cortex (LO) and middle occipital cortex (MO)] when participants viewed objects that were previously seen or previously felt. This finding suggests that ventral cortex might play a general role in object perception, perhaps independent of sensory modality. Indeed, Amedi et al. (2001) have provided strong support for exactly this notion in an fMRI study that looked at the response of LO to haptically presented objects as compared with response to textures; responses in LO were much greater to objects than to textures, suggesting a role for this region in constructing object representations from low-level somatosensory signals. Although these studies did not look at the metrics that are used in the perception of object size, the findings are consistent with a role for ventral cortex in haptic object perception.

To our knowledge, no studies have directly explored the neural substrates associated with somatosensory control of object-directed action. Nevertheless, there is reason to speculate that dorsal brain regions might be important for the control of movements to haptically explored objects. First of all, the primary somatosensory cortex is located in the post-central gyrus of the anterior parietal cortex, and receives many sensory signals that are important for the haptic sense (e.g. touch and pressure sensation, proprioception; Iwamura 1998). Moreover, neurons in the posterior parietal cortex [e.g., anterior intraparietal region (AIP), medial intraparietal region (MIP)] and frontal cortex (dorsal premotor cortex and ventral premotor cortex) are thought to integrate multiple sources of sensory information for the control of goal-directed arm movements (Andersen et al. 1997; Binkofski et al. 1998; Kalaska et al. 1997). It is possible that direct transformation of somatosensory signals into motor commands could occur within a distributed network of dorsal brain regions (parietal and frontal cortex), without contribution from ventral brain regions that are responsible for constructing perceptual object representations. Of course, a great deal more research will be necessary to identify the specific neural systems that underlie the processing of haptic information for the purpose of controlling hand movements.

In summary, we present evidence for a dissociation in the processing of (exclusively) haptic information for object perception and object-directed action. A haptic variation of a size-contrast illusion influenced size estimations but not grasping movements, even though equivalent sensory information was available in both tasks. Our findings are consistent with the view that sensorimotor systems utilize absolute metrics and egocentric frames of reference, whereas perceptual systems employ relative metrics and allocentric frames of reference. These arguments, although originally derived from

experiments in the visual domain, may apply equally well to multiple domains of sensory object processing. Segregation of action and perception systems might be a general organizational principle of sensory systems.

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