

## RESEARCH ARTICLE

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## Peripheral vision for perception and action

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**Abstract** Anatomical and physiological evidence suggests that vision-for-perception and vision-for-action may be differently sensitive to increasingly peripheral stimuli, and to stimuli in the upper and lower visual fields (VF). We asked participants to fixate one of 24 randomly presented LED arranged radially in eight directions and at three eccentricities around a central target location. One of two (small, large) target objects was presented briefly, and participants responded in two ways. For the action task, they reached for and grasped the target. For the perception task, they estimated target height by adjusting thumb-finger separation. In a final set of trials for each task, participants knew that target size would remain constant. We found that peak aperture increased with eccentricity for grasping, but not for perceptual estimations of size. In addition, peak grip aperture, but not size-estimation aperture, was more variable when targets were viewed in the upper as opposed to the lower VF. A second experiment demonstrated that prior knowledge about object size significantly reduced the variability of perceptual estimates, but had no effect on the variability of grip aperture. Overall, these results support the claim that peripheral VF stimuli are processed differently for perception and action. Moreover, they support the idea that the lower VF is specialized for the control of manual prehension. Finally, the effect of prior knowledge about target size on performance substantiates claims that perception is more tightly linked to memory systems than action.

**Keywords** Peripheral vision · Perceptual judgment · Reaching · Grasping · Prehension · Motor control

An object whose image falls on the fovea, a small area of densely packed photoreceptors covering about 2° of central vision (Palmer 1999), is perceived with greater crispness and clarity than an object that falls outside the fovea. Photoreceptor and retinal ganglion cell density is approximately 200% greater at the fovea than in the periphery (Curcio and Allen 1990). Central stimulus information is distributed more widely than peripheral stimulus information as it travels from the retina to the lateral geniculate nucleus (LGNd) and V1 (Connolly and Van Essen 1984; Van Essen et al. 1984; Wassle et al. 1990). Consequently, V1 cell receptive fields are more likely to include the foveal region than peripheral regions. This arrangement results in the *cortical magnification* of central vision. That is, more neural tissue is dedicated to processing centrally presented stimuli than peripherally presented stimuli. Therefore, the perceptual clarity associated with central vision can be explained by neuroanatomical differences between central and peripheral vision.

This account, while explaining why we see things best when we are looking directly at them, may not apply to all aspects of visual processing. According to the two visual systems account of Goodale and Milner (1992) and Milner and Goodale (1995), vision-for-perception and vision-for-action depend on distinct neural systems. Vision-for-perception, the visual processing that leads to conscious perception and recognition of scenes, faces, and objects in our environment, is served by the cortical stream leading from the primary visual cortex (area V1) to the temporal lobe. Vision-for-action, the visual processing that guides our physical interactions with the environment, like reaching and grasping objects, is served by the cortical stream leading from area V1 to the posterior parietal cortex. This distinction is supported by studies of neurological patients (Goodale et al. 1991) and healthy subjects (Brown et al. 2002; Haffenden and Goodale 1998, 2000), and by neuroimaging studies (Culham et al. 2003).

There is anatomical and physiological evidence that the ventral (perception) stream and the dorsal (action)

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stream represent the central and peripheral visual fields differently. At the dorsal lateral geniculate nucleus (LGNd), central vision is represented more densely in the parvocellular layers than in the magnocellular layers, and parvocellular density declines more rapidly with eccentricity than does magnocellular density (Azzopardi et al. 1999; Connolly and Van Essen 1984; Malpeli et al. 1996). In turn, parvo-dominated pathways synapse on layers of V1 (layers 4C $\beta$ , blobs, and interblobs) that project largely to ventral extrastriate areas, whereas magno-dominated pathways synapse on layers of V1 (layers 4C $\alpha$  and 4B) that project to both ventral and dorsal extrastriate areas (Van Essen and DeYoe 1995; Milner and Goodale 1995). Not surprisingly, ventral stream sub-areas have receptive fields that are more likely to include foveal regions than peripheral regions, and dorsal stream sub-areas, such as the parieto-occipital cortex, have receptive fields that represent central and peripheral visual fields relatively evenly (Colby et al. 1988). Thus, cortical magnification of the fovea may continue in the ventral (perception) stream, but not necessarily in the dorsal (action) stream.

The ventral and dorsal streams may also differ in their representation of upper and lower visual fields. The density of ganglion cells is 60% greater in the superior peripheral hemiretina (Curcio and Allen 1990) and these superior hemiretinal cells project more strongly (eventually) to the dorsal stream than to the ventral stream (Galletti et al. 1999; Maunsell and Van Essen 1987; for a review, see Danckert and Goodale 2003). This suggests that the location of a target stimulus in the upper or lower visual field may be a factor when considering the effects of stimulus eccentricity on vision-for-perception and vision-for-action.

Congruent with these differences between the representation of the central and peripheral vision in the two streams, several behavioural experiments suggest that peripheral visual information might be processed differently for perception and action. Goodale and Murphy (1997) compared perceptual judgments of object size and scaling of object-directed grasping for targets presented in the visual periphery. In their experiment, participants fixated markers positioned so that a central target object would be seen along the right horizontal meridian at eccentricities ranging between 10° and 70°. Targets of different sizes were presented for 100 ms and participants either categorized the target object by size (using a learned numerical scale), or reached out and grasped the object. Retinal eccentricity had quite different effects on the two tasks. Participants progressively underestimated target width as retinal eccentricity increased, a finding that was consistent with previously reported effects of increasing eccentricity on size perception (Bedell and Johnson 1984; Collier 1931; Newsome 1972; Schneider et al. 1978; Van Doorn et al. 1972). In contrast, when they reached out to grasp the object, maximum grip aperture increased with retinal eccentricity. Eccentricity did not influence the variability of performance in either task. Goodale and Murphy (1997) concluded that these

results reflected differences in the way size information was processed for perception and action in the visual periphery (but see Schlicht and Schrater 2003).

Several researchers (Danckert and Goodale 2001; Previc 1990) have investigated and reviewed how visual motor control is influenced by the visual field of target presentation. Using a pointing task with targets of variable width, they showed that speed accuracy trade-offs modeled by Fitts' Law (Fitts 1954) held only when the task was performed in the lower visual field rather than the upper visual field. They also showed that overall performance was better—faster and more accurate—when the task was performed in the lower visual field.

In this current study we repeated Goodale and Murphy's (1997) experiment and extended testing to include many locations in the peripheral visual field, including positions in both the upper and the lower visual fields. We measured perceptual judgments on a continuum by having each participant estimate object size by adjusting thumb-index finger separation. We eliminated the possibility that the eccentricity effects reported by Goodale and Murphy (1997) were due to a shift from binocular vision at near eccentricities to monocular vision at far eccentricities. We removed this confound by testing peripheral vision at locations that were always in the binocular range, between 10 and 40°. We expected perceived size and grip scaling would be differently affected by changes in target eccentricity. We also expected that there would be a lower visual field advantage for grasping but not perceptual judgments. In a final experiment, we tested the extent to which possible differences between the effects of eccentricity on perception and action may be because of greater stimulus uncertainty in the periphery by giving participants prior information about the size of the upcoming target. We expected that prior knowledge about object size would affect performance on estimation trials more than on grasping trials.

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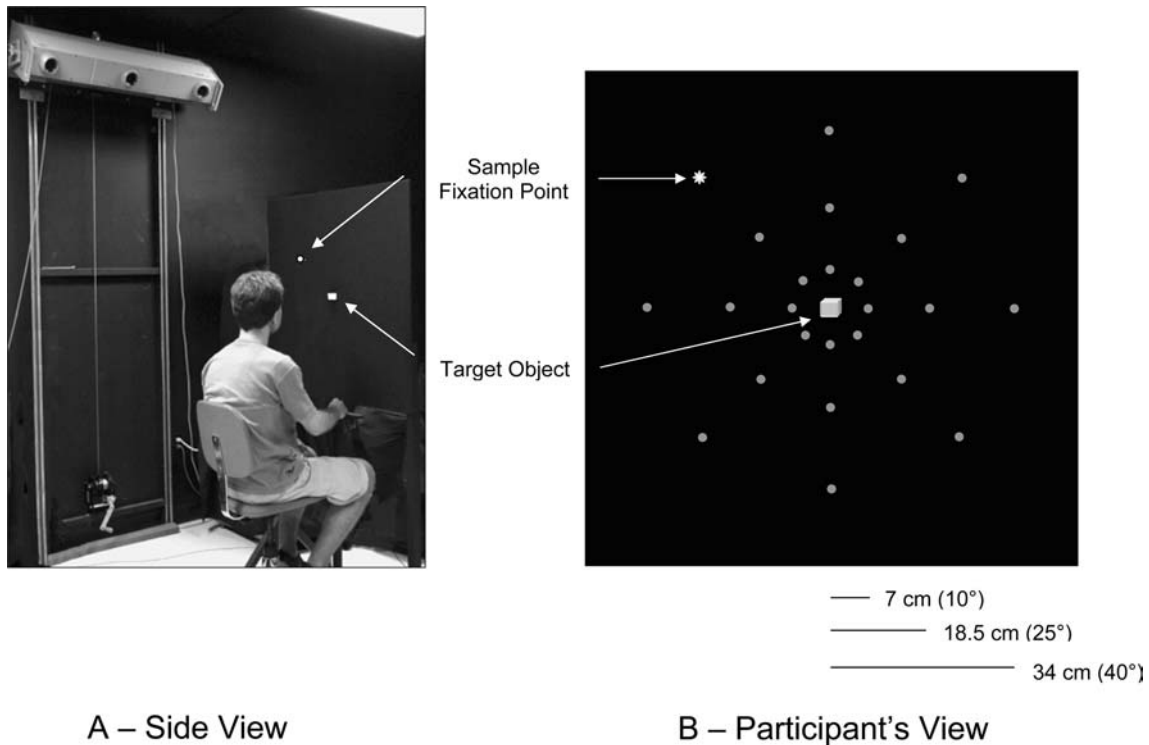
## Method

### Participants

Ten undergraduate students (four females, six males), aged 20–23, from the University of Western Ontario volunteered to participate. All participants reported being right-handed and had normal vision or vision corrected with contact lenses. The experiment was conducted in full compliance with the regulations of the University of Western Ontario Ethics Review Board.

### Materials

A vertical board (91.5 cm<sup>2</sup>) was used to display the fixation points and target objects (Fig. 1B). Twenty-four light-emitting diodes (LED) were embedded in the board at three eccentricities (10, 25, and 40° at a viewing distance of 40 cm) and in eight different directions (0, 45,



**A – Side View**

**B – Participant's View**

**Fig. 1** Experimental set-up. **A** Participant was seated directly in front of the vertical display board. The hand rested on a small stand placed at the participant's knee. The target object was placed in the center of the vertical board. One of 24 LED was illuminated for fixation. **B** The arrangement of the 24 fixation LED in eight directions and three eccentricities with respect to the central target object location. During the experiment, only one fixation point was visible on each trial. The three fixation eccentricities were designed to place the target object at 10, 25, or 40° eccentricity

90, 135, 180, 225, 270, 315°) with respect to a central target object location. The range of eccentricity ensured that the target object would always be viewed binocularly. The eight fixation directions allowed the target object to be seen in the lower, lower left, left, upper left, upper, upper right, right, and lower right visual fields, respectively. A 25th LED was located in the center of the board and was used to backlight the target object. The central target object location ensured that, irrespective of the location of the stimulus in the visual field, biomechanical requirements of the manual response would remain constant.

Six white-translucent plexiglass block objects of different sizes were used. To prevent viewers from using brightness as a cue for determining size, object surface area was held constant. The following object dimensions were used (height×width): 2.0×6.0, 2.5×4.8, 3.0×4.0, 3.5×3.4, 4.5×2.7, and 5.0×2.4 cm. Two of these objects (the 2.0 and 3.5 cm heights) were designated for later analysis and were presented a large number of times. The remaining four objects served as foils on randomly interleaved catch trials that were included to ensure that participants used vision to perform the tasks. On estimation trials participants always estimated the distance between the top and bottom (height) of the objects. On

grasping trials, they grasped the object across the same dimension (height). A clear plastic cube glued to the back of each object was designed to fit into a matching slot in the vertical board. This allowed the object to be placed over the central LED in the same way from trial to trial.

The participant sat in a chair of adjustable height, with his/her eye leveled and centered on the central LED of the vertical board (Fig. 1A). His/her hand rested on top of a stand, which sat between the participant's knees. An inactive button located on top of the stand served as the hand start location for each trial. Three infrared-emitting diodes (IRED) were attached to the participant's right thumb, index finger and wrist with medical adhesive tape. The IRED were tracked with an Optotrak 3D motion-analysis system (Northern Digital, Waterloo, Ont., Canada). The Optotrak recorded the 3D positions of the IRED at a frequency of 100 Hz. The positions were saved and later analyzed off-line.

### Design

The experiment used a two task (action, perception)×eight visual field (lower, upper, left, right, upper left, upper right, lower left, lower right)×three eccentricity (10, 25, 40°)×two object height (2.0 and 3.5 cm) within-participants design. Performance of each task was blocked and counterbalanced between participants. That is, five participants performed the action task before the perception task, and five performed the perception task before the action task. Visual field, eccentricity, and object height were randomly varied within each block of trials. Within each task, the

participant performed five blocks of trials. The first block consisted of five practice trials. The second, third, and fourth blocks each consisted of 53 trials. On 48 of those trials, the two objects designated for analysis were randomly presented at all combinations of visual field and eccentricity. On the remaining five trials, which were randomly interleaved, the foil objects were presented (10% catch trials). In the end, the participant repeated each possible trial combination three times. Finally, in the fifth block, we showed the 2-cm height object to the participant in advance and informed him/her that this same object would be presented on every trial. There were 48 trials in this fifth block with the participant performing each possible combination of visual field and eccentricity twice.

### Procedure

The participant was seated with the bridge of his/her nose 40 cm away from the vertical board. The room lights were extinguished and a small incandescent light was used for visibility as the trial was prepared. This light also prevented the participant from becoming dark-adapted. The experimenter used a cardboard shield to prevent the participant from viewing the target object as it was put in place.

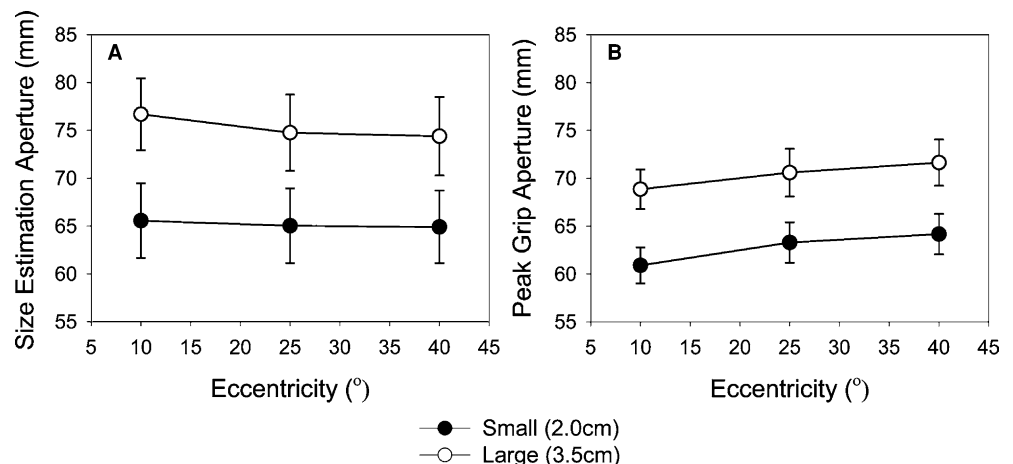
One of the 24 fixation LED was illuminated and the participant was given time to establish his/her gaze on the fixation point. The participant was instructed to maintain this fixation at all times. Once the target object was in place, and the experimenters were confident that the participant had adopted the correct gaze position, the light was extinguished and the room was completely dark for the remainder of the trial. The participant received a verbal ready signal from one experimenter, who then pressed a button that initiated the remaining trial sequence. The sequence started with a randomly chosen delay of 500, 750, 1,000, or 1,250 ms. This delay prevented the participant from anticipating the timing of target presentation. Following the delay, the target object was illuminated for 100 ms. The computer

generated an audible tone as the target LED was extinguished. The participant was instructed to initiate his/her response on hearing the tone. The Optotrak was triggered at the tone and the response was recorded. Participants were given 4 s to complete their response. At no time was this response duration insufficient.

Each participant performed two types of response. In the action task, the participant was instructed that, upon hearing the tone, he or she was to reach for and grasp the target object, remove it from the vertical board, and hand it to the experimenter. Given that iconic memory allows retinal image information to be maintained for approximately 300 ms (Averbach and Sperling 1960), and accurate specification of movement distance and direction takes 200–250 ms (Favilla et al. 1989), it is highly likely that performance was driven by concurrent retinal image information rather than by memory (Westwood and Goodale 2003).

For the perception task, the participant was told that upon hearing the tone, he or she should estimate object height as accurately as possible by adjusting the separation between the thumb and index finger (Amazeen and DaSilva 2005). The participant was told to keep the hand in contact with the start-button stand, and to make the estimate in the horizontal plane rather than the vertical plane. We asked participants to estimate object height in the horizontal plane in order to force them to compute the necessary vertical-to-horizontal transformation. This step was designed to increase the difference between the perception and action tasks, and thus strengthen our task manipulation. After the participant was satisfied with his/her estimate, he or she was instructed to close the finger and thumb together again. This action signaled that estimation was complete. Finally, the participant was asked to “help the experimenter” by handing the object over to her. The emphasis was placed on helping to prevent the participant from thinking that he or she was being asked to perform the action task after each perception trial. This step allowed us to provide the participant with tactile object size information on every trial in both the action and perception tasks.

**Fig. 2** Both SEA and PGA scaled with object size, and PGA increased with eccentricity. **A** For the perceptual size-estimation task, there was a non-significant trend for SEA to decrease with increasing eccentricity. **B** For the grasping task, PGA increased with increasing eccentricity



## Data analysis

The Optotrak system provided  $X, Y, Z$  positions over time for each IRED. Custom-designed analysis programs written with Matlab (The MathWorks, Natick, MA, USA) were used to define the beginning and end of each response and to calculate the Euclidean distance between the thumb and index finger IRED. Finally, Matlab was used to find the greatest distance between the thumb and index finger achieved for each response, the peak aperture (PA). This distance was designated the peak grip aperture (PGA) for the action task, and the size-estimation aperture (SEA) for the perception task.

The mean and standard deviation of these aperture measures were submitted to a two task (action, perception)  $\times$  eight direction (lower, lower left, left, upper left, upper, upper right, right, and lower right visual field)  $\times$  three eccentricity (10, 25, and 40°)  $\times$  two object size (2.0  $\times$  6.0, 3.5  $\times$  3.4 cm) repeated-measures analysis of variance (ANOVA,  $\alpha=0.05$ ). A separate analysis of these measures was carried out for the sub-experiment in which the participant had prior knowledge about object size. Interactions were decomposed by computing simple main effects for each interacting factor. Main effects of direction were further analyzed using planned comparisons ( $t$ -tests) of mean performance in the upper visual field versus the lower visual field and the right visual field versus the left visual field. Main effects of eccentricity were analyzed using planned comparisons ( $t$ -tests) between mean performance at all eccentricity levels.

## Results

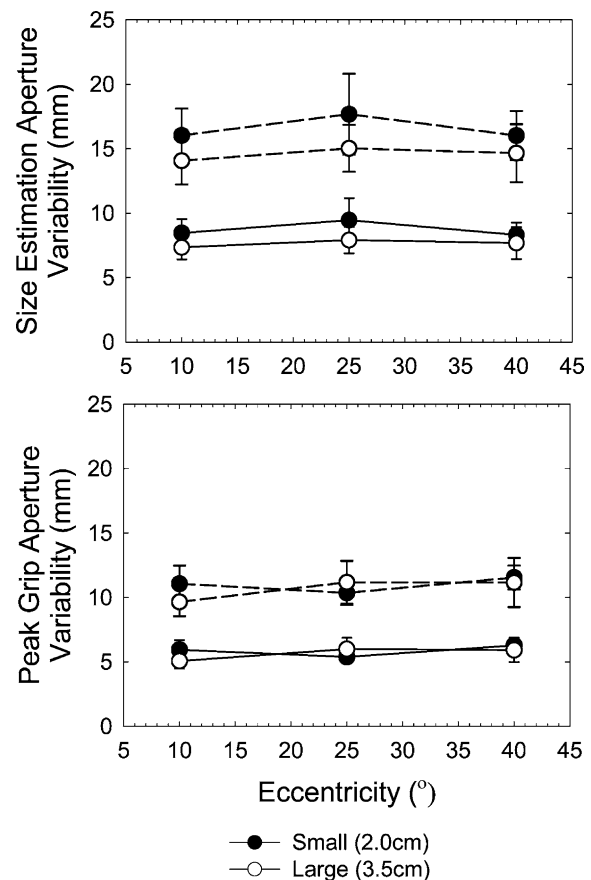
Both SEA and PGA were scaled to object size. Figure 2 shows SEA (panel A) and PGA (panel B) as a function of target eccentricity and object size. The overall mean aperture for the small object (mean  $\pm$  standard error = 63.98  $\pm$  1.78 mm) was significantly less than that for the large object (72.82  $\pm$  1.78 mm),  $F_{(1,9)}=70.86$ ,  $P<0.001$ . This scaling did not differ for perception and action ( $P=0.321$ ), and did not change with eccentricity ( $P=0.497$ ).

Eccentricity influenced grip aperture but not size-estimation aperture

While visual field had no significant influence on mean SEA or mean PGA,  $F_{(7,63)}=1.96$ ,  $P=0.130$ , target eccentricity had different effects on SEA and PGA,  $F_{(2,18)}=6.83$ ,  $P=0.006$ . Figure 2A shows a non-significant trend for SEA to decrease with eccentricity ( $P=0.119$ ). In contrast, Fig. 2B shows that PGA increased significantly with eccentricity,  $F_{(2,18)}=6.72$ ,  $P=0.017$ . Planned comparisons confirmed that mean PGA at 10° eccentricity (64.88  $\pm$  1.95 mm) was significantly smaller than mean PGA at 25° (66.94  $\pm$  2.26 mm,

$P=0.007$ ) and 40° (67.90  $\pm$  2.19 mm,  $P=0.021$ ) eccentricity. Mean PGA at 25° eccentricity did not differ from that at 40° ( $P=0.250$ ).

These results indicate that the effect of eccentricity on participants' perceptual size estimates was different from the effect of eccentricity on grasping. This finding is consistent with the hypothesis that vision-for-perception and vision-for-action depend on different neural systems and that these neural systems process peripheral stimuli in different ways. One alternative explanation for this finding is that PGA increased with eccentricity because uncertainty about object size increased with eccentricity (Schlicht and Schrater 2003). Indeed, it has been well documented that grip aperture is larger when visual information is degraded than when it is not degraded (Jakobson and Goodale 1991). One way in which we tested this hypothesis was to analyze the inter-trial variability (standard deviation and range) of SEA and PGA within each subject and each condition. If uncertainty about object size increased with eccentricity, then the standard deviation and range of both SEA and PGA should also increase with eccentricity.



**Fig. 3** SEA variability and PGA variability as a function of task, eccentricity, and object size. *Solid lines* show standard deviation values and *dashed lines* show range values. Variability did not increase with eccentricity for either the perception task (A) or the action task (B)

Figure 3 shows SEA variability (panel A) and PGA variability (panel B) as a function of target eccentricity and object size. Importantly, neither SEA variability nor PGA variability increased with eccentricity,  $F_{(2,18)} = 1.43$ ,  $P = 0.265$ . Pearson correlations showed there was no relationship between eccentricity and SEA variability for the perception task,  $r = 0.007$ ,  $P = 0.887$ , and that there was no relationship between eccentricity and PGA variability for the action task,  $r = 0.060$ ,  $P = 0.192$ . Thus, it is unlikely that the observed increase in mean PGA with eccentricity can be attributed solely to an increase in uncertainty with eccentricity.

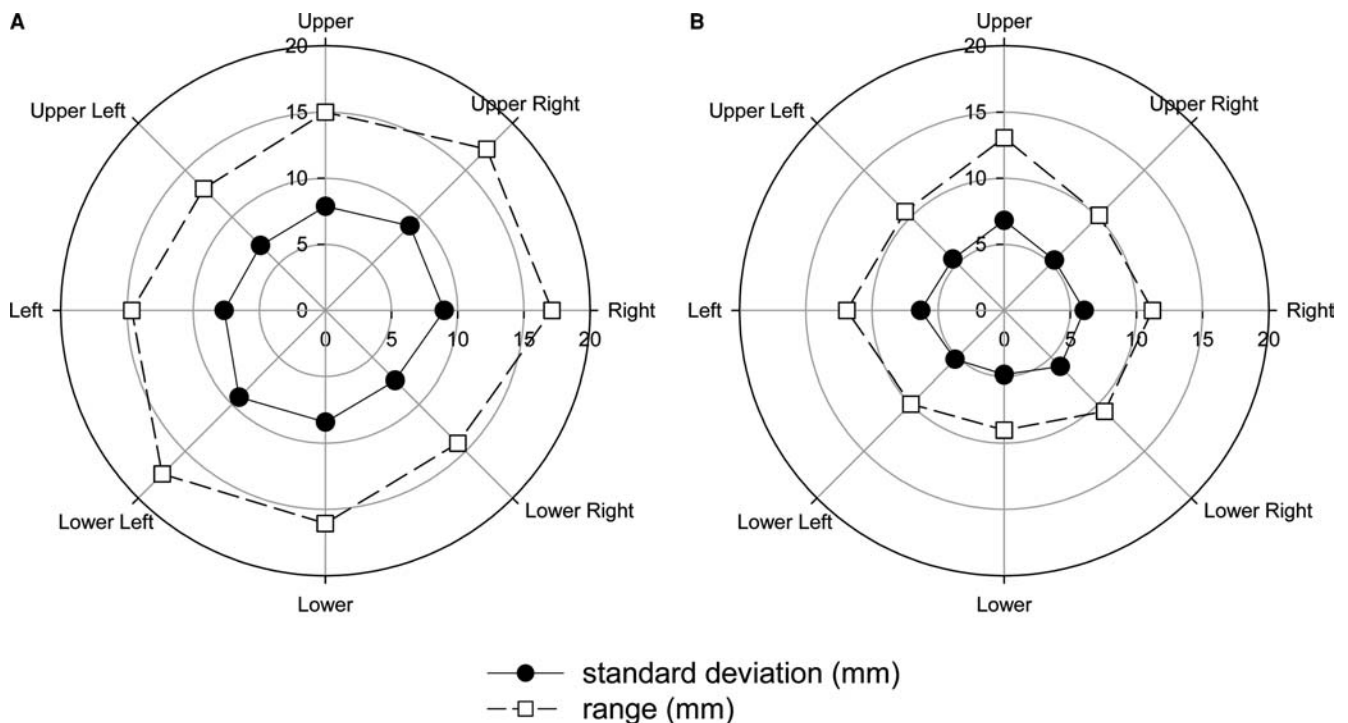
We also considered the possibility that PA varied with eccentricity for action but not perception, because participants took more or less time to plan their response during action than during perception. This was not the case, however. Reaction time (RT), the time between the go signal (tone) and response initiation, was not different for action ( $439 \pm 5$  ms) and perception ( $442 \pm 3$  ms), and it did not vary with eccentricity ( $P = 0.215$ ). Consequently, it does not seem that participants performed differently during the perception and action tasks because they invested more time preparing one task over the other.

Aperture variability shows visual field effects that differ for perception and action

Although response variability did not change as a function of eccentricity, it did vary with task and with visual field. Figure 4 shows the standard deviation and range of SEA (panel A) and PGA (panel B) plotted as a function of the visual field in which the target object appeared. Here one can see that the overall variability, represented by the plot area, is greater for perception than for action. This pattern was confirmed by a main effect of task,  $F_{(1,9)} = 14.73$ ,  $P = 0.004$ . In addition, there was a significant interaction between task and direction,  $F_{(7,63)} = 2.27$ ,  $P = 0.04$ . Planned comparisons indicated that for perception, mean SEA variability was significantly greater when the target object appeared in the right visual field ( $SD = 8.99 \pm 1.24$  mm) than in the left visual field ( $SD = 7.64 \pm 1.12$  mm,  $P = 0.027$ ), but did not differ when the target appeared in the upper ( $SD = 7.86 \pm 1.27$  mm) and lower ( $SD = 8.40 \pm 0.96$  mm) visual fields ( $P = 0.567$ ). By contrast, for action, PGA variability did not differ when the target appeared in the left ( $SD = 6.31 \pm 1.18$  mm) and right ( $SD = 6.05 \pm 0.72$  mm) visual fields ( $P = 0.823$ ), but PGA variability was greater when the target appeared in the upper visual field ( $SD = 6.80 \pm 0.42$  mm) than in the lower visual field ( $SD = 4.85 \pm 0.54$  mm,  $P = 0.002$ ). As can be seen in Fig. 4, analyses of range yielded the same pattern of results.

To summarize, analyses of response means and variability demonstrated different patterns in the perception and action conditions. Mean PGA increased significantly with eccentricity, but SEA did not vary with eccentricity. Aperture variability was greater during the

**Fig. 4** SEA (A) and PGA (B) as a function of visual field of target presentation. *Solid lines* show standard deviation values and *dashed lines* show range values. Overall variability was greater for SEA (perception) than for PGA (action). **A.** SEA was significantly more variable when the target appeared in the right visual field than in the left visual field. Upper and lower visual fields did not differ. **B.** PGA was significantly more variable when the target appeared in the upper visual field than in the lower visual field. Right and left visual fields did not differ



perception task than it was during the action task. Moreover, PGA variability was greater when the target object was presented in the upper visual field than the lower visual field, whereas SEA variability was greater when the target object was presented in the right visual field than the left visual field for perception. These results support the hypothesis that peripheral stimuli are processed differently for perception and action, and that grasping responses are more precise when the visual stimulus is presented in the lower visual field rather than in the upper visual field.

Prior knowledge of size reduces aperture variability for perception, but not action

To assess the influence of prior knowledge on both size estimation and grasping, performance on trials in which the small target object was randomly interleaved with other object sizes was compared with performance on trials in which the small target object was shown on every trial. The performance measures were submitted to a 2 (task) $\times$ 8 (visual field) $\times$ 2 (knowledge: yes, no) repeated-measures ANOVA. The results, shown in Fig. 5, indicated that prior knowledge did not have a significant overall effect on either mean SEA (panel A) or PGA (panel B),  $F_{(1,9)}=0.55$ ,  $P=0.479$ . Further, despite having prior knowledge about object size, participants continued to show a significant increase in mean PGA with eccentricity. In short, the significant interaction of task and eccentricity shown in Fig. 2 was still apparent even when object size did not vary,  $F_{(2,18)}=7.215$ ,  $P=0.005$ . This interaction was not influenced by prior knowledge about object size ( $P=0.374$ ).

These results can also be used to address the issue of uncertainty about object size. Typically, PGA is greater when uncertainty is high than when uncertainty is low because participants factor an additional margin for error into their grip space. If uncertainty contributed to aperture formation, then PGA should have been larger during conditions of random target size presentation (high uncertainty about object size) than during

conditions of constant target size presentation (low uncertainty about object size). Figure 5B shows, however, that there is no tendency for PGA to be larger during random target size presentation than constant size presentation. This result indicates, that at least under the conditions tested in this experiment, mean peak grip was not sensitive to uncertainty about object size.

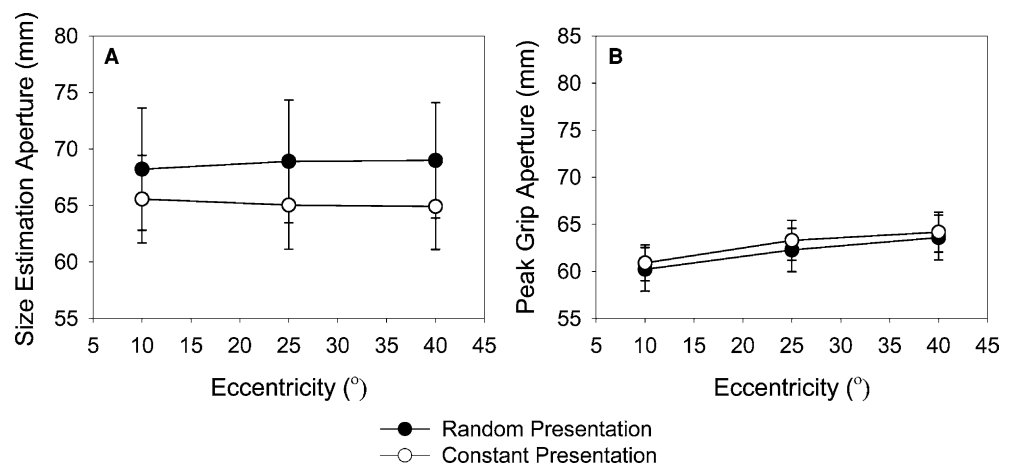
Prior knowledge of object size had a significant effect on performance variability  $F_{(1,9)}=5.93$ ,  $P=0.045$ . But as Fig. 6 shows, this was true only for the perception task, where prior knowledge about the size of the target object reduced SEA variability (panel A) from  $7.83 \pm 1.27$  to  $3.55 \pm 0.77$  mm,  $F_{(1,8)}=17.80$ ,  $P=0.003$ . The variability of PGA (panel B) was unaffected by such prior knowledge,  $F_{(1,8)}=0.41$ ,  $P=0.544$ . Altogether, prior knowledge helped participants increase the precision of their size estimates but did not change the precision of their grasp.

## Discussion

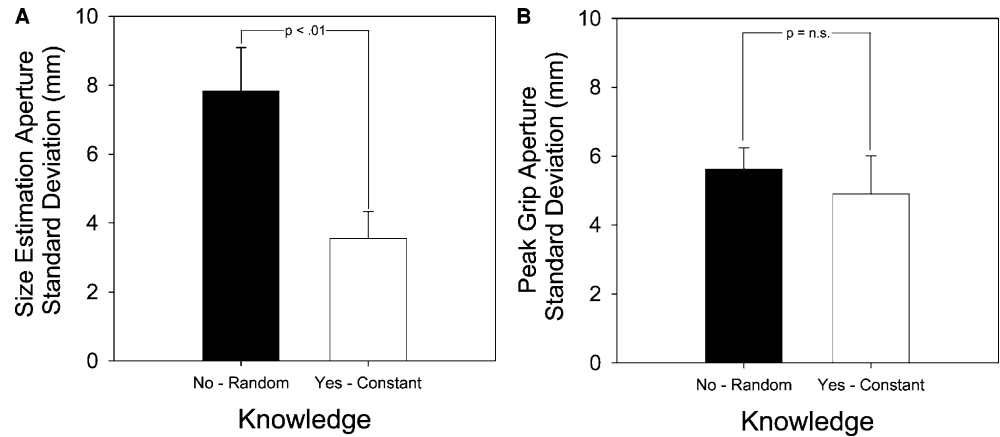
The current study examined how peripheral visual information presented at three eccentricities and in different visual field locations was used for perception and action. We found that perceptual size estimates did not change as target eccentricity increased but that PGA did increase with target eccentricity. Performance was more variable for the perception task than for the action task. The variability of SEA and grip aperture remained unchanged with target eccentricity but did change with visual field. Grip aperture formation was more variable when the target was presented in the upper visual field than in the lower visual field. In contrast, SEA was more variable when the target was presented in the right visual field than in the left visual field. Finally, giving participants information about object size beforehand reduced size-estimate variability but did not change grip aperture variability. An interpretation of these results follows.

One reason why PGA might increase with target eccentricity is that participants become less certain about the object's location and size at more eccentric target locations. In other words, because of uncertainty

**Fig. 5** Prior knowledge of object size did not have a significant effect on SEA (A) or PGA (B)



**Fig. 6** The effect of prior knowledge of object size on response variability (standard deviation) depended on task. **A** Prior knowledge significantly reduced SEA variability in the perception task. **B** Prior knowledge did not significantly reduce PGA variability in the action task



about these object properties, individuals increased their grip aperture to avoid an unwanted collision with the object. Indeed, this explanation has been put forward by others who have examined the effects of eccentricity on grasping (Schlicht and Schrater 2003). We tested this uncertainty hypothesis in two ways. For our first test, we reasoned that if the “uncertainty hypothesis” is correct then one would expect the variability of grip aperture to also increase with eccentricity. As Fig. 3 shows, however, there was absolutely no indication of such an increase. For our second test, we reasoned that if uncertainty about target size contributed to aperture formation, then PGA should be larger and more variable when target size was presented randomly (high level of uncertainty) than when target size was presented constantly. As Figs. 5B and 6B show, neither mean peak grip aperture nor PGA variability were significantly reduced when participants had advance information about target size. These converging pieces of evidence suggests that the observed increase in PGA as targets became more eccentric does not reflect a strategy used by participants to deal with uncertainty about target size.

Although the uncertainty hypothesis as it pertains to target size seems an unlikely explanation, it is still possible that PGA increased with eccentricity because of increasing uncertainty about target location. Indeed, it has been well documented that people tend to overestimate the eccentricity of peripherally presented targets (Bock 1986; Henriques et al. 1998; Henriques and Crawford 2001) and this error may have led to location uncertainty in our participants. At this time, we cannot address this issue because we did not vary target location. We do note, however, that past experiments in which target location was randomly varied (Roy et al. 2002; Meulenbroek et al. 2001) or perturbed upon movement initiation (Paulignan et al. 1991) have found that grasping (PGA), in comparison to measures of reaching, is relatively unaffected by manipulations of target location. These findings argue against the idea that the eccentricity-dependent increase in PGA is because of uncertainty about target location. Nevertheless, further testing is required.

Another possible explanation for the observed increase in PGA with eccentricity is that grip aperture may

have varied with gaze position irrespective of retinal eccentricity. Recall that placing the target at increasingly eccentric retinal locations required participants to adopt increasingly rotated gaze directions relative to the central gaze direction. It may be that holding the head and eyes away from the canonical forward gaze position caused participants to compute their limb position differently. Schlicht and Schrater (2003) asked participants to reach for and grasp a remembered target while adopting the eye positions necessary to place that target at increasingly eccentric retinal locations. For some participants, grip aperture increased with eye position eccentricity even though the target was never seen.

One prediction of this “gaze-position hypothesis” is that in addition to the effect of eccentricity, PGA would also be influenced by visual field. For example, Henriques and Crawford (2000) found that with eccentric fixation participants overestimated target eccentricity more for gaze directions that fell along the cardinal axes than for oblique gaze directions. If gaze position was a factor influencing performance in the current experiment, we might have expected performance to vary with both gaze direction and eccentricity. We saw no indication of this in our data, however, but again further research into how eye and gaze position affect grip formation is required.

Action-task performance is less variable than perception-task performance

Performance was less variable for the action task than for the perception task. This result is consistent with anatomical and neurophysiological data showing that a peripheral stimulus is represented with greater resolution in the dorsal stream than in the ventral stream. The different distribution of parvo-dominated and magno-dominated projections to the ventral and dorsal streams might play a role here. Recall that parvocellular layers of the LGN are characterized by a rapid eccentricity-dependent decline in density and that parvo-dominated pathways project more strongly to the ventral than the dorsal stream. The density of the magnocellular layers in the LGN does not decline nearly so rapidly with



eccentricity as density of the parvocellular layers (Azzopardi et al. 1999; Connolly and Van Essen 1984; Malpeli et al. 1996), however, and magno-dominated pathways project both to the dorsal stream and to the ventral stream (Milner and Goodale 1995; Van Essen and DeYoe 1995). Therefore, whereas the ventral (perceptual) stream devotes more cells to central than to peripheral coding, the dorsal (action) stream codes the peripheral and central visual fields more uniformly.

#### Superior performance in the lower visual field during the action task

PGA precision was greater when the target object was presented in the lower visual field than in the upper visual field along the vertical meridian. There was no difference between the upper and lower visual fields for size-estimation precision. This finding helps to strengthen the impression that visuomotor performance is better in the lower visual field than in the upper visual field (Danckert and Goodale 2001, 2003; Previc 1990). The result is consistent with anatomical and physiological research showing that retinal ganglion cell density is greater in the superior hemiretina than in the inferior hemiretina (Curcio and Allen 1990), and that the superior hemiretina projects more strongly to the dorsal stream than to the ventral stream (Danckert and Goodale 2003; Galletti et al. 1999; Maunsell and Van Essen 1987; Previc 1990). The combined influences of increased density of coding in the lower visual field and greater transmission of lower visual field stimulation to the dorsal stream than to the ventral stream can explain how precision is better in the lower visual field than the upper visual field for action but not perception.

#### Superior performance in the left visual field during the perception task

The precision of SEA was greater when the target object was presented in the left visual field than in the right visual field along the horizontal meridian. This finding is consistent with the widely held notion that visuospatial processing is better in the right hemisphere than in the left hemisphere (Corballis 2003). For example, split-brain patients are better able to make fine spatial discriminations about line orientation or vernier offset (Corballis et al. 2002) and they are better able to make perceptual judgments about whether two images are identical or mirror reversed (Funnell et al. 1999) when the visual stimulus is presented in the left visual field than in the right visual field. This hemispheric asymmetry for visuospatial processing does not seem to apply equally to visual perceptual judgments and the visual control of manual actions, however. Visuomotor disorders like optic ataxia are just as likely to follow a left-hemisphere lesion as they are to follow a right-hemisphere lesion (Perenin and Vighetto 1988), suggesting that visuomotor control is not characterized

by hemispheric specialization. Indeed, given the spatio-temporal demands of visuomotor control, one would not expect to see hemispheric specialization. Our finding that grasping variability did not differ in the left and right visual fields is consistent with this idea.

#### Prior knowledge of target size

Size-estimate variability was significantly reduced when participants were given information about target size in advance. PGA variability, in contrast, did not change with prior knowledge of target size. These findings are consistent with the two visual systems hypothesis (Goodale and Milner 1992; Milner and Goodale 1995). According to this hypothesis, vision-for-action and vision-for-perception make different demands on memory. Whereas vision-for-perception creates an object representation from both past and current object and contextual information, vision-for-action requires that information about position, orientation, and affordances of the object be continually updated as the body moves, with little or no storage of past information. Accordingly, one reason why participants estimated target size more precisely when they had prior information about target size than when they did not is that they were able to use this information to form a more reliable percept of the object. Alternatively, they may have performed more consistently after receiving advance information about the target's size simply because they repeated the same estimate on every trial. But whatever was actually going on during the size-estimation trials, it is important to note that when participants reached out and grasped the object, advance information had absolutely no effect on the variability of their grip aperture. Nor did it change the slope of the eccentricity effect on grip aperture; participants continued to open their hand wider at more eccentric fixations, even though the participant knew the size of the target they were grasping. In short, there was no evidence that the visuomotor system was capable of capitalizing on the participant's prior knowledge of target size—which, as Goodale and Milner (1992) have argued, is exactly what you would expect from a system that works entirely in real time.

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## Conclusion

Overall, our results support the notion that peripheral visual information is processed differently for perception and action. The findings also show that grasping is more precise when the goal object is presented in the lower visual field than in the upper visual field. In addition, the data also show that prior knowledge of the size of the goal object seems to reduce variability in perceptual judgments of size but not the scaling of grasping movements. This observation is consistent with a visuomotor system that must compute target data in real time.

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