THE ROYAL SOCIETY

Evidence for dissociation between the perceptual and visuomotor systems in humans

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When a visual stimulus is continuously moved behind a small stationary window, the window appears displaced in the direction of motion of the stimulus. In this study we showed that the magnitude of this illusion is dependent on (i) whether a perceptual or visuomotor task is used for judging the location of the window, (ii) the directional signature of the stimulus, and (iii) whether or not there is a significant delay between the end of the visual presentation and the initiation of the localization measure. Our stimulus was a drifting sinusoidal grating windowed in space by a stationary, two-dimensional, Gaussian envelope ($\sigma = 1$ cycle of sinusoid). Localization measures were made following either a short (200 ms) or long (4.2 s) post-stimulus delay. The visuomotor localization error was up to three times greater than the perceptual error for a short delay. However, the visuomotor and perceptual localization measures were similar for a long delay. Our results provide evidence in support of the hypothesis that separate cortical pathways exist for visual perception and visually guided action and that delayed actions rely on stored perceptual information.

Keywords: vision; illusion; motion; action

1. INTRODUCTION

Gibson's (1979) ecological approach to the psychology of perception highlighted the importance of vision in the control of action. Today, the close relationship between vision and action is once again being championed as a vital component of behaviour. In an elegant reworking of the 'two visual systems' idea (Trevarthen 1968; Schneider 1969; Ungerleider & Mishkin 1982), Milner & Goodale (1995) proposed that the division of labour within vision is balanced between a perceptual system responsible for conscious awareness of objects and their surroundings and a visuomotor system responsible for controlling visually guided actions. Both systems process information about the spatial locations of objects, though the transformations carried out by each reflect the different purposes for which they have evolved (Milner & Goodale 1995). For example, there is an immediate correspondence of visual information and motor behaviour with the visuomotor system, but not with the perceptual system (Bridgeman *et al*. 1997). Because the relationship between observers and goal objects is usually a dynamic one, it is conceivable that the object location signal generated by one system may differ from that generated by the other.

It is known that, when a visual stimulus is continuously moved behind a small stationary window, the window appears displaced in the direction of motion of the stimulus (Ramachandran & Anstis 1990; DeValois & DeValois 1991). The magnitude of the illusory displacement is greatest for eccentrically viewed stimuli (DeValois & DeValois 1991). Anstis & Ramachandran (1995) suggested that, from an ecological perspective, this

perceptual illusion might reflect compensation for the physical displacement a moving object would undergo during the delay associated with visual processing. If an observer was required to grasp the moving object, it is reasonable to assume that compensation may also be required for the added delay needed to process and execute motor commands. For example, in order to grasp a rapidly approaching object successfully, in comparison with the perceptual system's location signal, the visuomotor system's signal may be displaced towards the observer along the path of the object's trajectory.

We sought to provide evidence in support of this hypothesis by examining whether the magnitude of the spatial illusion described above (Ramachandran & Anstis 1990; DeValois & DeValois 1991) varies depending on whether a perceptual or visuomotor task is used for assessing it. Our stimulus was a drifting (or flickering) sinusoidal grating windowed in space by a stationary, two-dimensional, Gaussian envelope ($\sigma = 1$ cycle of sinusoid). It was presented for 500 ms at a retinal eccentricity of 10°. Following the stimulus presentation, the perceptual measure was accomplished by localizing the remembered target with reference to a ruler imaged on the display monitor. The visuomotor measure involved localizing the remembered target using a manual-pointing paradigm in which observers were unable to see their hand or arm. Because the visuomotor system is believed to operate in real time (Milner & Goodale 1995), significantly delayed actions directed at remembered targets are thought to rely on stored perceptual memories (Goodale & Haffenden 1998; Hu *et al*. 1999a,b; Milner 1999). For this reason, localization measures were made both with and without a significant delay (4 s) following the stimulus presentation.

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2. METHODS

(a) *Stimuli*

Sinusoidal gratings of 0.5 cycles deg^{-1} periodicity and 50% Michelson contrast were generated using a VSG2/3 graphics card (Cambridge Research Systems, Rochester, Kent, UK) and displayed on a Sony GDM-F500 monitor with a resolution of 600 lines × 800 pixels. They were orientated vertically and spatially windowed using a stationary, two-dimensional, Gaussian envelope with $\sigma = 1$ cycle of sinusoid (2°). The mean luminance (25.8 cd m^{-2}) and colour (yellow) of the grating patch was matched to that of the surround, which extended to 30° vertically by 37° horizontally. The temporal frequency of the sinusoid was 1.56, 3.13 or 6.25 Hz, either flickering or drifting to the left or right. A small fixation target was viewed binocularly. The grating patches were presented for 500 ms at an eccentricity of $10 \pm 1.5°$ along the horizontal meridian in the right visual field. The display screen was positioned to the side of the observer and viewed in a front-silvered mirror angled at 45° to the screen (see figure 1 for arrangement of the apparatus). The optical viewing distance was 50 cm.

(b) *Procedure*

Ability to localize the sinusoidal patches was assessed using either a perceptual or manual-pointing paradigm. Observers maintained central fixation during stimulus presentation with both paradigms. A method of constant stimuli was used. In the perceptual paradigm, a ruler was displayed on the screen either 200 ms (short-delay condition) or 4.2 s (long-delay condition) after the end of stimulus presentation. The ruler was 18° long, graded in 0.5° steps and centred at 10° eccentricity along the horizontal meridian. The presentation of the ruler was accompanied by an audible tone, which was the signal for the observer to disengage fixation and report the perceived location of the patch with reference to the ruler. In the manual-pointing paradigm, observers were again cued by a tone produced 200 ms or 4.2 s after the end of stimulus presentation to disengage fixation and mark a board positioned behind an opaque screen using a fine-tipped pen held in their right hand (see figure 1). Central fixation was not maintained because pointing responses are more reproducible if the eyes are aimed towards the remembered location of a peripheral target (Enright 1995). Between trials and during the stimulus presentation, the observer's arm lay rested on a table that supported the viewing mirror and opaque screen. In this position, the observer's hand was *ca.* 30 cm away from the marking board. It should be noted that observers were unable to see their arm and/or hand while in this position of rest or during the movement required for stimulus localization. For some control measures, the rest position of the observer's arm was down the side of the body, requiring a hand movement of *ca.* 110 cm in order to mark the perceived location of the stimulus.

Each set of measures comprised a block of 60 trials for both paradigms: 20 trials of rightward-drifting gratings, 20 trials of leftward-drifting gratings and 20 trials of flickering gratings. The stimulus type and position (range 3° and centred at 10° eccentricity) was randomized between trials. This procedure was repeated three times for each stimulus temporal frequency (1.56, 3.13 or 6.25 Hz), yielding 60 trials per datum.

(c) *Subjects*

Two subjects who were naive to the aims of the experiments were employed. Observer F.S. had normal visual acuity and
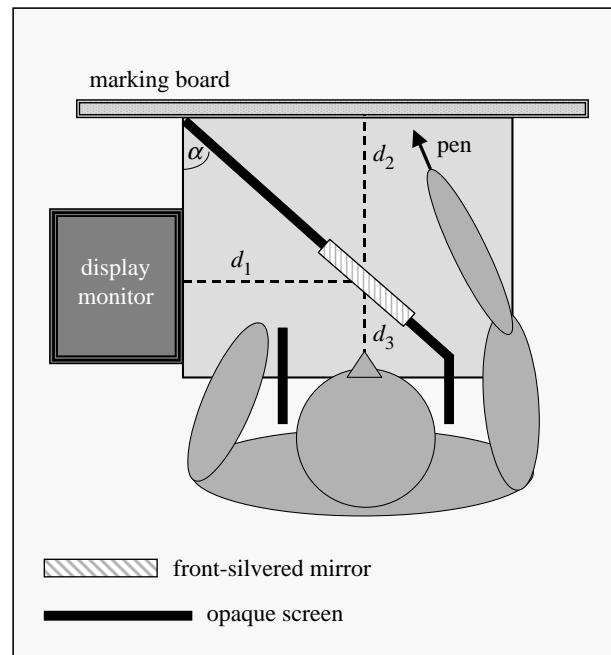

Figure 1. Schematic of the experimental set-up showing the position of the observer in relation to the display monitor, marking board, front-silvered mirror, table and opaque screening. The screening near the observer's right eye prevented the perception of any limb movement during the visuomotor localization task while that near the left eye prevented any direct perception of the stimulus. Values: $d_1 = d_2 = 35$ cm, $d_3 = 15$ cm and $\alpha = 45°$.

observer Y.K. had corrected to normal acuity using spectacles. Both subjects had normal visual fields and both were right-handed.

3. RESULTS

All of the results reported here for the visuomotor localization paradigm were based on a hand movement of *ca.* 30 cm (see § 2). Control measures requiring a hand movement of 110 cm yielded similar results.

(a) *Stimulus localization following a short post-stimulus delay (200 ms)*

Figure 2 shows the perceptual (open symbols) and visuomotor errors (solid symbols) in localizing eccentrically viewed patches of a sine-wave grating for two observers. Each localization task was instigated following a short (200 ms) post-stimulus delay. The grating (not the patch) was drifting either towards or away from the fovea or flickering at a temporal frequency of 1.56, 3.13 or 6.25 Hz (figure 2a–c, respectively). The results for drifting gratings are shown with respect to the location measure for the flickering gratings, which was normalized to zero. Positive location errors indicate a perceived displacement away from the fovea and negative errors indicate a perceived displacement towards the fovea. The size of the visuomotor error at each temporal frequency was approximately independent of stimulus direction but the perceptual error was usually greatest for stimuli drifting towards the fovea. Indeed, under most test conditions there was no significant perceptual error for stimuli drifting away from the fovea. The sign (positive or
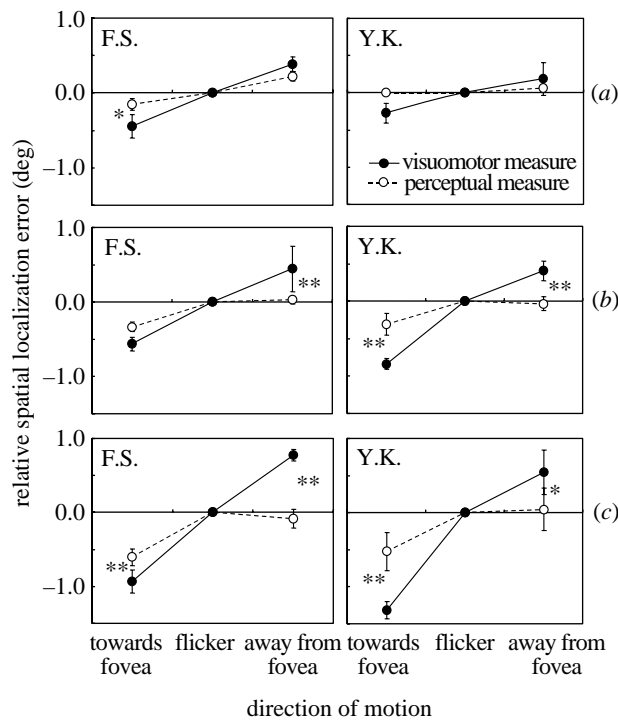
Figure 2. Visuomotor (solid symbols) and perceptual (open symbols) localization errors made following a short (200 ms) post-stimulus delay. Results are shown for observers F.S. (left-hand panels) and Y.K. (right-hand panels) for grating drift (or flicker) rates of (*a*) 1.56 Hz, (*b*) 3.13 Hz and (*c*) 6.25 Hz. The results for the drifting gratings are shown with respect to the location measure for the flickering gratings, which was normalized to zero. Positive location errors indicate a perceived displacement away from the fovea and negative errors towards the fovea. The perceived location of the flickering stimulus relative to its actual location was $0.32 \pm 0.21°$ for the visuomotor task and $0.75 \pm 0.05°$ for the perceptual task for observer F.S. The perceived location of the flickering stimulus was $3.58 \pm 0.15°$ for the visuomotor task and $0.48 \pm 0.15°$ for the perceptual task for observer Y.K. The vertical error bars show ± 1 s.e. of the mean. The asterisks indicate a significant difference between the visuomotor and perceptual localization measures ($^*p < 0.05$, $^{**}p < 0.01$) (unpaired *t*-statistic, two-tailed).

negative) of significant visuomotor and perceptual errors always coincided with the directional signature of the grating and the magnitude of the errors increased as the drift rate increased. Importantly, under most test conditions the visuomotor localization error was significantly greater than the perceptual error ($p < 0.05$). Details of the statistical analyses are reported in the legend to figure 2.

(b) *Stimulus localization following a long post-stimulus delay (4.2 s)*

The experiment reported above was repeated for localization measures instigated following a long (4.2 s) post-stimulus delay. The results are shown in figure 3 for the same two observers (F.S. and Y.K.) for grating drift or flicker rates of 1.56, 3.13 or 6.25 Hz (figure 3*a*–*c*, respectively). The open and solid symbols are the perceptual and visuomotor localization errors, respectively, plotted using the same format as in figure 2. As in the short-delay condition, the magnitude of the localization errors
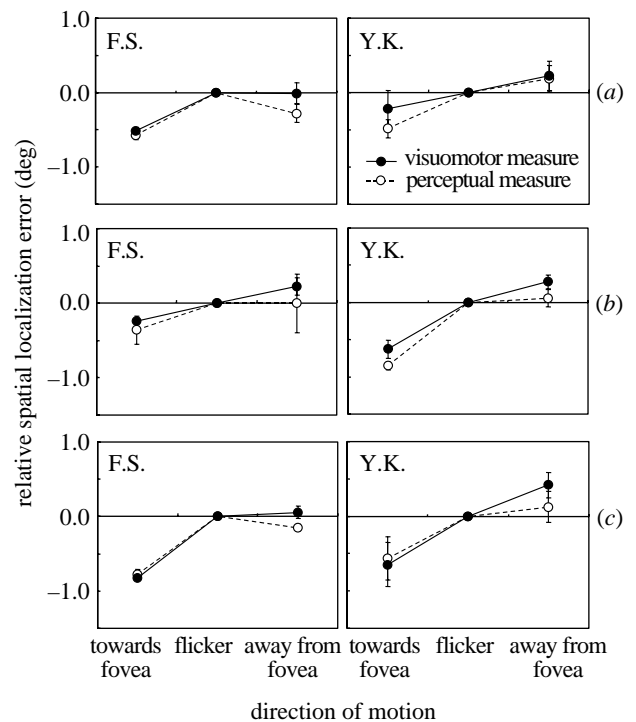
Figure 3. As in figure 2 for visuomotor (solid symbols) and perceptual (open symbols) localization errors made following a long (4.2 s) post-stimulus delay. The perceived location of the flickering stimulus relative to its actual location was $0.31 \pm 0.13°$ for the visuomotor task and $-0.21 \pm 0.20°$ for the perceptual task for observer F.S. The perceived location of the flickering stimulus was $3.75 \pm 0.49°$ for the visuomotor task and $-0.30 \pm 0.22°$ for the perceptual task for observer Y.K. The vertical error bars show ± 1 s.e. of the mean. There was no significant difference between the visuomotor and perceptual localization measures for each test condition ($p > 0.05$) (unpaired *t*-statistic, two-tailed).

in the long-delay condition was greatest for a stimulus drift rate of 6.25 Hz. In addition, the pattern of the perceptual errors was qualitatively similar in the short- and long-delay conditions, i.e. it was asymmetrical with the largest errors being evident for stimuli drifting towards the fovea. However, unlike the short-delay condition there was no significant difference between the visuomotor and perceptual localization measures, regardless of the stimulus drift rate or direction of motion ($p > 0.05$).

(c) *Comparison of the short- and long-delay conditions*

The differences between the short- and long-delay conditions for both localization paradigms are shown more clearly in figure 4. The 'localization error range', which was calculated as the absolute sum of the location errors for the rightward- (away from fovea) and leftward (towards fovea)-drifting gratings, is plotted as a function of grating speed for both observers. The top panels show the results for the short-delay condition (based on the data in figure 2) and the bottom panels show the results for the long-delay condition (based on the data in figure 3). Some individual differences were apparent. The perceptual error range for observer F.S. was largely unaffected by the length of the post-stimulus delay, while

that for observer Y.K. was greater in the long-delay condition than the short-delay condition by a factor of *ca.* 3.1 (averaged across stimulus drift rates). The visuomotor error range was less in the long-delay condition than in the short-delay condition by factors of 1.84 and 1.3 for observers F.S. and Y.K., respectively (averaged across stimulus drift rates).

However, the results for both observers were qualitatively similar. The localization error range was significantly greater for visuomotor than perceptual measures in the short-delay condition at each drift rate employed. However, the visuomotor and perceptual measures were approximately the same in the long-delay condition. The results of a two-way analysis of variance (ANOVA) are reported in the legend to figure 4.

4. DISCUSSION

Our results show that the extent to which a peripherally viewed stimulus is mislocalized in space varies depending on (i) the directional signature of the stimulus, (ii) whether a perceptual or visuomotor task is used for judging its location, and (3) the immediacy of the observer's response following stimulus presentation.

Under most test conditions, significant perceptual localization errors were only evident for stimuli drifting towards the fovea. The reason for this is not clear, although it might relate to the fact that there are significant differences in sensitivity in favour of centripetal motion at eccentricities of 5–12.5° (Raymond 1994; Fawcett *et al.* 1998). Raymond (1994) suggested that heightened sensitivity to stimuli drifting towards the fovea might act to facilitate figure/ground segmentation in the presence of optic flow signals that accompany forward locomotion. Visuomotor localization errors, on the other hand, were evident for stimuli drifting either towards or away from the fovea. The direction of visuomotor mislocation always coincided with that of the stimulus. The marked difference in the qualitative nature of the perceptual and visuomotor localization errors immediately suggests that the perceptual system uses a different representation of object location than the motor system. Milner & Goodale (1995) argued that separate representations might be required because object-centred coding is needed for perception while viewer-centred coding is needed for action.

The visuomotor location error was significantly greater than the perceptual error for near immediate responses (figure 2). Again, a difference between perceptual and visuomotor location signals is indicative that different cortical mechanisms are responsible for their generation. Such a conclusion is consistent with the hypothesis that separate cortical pathways exist for visual perception and visually guided action (Milner & Goodale 1995). However, the visuomotor localization measure was approximately the same as the perceptual measure for delayed responses (figure 3). This result is to be expected if it is the case that, because computations by the visuomotor system decay rapidly (Milner & Goodale 1995), significantly delayed actions directed at remembered targets rely on stored perceptual memories (Goodale & Haffenden 1998; Hu *et al.* 1999a,b; Milner 1999).
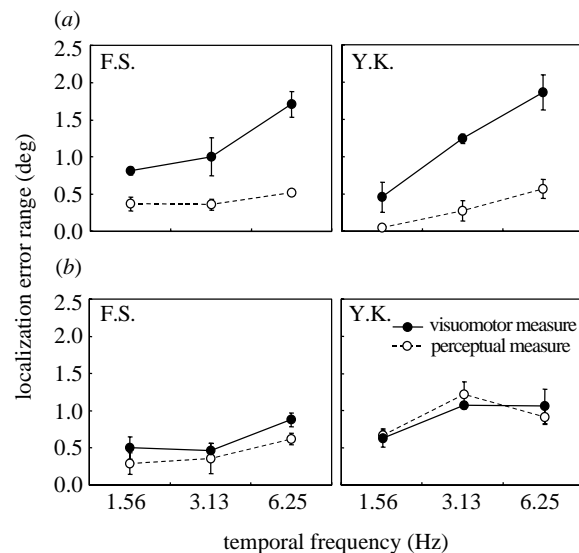
Figure 4. Summary of the results from figures 2 and 3. The localization error range, which was calculated as the absolute sum of the location errors for the rightward- (away from the fovea) and leftward (towards the fovea)-drifting gratings, is plotted as a function of the grating speed for observers F.S. (left-hand panels) and Y.K. (right-hand panels). Results are shown for both visuomotor (solid symbols) and perceptual (open symbols) localization measures. The panels show the results for (a) the short-delay condition and (b) the long-delay condition. The vertical error bars show ± 1 s.e. of the mean. A two-way ANOVA revealed significant effects of grating speed ($F_{2,12} = 13.93$ and $p < 0.01$ for subject F.S. and $F_{2,12} = 19.65$ and $p < 0.01$ for subject Y.K.), localization measure ($F_{1,12} = 57.69$ and $p < 0.01$ for subject F.S. and $F_{1,12} = 51.36$ and $p < 0.01$ for subject Y.K.) and the interaction ($F_{2,12} = 6.50$ and $p < 0.05$ for subject F.S. and $F_{2,12} = 4.92$ and $p < 0.05$ for subject Y.K.) for the short-delay condition, but a significant effect of grating speed only ($F_{2,12} = 4.42$ and $p < 0.05$ for subject F.S. and $F_{2,12} = 16.99$ and $p < 0.01$ for subject Y.K.) for the long-delay condition.

Our extraordinary ability to reach and grasp moving objects is seemingly at odds with the fact that our sensory experiences lag behind the physical changes in the environment that give rise to them. We must be 'living in the past' because retinal processing and the transfer of information along the optic nerve to the brain can take as long as 30–100 ms (Maunsell & Gibson 1992; Cavanagh 1997). Under certain circumstances, such as those where actions are required to grasp or avoid a fast-moving object, the temporal asynchrony between environmental change and sensory experience could have serious consequences for survival. The inability to localize visual targets of the type described above accurately may reflect the fact that the human visual system has mechanisms in place for compensating for the effects of this asynchrony. Anstis & Ramachandran (1995) argued that the illusory displacement of such targets reflects compensation for the physical displacement a moving object would undergo during the delay associated with visual processing. Presumably, compensation is also required for the added delay needed for processing and executing motor commands and this may be why, when a near immediate response is required, visuomotor localization errors exceed perceptual errors.

For example, for a carrier of 0.5 cycles deg^{-1} periodicity travelling at 6.25 Hz towards the fovea, the perceptual error was 0.55° (figure 2c) (results averaged across observers). Therefore, at our viewing distance of 50 cm, the perceptual error for a target travelling at 10.9 cm s^{-1} was 0.48 cm, which would compensate for a temporal delay of 44 ms. Under the same conditions, the visuomotor error was 1.18° (1.03 cm), which would compensate for a temporal delay of 95 ms.

Some studies have suggested that the visual system corrects for transmission delays using operations akin to extrapolation, whereby the perceived position of a moving object is extrapolated forwards in time based on its speed, trajectory and neural latency (Nijhawan 1994; Khurana & Nijhawan 1995; Sheth *et al.* 2000). The extrapolation hypothesis was based on studies of the 'flash-lag phenomenon', in which a continuously moving bar is perceived to be ahead of a stationary flashed (stroboscopically illuminated) bar when the two images are spatially aligned on the retina. Although other explanations for this phenomenon have been advanced (Baldo & Klein 1995; Purushothaman *et al.* 1998; Brenner & Smeets 2000; Whitney *et al.* 2000), the extrapolation hypothesis is supported by the results of this study. The ecological advantage of such operations for both perception and action is clear. It is also clear that optimal performance is likely to be achieved if correctional operations were implemented early, before the merger of information from various visual areas and indeed other sensory systems. Interestingly, Berry *et al.* (1999) recently showed that the spiking activity in a population of ganglion cells elicited by a moving bar travels near the leading edge of the bar rather than lagging behind it. They concluded that the extrapolation of a moving object's trajectory might begin in the retina. Any higher order correctional operations are likely to take place within the dorsal stream, which is thought to play a vital role in transforming visual information into motor behaviour (Ellermann *et al.* 1998).

REFERENCES

Anstis, S. M. & Ramachandran, V. 1995 At the edge of movement. In *The artful eye* (ed. R. Gregory, J. Harris, P. Heard & D. Rose), pp. 232–248. Oxford University Press.

Baldo, M. V. C. & Klein, S. A. 1995 Extrapolation or attentional shift? *Nature* **378**, 565–566.

Berry, M. J., Brivanlou, I. H., Jordan, T. A. & Meister, M. 1999 Anticipation of moving stimuli by the retina. *Nature* **398**, 334–338.

Brenner, E. & Smeets, J. B. J. 2000 Motion extrapolation is not responsible for the flash-lag effect. *Vision Res.* **40**, 1645–1648.

Bridgeman, B., Peery, S. & Anand, S. 1997 Interaction of cognitive and sensorimotor maps of visual space. *Percept. Psychophys.* **59**, 456–469.

Cavanagh, P. 1997 Predicting the present. *Nature* **386**, 19–21.

DeValois, R. L. & DeValois, K. K. 1991 Vernier acuity with stationary moving gabors. *Vision Res.* **31**, 1619–1626.

Ellermann, J. M., Siegal, J. D., Strupp, J. P., Ebner, T. J. & Ugurbil, K. 1998 Activation of visuomotor systems during visually guided movements: a functional MRI study. *J. Magnet. Res.* **131**, 272–285.

Enright, J. T. 1995 The non-visual impact of eye orientation on eye–hand coordination. *Vision Res.* **35**, 1611–1618.

Fawcett, S., Raymond, J. E., Astle, W. F. & Skov, C. M. B. 1998 Anomalies of motion perception in infantile esotropia. *Invest. Ophthalmol. Visual Sci.* **39**, 724–735.

Gibson, J. J. 1979 *The ecological approach to visual perception.* Boston: Houghton Mifflin.

Goodale, M. A. & Haffenden, A. 1998 Frames of reference for perception and action in the human visual system. *Neurosci. Biobehav. Rev.* **22**, 161–172.

Hu, Y., Eagleson, R. & Goodale, M. A. 1999a The effect of delay on the kinematics of grasping. *Exp. Brain Res.* **126**, 109–116.

Hu, Y., Eagleson, R. & Goodale, M. A. 1999b Relative size information influence after a delay. *Invest. Ophthalmol. Visual Sci.* **40**, S412.

Khurana, B. & Nijhawan, R. 1995 Extrapolation or attentional shift? *Nature* **378**, 565–566.

Maunsell, J. H. & Gibson, J. R. 1992 Visual response latencies in striate cortex of the macaque monkey. *J. Neurophysiol.* **68**, 1332–1344.

Milner, A. D. 1999 Neuropsychological studies of perception and visuomotor control. In *Attention, space and action* (ed. G. W. Humphreys, J. Duncan & A. Treisman), pp. 217–231. Oxford University Press.

Milner, A. D. & Goodale, M. A. 1995 *The visual brain in action.* Oxford University Press.

Nijhawan, R. 1994 Motion extrapolation in catching. *Nature* **370**, 256–257.

Purushothaman, G., Patel, S. S., Bedell, H. E. & Ogmen, H. 1998 Moving ahead through differential visual latency. *Nature* **396**, 424.

Ramachandran, V. & Antis, S. M. 1990 Illusory displacement of equiluminous kinetic edges. *Perception* **19**, 611–616.

Raymond, J. E. 1994 Directional anisotropy of motion sensitivity across the visual field. *Vision Res.* **34**, 1029–1037.

Schneider, G. E. 1969 Two visual systems: brain mechanisms for localization and discrimination are dissociated by tectal and cortical lesions. *Science* **163**, 895–902.

Sheth, B. R., Nijhawan, R. & Shimojo, S. 2000 Changing objects lead briefly flashed ones. *Nature Neurosci.* **3**, 489–495.

Trevarthen, C. B. 1968 Two mechanisms of vision in primates. *Psychol. Forschung* **31**, 299–337.

Ungerleider, L. G. & Mishkin, M. 1982 Two cortical visual systems. In *Analysis of visual behavior* (ed. D. J. Ingle, M. A. Goodale & R. J. W. Mansfield), pp. 549–586. Cambridge, MA: MIT Press.

Whitney, D., Murakami, I. & Cavanagh, P. 2000 Illusory spatial offset of a flash relative to a moving stimulus is caused by differential latencies for moving and flashed stimuli. *Vision Res.* **40**, 137–149.