

Dirk Kerzel · Karl R. Gegenfurtner

Motion-induced illusory displacement reexamined: differences between perception and action?

Received: 12 May 2004 / Accepted: 8 October 2004 / Published online: 8 December 2004
© Springer-Verlag 2004

Abstract The position of a drifting sine-wave grating enveloped by a stationary Gaussian is misperceived in the direction of motion. Previous research indicated that the illusion was larger when observers pointed to the center of the stimulus than when they indicated the stimulus position on a ruler. This conclusion was reexamined. Observers pointed to the position of a small Gabor patch on the screen or compared its position to moving patches, stationary lines, or flashed lines. With moving patches, the illusion was larger with probe than with motor judgments; with stationary lines, the illusion was about the same size; and with flashed lines, the illusion was smaller with probe than with motor judgments. Thus, the comparison between perceptual and motor measures depended strongly on the methods used. Further, the target was mislocalized toward the fovea with motor judgments, whereas the target was displaced away from the fovea relative to line probes.

Keywords Action · Extrapolation · Illusion · Motion · Perception · Pointing · Position judgments

Introduction

It has been proposed that different visual processing streams use the same input from early vision for different computations (Goodale and Milner 1992). In the ventral route from V1 to the ventral temporal cortex, visual representations for object recognition are built. To this end, information about surrounding objects is taken into account. The ventral route is therefore believed to operate in world-centered (allocentric) coordinates. In the dorsal route from V1 to the posterior parietal cortex, information

about the position and velocity of objects is transformed to guide action. Most importantly, this requires the transformation of retinotopic into viewer-centered (egocentric) coordinates while ignoring information about other objects. Therefore, the spatio-temporal context is expected to influence action to a smaller degree than perception.

A size-illusion provided initial support for this view. In the Ebbinghaus-illusion, the perceived size of a circle is affected by the size of surrounding context elements. The central target circle appears smaller when large context elements surround the target and larger when small context elements surround it. When perceptual and motor size judgments were compared, it was found that grasping movements were not as strongly affected by the surrounding stimuli as perceptual judgments (Aglioti et al. 1995). The conclusion was that action resists illusions. However, this finding has been criticized on methodological grounds.

Among other things (overview in Franz 2001), the size of the illusion in perception changes as a function of the method used to measure it. Therefore, the illusion may be larger in perception than in action, or may be of equal size (Franz et al. 2000). To illustrate the difficulty of matching perception and action, two methods to measure the Ebbinghaus illusion in perception will be briefly described. First, a circle in isolation was matched to a circle surrounded by small context elements or to a circle surrounded by large context elements (single context condition). The (unsigned) deviations of the matched circle from the true size were then averaged across the large and small context conditions. A second method to measure the perceptual illusion was to match the size of a circle surrounded by small context elements to the size of a circle surrounded by large context elements (two context condition). If the illusion was additive, the size difference required to match the two circles in the two context condition would be twice the size difference required to match the circles in the single context condition: when both circles have a context, the small and the large context elements contribute to the illusion at the same time. However, it turned out that the adjusted size of the illusion

D. Kerzel (✉) · K. R. Gegenfurtner
FB 06 Psychologie und Sportwissenschaft, Abteilung
Allgemeine Psychologie, Justus-Liebig-Universität Gießen,
Otto-Behaghel-Str. 10F,
35394 Giessen, Germany
e-mail: dirk.kerzel@psychol.uni-giessen.de
Tel.: +49-641-9926107
Fax: +49-641-9926119

was larger in the two context condition compared with the single context condition, indicating that the illusion was over-additive. In contrast, the grasping condition does not require a comparison stimulus, and it is therefore difficult to say which of the two context conditions provides the more adequate comparison. In any case, a comparison between perception and action using the two context condition showed a larger illusion in perception than in action, while a comparison using a single context condition indicated no difference between perception and action.

Thus, the answer to the question of whether the size illusion is larger in perception than in action may be elusive because motor action only requires a single target, whereas perceptual judgments mostly need a probe stimulus in addition to the target and it is unclear which probe stimulus is the most adequate.

In the present study, we will further investigate an illusion of position that was taken as evidence for the theory of two separate visual streams. When a drifting sine-wave grating is seen through a stationary Gaussian window (i.e., a Gabor patch), the perceived position of the stationary window is shifted in the direction of motion (De Valois and De Valois 1991; Ramachandran and Anstis 1990). It has been shown that the illusory displacement of the Gabor patch is larger for action (pointing) than for perception (comparison to a ruler, Yamagishi et al. 2001): displacement in the direction of motion was larger for motor action than for perception. Contrary to Goodale and Milner's (1992) claim that action is more accurate than perception, the error was larger for action than for perception. However, the findings provide evidence for the claim of separate visual processing for perception and action.

The first goal of the present study was to reexamine whether the difference between perception and action for motion-induced displacement depends on the comparison (probe) stimulus used in the perceptual task. As outlined for the Ebbinghaus-illusion above, there are multiple ways to measure a perceptual illusion, and the outcome of the comparison between perception and action may depend on which probe stimulus is used in the perceptual task. Therefore, we used a drifting Gabor (Exp. 1), and continuous or flashed lines (Exps. 2 and 3) as probe stimuli. Observers' task in the perceptual (probe) condition was to compare the horizontal position of the target patch to two probe stimuli above and below the target (see Fig. 1). The size of the perceptual illusion was then compared to the size of the illusion in the motor system. Observer's task in the motor condition was to point to the center of the target patch (manual estimation: Exps. 1 and 4) or to saccade to the target (ocular estimation: Exp. 5). Pointing movements were executed with full vision of the hand (Exp. 1) or in the dark (Exp. 4).

The second goal was to track the time course of the perceptual illusion. To this end, the probe either appeared simultaneous with the target or 500 ms after target offset (see Fig. 1). Simultaneous presentation ("perceptual localization") allows for relative judgments in a retinotopic

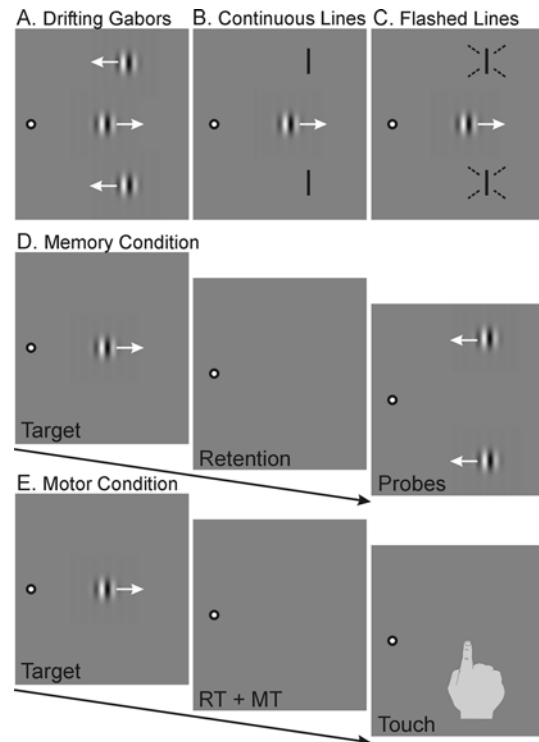


Fig. 1a–e Schematic drawing of the stimuli (not drawn to scale) and procedure. **a–c** Observers fixated a bull's eye and judged whether the probe stimuli at 3° above and below the vertical midline were to the left or right of the central Gabor patch. The eccentricity of the Gabor was $6 \pm 0.55^\circ$. Moving Gabor patches, continuously visible lines or flashed lines were used as probes. In the perceptual condition, target and probe stimuli were simultaneously visible. With flashed lines, the time interval between target onset and flash was varied. **d** In the memory condition, the probe stimuli were present after a retention interval of 500 ms. **e** In the motor condition, observers released the home key as soon as they detected target motion. The time from target onset to release of the home key is referred to as reaction time (RT). RT and movement time (MT) add up to the total time

coordinate frame, whereas the delayed condition ("memory-based localization") requires storage of the object's position in visual short-term memory. Research on visual short-term memory suggests that the illusion may be larger in the memory compared with the perceptual condition: when observers are asked to localize the final position of a moving object, they tend to judge the object further in the direction of motion than it actually was (overview in Hubbard 1995). It was suggested that observers are unable to stop the mental representation of motion instantaneously ("representational momentum") and continued the motion of the target mentally. If there was "representational momentum" for motion-induced illusory displacement, larger motion-displacement is expected with a delayed probe stimulus. However, if there was a time course, this would make a comparison between perception and action more complicated. While the presentation of probe stimuli may be fully controlled, it is less clear which time interval is most relevant for the pointing movement.

Third, we determined mislocalization of the target relative to the fovea. Previous reports showed mixed

findings: some studies demonstrated that a peripheral target was localized toward the fovea (e.g., Kerzel 2002; Sheth and Shimojo 2001), whereas other studies demonstrated mislocalization away from the fovea (e.g., Bock 1986; Henriques et al. 1998). We do not intend to clarify this apparent contradiction between previous studies, but we will look for differences between perception and action with respect to biases away or toward the fovea. However, it has to be kept in mind that perceptual mislocalization toward or away from the fovea is always relative to the probe stimulus (allocentric), whereas motor mislocalization is egocentric without vision of the hand (Exp. 4) and a mixture of allocentric and egocentric with vision of the hand (Exp. 1).

Fourth, we made an attempt to improve the methods used by Yamagishi et al. (2001), which employed a rather large Gabor patch as a stimulus. The standard deviation of the Gaussian was 2° such that the patch had a diameter of 2–4 times the standard deviation. Because the contrast drops off gradually with a Gaussian envelope, the size of the Gabor patch is difficult to determine. If 5% contrast is considered a cut-off criterion, the diameter of the stimulus was 6° . At a viewing distance of 50 cm in Yamagishi et al., this translates into a stimulus size of 5.3 cm. For pointing movements, this stimulus is not ideal because the tip of the fingers is only about 1.5–2 cm wide. Consequently, observers have to determine the center of the stimulus before they can actually point to it. With smaller diameters, the stimulus determines the goal of the pointing movement in a more direct manner (i.e., observers may try to “cover” the stimulus with their finger). Similarly, the perceptual measure used by Yamagishi et al. required a rather indirect judgment: observers had to determine the position of the moving stimulus on a ruler after target offset.

In the present study, a small Gaussian with a standard deviation of 0.6° and a sine wave with a spatial frequency of 1.3 cycles/deg were used. The resulting Gabor patch provided a more adequate stimulus for pointing movements because of its smaller diameter (about 1.8 cm). The Gabor patch was either moving or stationary and was presented for only 350 ms. In the motor condition, observers were asked to point to the target as rapidly and accurately as possible. Yamagishi et al. (2001) reported that the difference between perception and action vanished with a delay of 4 s, presumably because delayed motor judgments are based on perceptual memories. Further, the perceived position was estimated using probe judgments and a two-alternative, forced-choice protocol (2AFC). As outlined above, the nature of the probe stimulus and the relative timing of target and probe were varied.

Three dependent measures were analyzed. First, the deviation along the direction of motion indicates the magnitude of illusory displacement. Here, positive values indicate that the moving object was localized too far in the direction of motion. Second, the deviation with respect to the fovea indicates whether the target was localized closer to the fovea than it actually was. Here, positive values indicate that the target was localized further away from the

fovea. Finally, the variability of the judgments was considered. To this end, the width of the psychometric function fit to the probe judgments was compared with the width of the distribution of motor judgments.

General methods

Participants

Students at the Justus-Liebig-University of Giessen were paid for their participation, reported normal or corrected-to-normal vision and were naive as to the purpose of the experiment. Some students participated in more than one experiment. Prior to the inclusion in the study, all subjects gave their informed consent. The work was approved by the local ethics committee.

Stimuli and apparatus

The stimuli were presented on a 21-inch (diagonal) CRT-display with a resolution of 1,280 (H) \times 1,024 (V) pixels at a refresh rate of 100 Hz. One pixel measured about 0.03° . The stimuli were presented on a light gray background of 32 cd/m² in a fully illuminated room. Observers' head position was stabilized with a chin rest at 49 cm from the screen. The position of one eye was monitored with a head-mounted, video-based eye tracker at a frequency of 250 Hz (EyeLink II, SR-Research, Canada). Observers were instructed to fixate a bull's eye (0.6° diameter) in the center of the screen, and eye movements larger than 1° were considered a fixation error. Pointing movements to the screen were recorded by an ELO Touchsystems (Fremont, CA, USA) touch interface at the pixel resolution of the monitor. To reach the screen, participants had to move the hand from a start button about 22 cm below and 17 cm in front of the screen center (distance of ~ 26 cm).

The main stimulus was a sine-wave grating with a spatial frequency of 1.3 cycles/deg and 100% contrast that was windowed by a Gaussian with a standard deviation of 0.64° (H) \times 0.56° (V). The contrast of the patch was modulated in time by a Gaussian with a standard deviation of 65 ms. The Gaussian was clipped 170 ms before and 170 ms after maximum contrast. That is, the complete sequence took 350 ms (2 * 170 ms + 10 ms at max. contrast). The Gabor patch was either stationary or drifted at a temporal frequency of 4 Hz. The target stimulus was presented randomly to the left or right of the fixation mark at an eccentricity of $6 \pm 0.55^\circ$. In conditions with relative judgments, two probe stimuli were presented 3° above and 3° below (center-to-center) the target stimulus (see Fig. 1). The horizontal offset of the probe stimuli was adjusted for each condition. In conditions with motor responses, the probe stimuli were absent.

Procedure and design

At the beginning of each trial, observers were asked to look at the fixation bull's eye. To initiate a trial, observers pressed a designated button on a game pad in front of them. Then, the EyeLink system performed a drift correction. When it was successful, the bull's eye changed into a small filled circle (0.18° diameter). One hundred milliseconds later, the target appeared. In conditions with probe judgments, the probes appeared simultaneously with the target or some time later. The observers' task was to decide whether the probe was to the left or right of the target stimulus by pressing the left or right mouse button. In conditions with motor responses, observers initiated a goal directed movement as soon as they detected the stimulus. Observers were instructed to keep the start button depressed until they initiated the response. If the motor response was too early or too late (for definitions, see below), or inaccurate (deviation of more than 3° from the true target position), visual error feedback was provided.

Data analysis

Trials with saccades and eye blinks were removed when eye fixation was to be maintained. Table 1 shows the proportion of excluded trials. For moving stimuli, the left-right judgments were transformed into "further" judgments which indicate whether observers judged the probe to be further in the direction of motion relative to the target position. For each condition and observer, a cumulative normal distribution was fit to the proportions of "further" judgments (PROBIT). The normal distribution is characterized by two parameters. The peak of the normal distribution, μ , indicates the point of subjective equality (PSE) between the target and the probe position. The width of the distribution, σ^2 , indicates the sensitivity or variability of the judgments (measured as standard deviation).

Table 1 Percentage of trials that were excluded due to fixation errors (including blinks), late responses, anticipations, and outliers (more than two SD from condition mean). In the experiment with saccadic responses, a fixation error refers to the fact that no saccade larger than 1° was detected. Note that more than one error type may have occurred in a given trial

| Experiment | Fixation error | Anticipation | Late | Outlier | Total |
|-------------|----------------|--------------|------|---------|-------|
| 1 Probe | 1.7 | - | - | - | 3.2 |
| Motor | 2.4 | 2.5 | 8.6 | 3.8 | 14.0 |
| 2 Probe | 3.2 | - | - | - | 1.7 |
| 3 Probe | 1.1 | - | - | - | 1.1 |
| 4 Feedback | 4.9 | 2.6 | 7.6 | 3.5 | 15.0 |
| No feedback | - | 3.1 | 5.9 | 4.5 | 10.6 |
| 5 Saccade | 3.0 | 0.4 | 2.1 | 3.5 | 5.0 |

PSE and standard deviation were determined for motion toward and away from the fovea. Positive values would indicate displacement in the direction of motion, and negative values would indicate displacement opposite the direction of motion. The average PSE for motion toward and away from the fovea estimated the net motion-induced displacement: $[PSE(away) + PSE(toward)]/2$. To estimate whether the patch was mislocalized toward or away from the fovea relative to the probe, the sign of the displacement for motion toward the fovea was reversed such that positive (negative) values indicate displacement away (toward) from the fovea: $[PSE(away) - PSE(toward)]/2$. This measure is referred to as foveal displacement. Similarly, the PSE for stationary stimuli was determined such that positive (negative) PSEs indicate displacement away from (toward) the fovea. To this end, the left-right judgments were transformed into judgments about whether the target was judged further away from the fovea.

In the analysis of the motor judgments, late and early trials, fixation errors and blinks were removed (critical time intervals are given below). Then, the deviation of the true center of the stimulus from the endpoint of the

Fig. 2 Mean motion-displacement and between-subjects standard error in the various experimental conditions. The number of the respective experiment is given after the hyphen. Positive values indicate that the target was localized too far in the direction of motion relative to the true target position. For probe judgments, the values were obtained by fitting a cumulative normal distribution to the psychometric function. For motor judgments (hand or eye), the values were obtained by calculating the mean

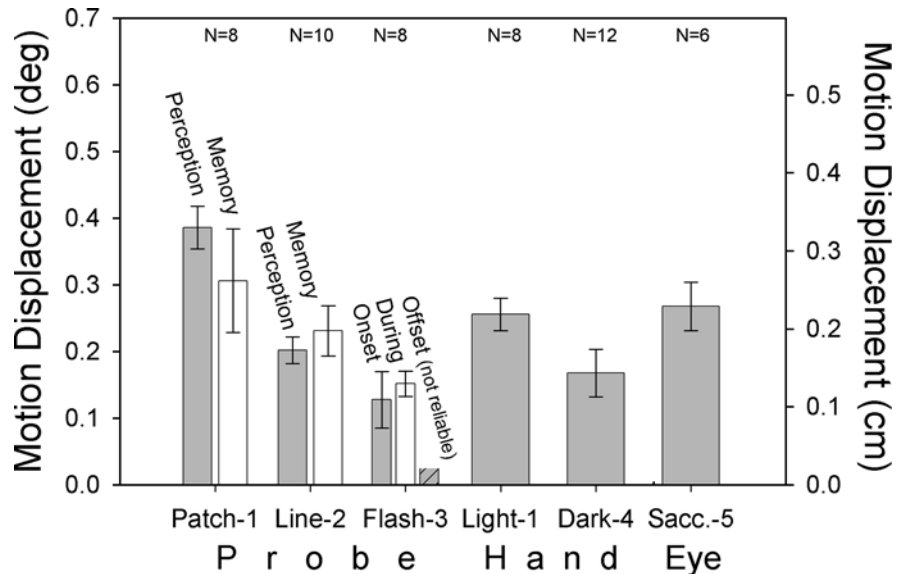


Fig. 3 Mean foveal displacement and between-subject standard error of the mean for the experimental conditions. Positive values indicate that the target was localized too far away from the fovea relative to the probe. The number of the respective experiment is given after the hyphen

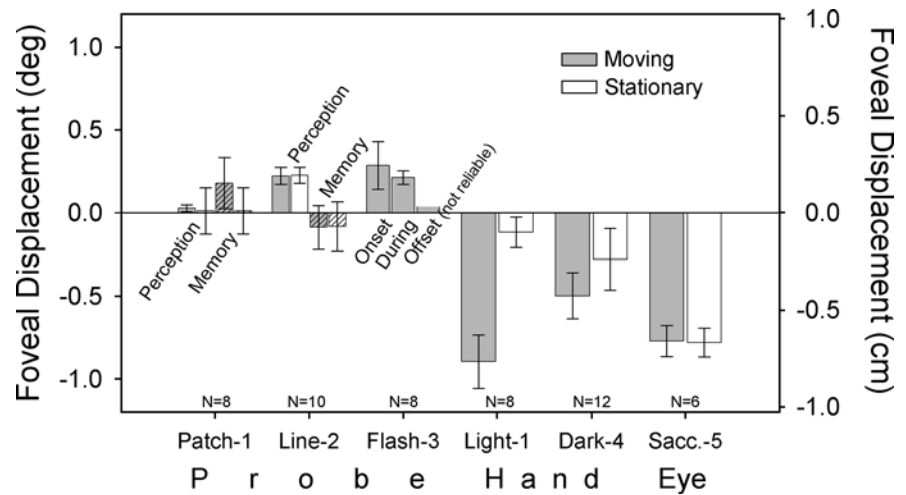
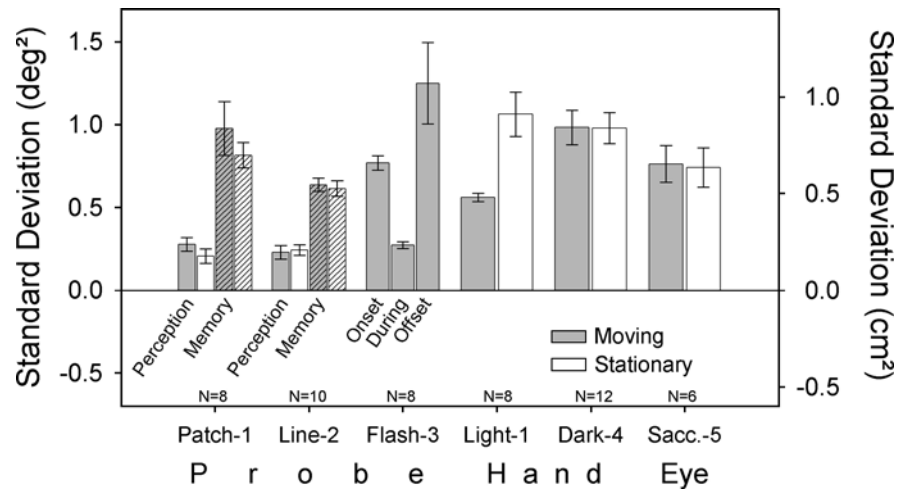


Fig. 4 Mean standard deviation and between-subject standard error for the experimental conditions. For probe judgments, the standard deviation indicates the width of the cumulative normal distribution fit to the data. For motor judgments (hand or eye), the deviation of the endpoints of the movement from the condition mean were computed. The number of the respective experiment is given after the hyphen



pointing movement or saccade was determined. The preliminary mean and preliminary standard deviation of the errors was computed. Responses that differed by more than two preliminary standard deviations from the preliminary condition mean were considered outliers and were excluded from the analysis. Then, the final condition means and standard deviations were computed. Latencies were determined with respect to the onset of the stimulus. If the latency was smaller than 50 ms, both manual and ocular responses were considered anticipatory. The time between onset of the stimulus and contact with the screen (manual responses) is referred to as total time. If it was longer than 800 ms (in the light) or 900 ms (in the dark), the response was considered late. Saccadic responses with latencies longer than 500 ms were considered late.

The comparison of motion and foveal displacement is straightforward. In both cases, the best estimate of the expectancy value, μ , is used: the average deviation for motor responses and the peak of the normal distribution fit to the probe judgments. The underlying assumption is that both measures have a normal distribution. To compare the variability of the judgments, the best estimate of the variance, σ^2 , is used: the standard deviation for motor judgments and the width of the normal distribution fit to the probe judgments.

For all experiments, motion displacement is shown in Fig. 2, foveal displacement is shown in Fig. 3, and the standard deviation is shown in Fig. 4. The percentage of excluded trials is shown in Table 1.

Experiment 1: drifting Gabors as probe stimuli

Perceptual and motor localization of moving and stationary Gabor patches was investigated. To measure localization without motor components, observers were asked to localize the horizontal position of a central target Gabor relative to two probe Gabors that were presented above and below (see Fig. 1). When the Gabor patches were moving, the probe patches moved in exactly the same manner into the opposite direction. Thus, illusory position shifts of the target and probe patches add up. In the motor condition, observers were asked to point to the center of the stimulus. In contrast to Yamagishi et al. (2001), who blocked vision of the hand, this was done with full vision of the hand. To make probe and motor judgments as comparable as possible, observers had to maintain fixation in both conditions. Typically, observers first look to where they point and gaze direction and pointing movement are tightly coupled (Neggers and Bekkering 2000). This is not

the case for probe judgments. Further, a condition with stationary target and probe patches was run as a control condition.

Method

Motor and probe judgments were compared in a group of eight participants. The probe stimuli were the same as the target stimulus. That is, either moving or stationary Gabor patches were shown as test and probe patches. The time course of the contrast modulation was identical for probe and target patches. In the perceptual condition, the target was shown at the same time as the probe. In the memory condition, the probes were shown 500 ms after target offset. The horizontal probe offset was 0, ± 0.33 , ± 0.65 , or $\pm 0.97^\circ$ in the perceptual condition and 0, ± 0.65 , ± 1.30 , or $\pm 1.95^\circ$ in the memory condition. The spacing of the probes was chosen so as to adequately sample the distribution with an equal number of conditions. The width of the distribution was gauged in pilot experiments. In the motor condition, only the target patch was shown. Observers had to maintain fixation until they made contact with the screen. The perceptual and motor conditions were run on separate days and 504 trials were run for each condition for each observer. The probability of target motion toward the fovea, motion away from the fovea, or no motion was 1/3.

Results

Because both target and probe were moving, the size of the illusion is half the PSE. For this experiment, these corrected values are reported. Condition means were compared by t-test. T-tests were two-tailed and paired unless noted otherwise. Motion-displacement was significantly different from zero with probe judgments that were presented simultaneous with the target and some time later, $t_{(7)} > 7.6$, $ps < .0001$. The size of the illusion was on the order of 0.35° and the difference between the perceptual and the memory condition of 0.08° did not reach significance, $t_{(7)} = 0.8$, $p > .4$. Foveal displacement did not differ significantly from zero, $t_{(7)} < 1.3$, $ps > .24$, and there was no difference between the perceptual and the memory conditions, $t_{(7)} = 1.0$, $p > .34$. Similarly, there was no foveal displacement with the stationary stimulus, $t_{(7)} < 1$, $ps > .3$. The standard deviation of the psychometric functions was larger in the memory than in the perceptual condition by 0.7 deg^2 with moving stimuli, $t_{(7)} = 4.8$, $p < .005$, and by 0.61 deg^2 with stationary stimuli, $t_{(7)} = 7.6$, $p < .005$.

In the motor condition, motion-displacement was 0.26° and significantly different from zero, $t_{(7)} = 10.8$, $p < .0001$. There was significant displacement toward the fovea of -0.89° , $t_{(7)} = 5.5$, $p < .001$, with moving stimuli, but not with stationary stimuli, $t_{(7)} = 1.3$, $p > .2$. The difference of 0.78° in foveal displacement between moving and stationary stimuli reached significance, $t_{(7)} = 4.2$, $p < .005$.

The mean reaction (total) time did not differ across conditions and was 326 ms (681 ms), $F_{(2,14)} = 1.44$, $p > .2$.

Before comparing probe and motor judgments, the displacement values obtained with perceptual and memory-based probe judgments were averaged. Motion-displacement was 0.09° larger with probe than with motor judgments, $t_{(7)} = 3.9$, $p < .01$. The foveal displacement with moving stimuli was 1.0° more negative with motor judgments than with probe judgments, $t_{(7)} = 6.1$, $p < .001$. With stationary stimuli, the foveal bias did not differ significantly between probe and motor judgments, $t_{(7)} = 0.9$, $p > .13$.

For moving stimuli, the standard deviation of motor judgments was larger by 0.28 deg^2 compared with perceptual probe judgments, $t_{(7)} = 4.8$, $p < .005$, but smaller by 0.42 deg^2 compared with memory-based probe judgments, $t_{(7)} = 2.6$, $p < .05$. For stationary stimuli, the standard deviation of motor judgments to stationary stimuli was larger by 0.85 deg^2 compared with perceptual probe judgments, $t_{(7)} = 6.4$, $p < .001$; however, it did not differ from memory-based probe judgments, $t_{(7)} = 1.5$, $p > .18$. Thus, the variability of motor judgments in the light falls in between perceptual and memory-based probe judgments.

Discussion

Both probe and motor judgments were significantly biased in the direction of motion. This finding replicates illusory displacement in perception, visual short-term memory, and action. Comparison of probe and motor judgments showed that the illusion was *larger* in perception than in action. This finding is contrary to the results of Yamagishi et al. (2001), who reported *smaller* displacement in perception than in action. However, a number of methodological differences exist. Maybe the most important are that Yamagishi et al. used a stationary probe stimulus (a ruler) and blocked vision of the hand. Effects of probe type were investigated in Exps. 2 and 3, while effects of visual feedback about the hand movement were investigated in Exp. 4.

There was no time course of the illusion with probe judgments, indicating that there was no "representational momentum" with illusory position shifts. Rather, the illusion was the same for perception and memory (see also Sheth and Shimojo 2003). This finding makes it unlikely that the presence of a second stimulus during presentation of the target explained differences between perception and action: with delayed probe presentation, the target was initially presented in isolation and the probe appeared a substantial time later. Because there was no time course, it was justified to average the perceptual and memory condition, and to compare this value with the motor condition.

Further, there was no foveal displacement in the probe task, but significant displacement toward the fovea with motor judgments and moving stimuli. With stationary stimuli and motor judgments, there was no displacement

toward the fovea. This indicates that motor judgments were not per se biased toward gaze direction, but that the illusion in motor judgments was stronger for motion toward the fovea than for motion away from it. Such a difference was not observed for probe judgments. Thus, perception and action differ with respect to foveal displacement. However, it should be kept in mind that the two tasks involved egocentric and allocentric judgments to a different degree.

Experiment 2: lines as probe stimuli

In Exp. 1, drifting Gabor patches were used as probe stimuli and the illusion was found to be larger in perception than in action. In the present experiment, two aspects of the probe stimuli were changed: the stimuli were stationary (vs. drifting) and narrow (vs. extended) lines (vs. patches) that were presented without contrast modulation. This was done to make the methods more similar to Yamagishi et al. (2001), who used a ruler as a comparison. The question was whether the change to a stationary probe stimulus would affect the size of the perceptual illusion. If the illusion was additive, no difference should emerge. If it was over-additive, a larger illusion would result when moving Gabor patches are compared with moving probe patches (cf. Exp. 1). This reasoning is similar to previous studies on the Ebbinghaus illusion (see Introduction). Of course, because the nature of the probe stimuli was changed at the same time, other factors may also contribute such as the smaller extent of the probe stimuli (patches vs. lines).

Method

Probe judgments were measured in a group of ten observers. The probe stimuli were one-pixel, black (~ 0 cd/m²) vertical lines that approximately matched the vertical extent of the Gabor patch. The length was 1.5° at 3° above and below the target patch. There was no contrast modulation over time. In the perceptual condition, the lines were visible for 350 ms (i.e., during target presentation). In the memory condition, the lines appeared 500 ms after target offset and stayed on until a response was given. The horizontal probe offset was 0, ± 0.22 , ± 0.43 , $\pm 0.65^\circ$ in the perceptual condition and 0, ± 0.43 , ± 0.87 , $\pm 1.3^\circ$ in the memory condition.

Results

Motion-displacement was significantly different from zero with probes that were presented simultaneous with the target and some time later, $t_{(9)} > 6.1$, $p_s < .0005$. The size of the illusion was on the order of 0.22° and the difference between the perceptual and the memory condition of 0.03° did not reach significance, $t_{(9)} = 0.8$, $p > .4$. In a between-subject comparison, the probe judgments from the current

experiment were compared with the motor judgments from Exp. 1. One participant was excluded from this comparison because she had participated in both experiments. This left 16 independent observations. M-displacement was of the same magnitude as in the motor condition of Exp. 1 (0.22 vs. 0.26°), $t_{(14, \text{unpaired})} = 1.4$, $p > .18$.

There was significant displacement of 0.22° away from the fovea in the perceptual condition, $t_{(9)} = 4.4$, $p < .005$. In the memory condition, foveal displacement was not significant (-0.09°), $t_{(9)} = 0.7$, $p > .5$, but the difference in foveal displacement between perception and memory was reliable (0.31°), $t_{(9)} = 2.6$, $p < .05$.

The standard deviation of the psychometric function for the moving stimuli was larger by 0.41 deg² in the memory condition than in the perceptual condition, $t_{(9)} = 7.4$, $p < .001$. Similarly, the standard deviation for the stationary stimulus was larger by 0.37 deg² in the memory compared with the perceptual condition, $t_{(9)} = 7.5$, $p < .001$.

Discussion

When lines were used as probe stimuli, the illusion was somewhat smaller than with drifting Gabors as probes, and not significantly different from the pointing data in Exp. 1. Thus, the present method would suggest that there is no difference between perception and action. This may be due to the fact that the illusion is not completely additive: with a moving target and moving probes the illusion (PSE adjusted by factor 0.5) is slightly larger than with stationary lines. Thus, the difference between perception and action depends on which allocentric reference is chosen in the perceptual task.

However, a different conclusion would have to be drawn with respect to the foveal bias. With lines as probes, the target was localized away from the fovea, whereas there was a bias toward the fovea with motor judgments. Thus, on the basis of the present experiment, one would have to conclude that perception and action differ with respect to the bias toward or away from the fovea. A very simple explanation for the bias away from the fovea with lines as probe stimuli would refer to the increase of receptive field size with eccentricity. The larger stimulus (the target) will excite more eccentric neurons than the smaller stimulus (the probe). Because the more eccentric neurons have a larger receptive field, the center of activation will be biased away from the fovea. Further experiments in our lab (not reported here) indicate that it is the size, rather than the absence of high spatial frequencies that causes the bias to the outside.

Experiment 3: flashed lines as probe stimuli

Experiment 1 showed that the illusion was larger in perception than in action when moving probes were employed. Experiment 2 showed no difference between perception and action when stationary line probes were used. Both experiments have in common that the probes

were present for an extended period of time. However, it may be equally legitimate to compare a moving stimulus with a briefly presented flash. This procedure was extensively used in research on the flash-lag effect. In the flash-lag effect, the position of a moving object appears to lag behind the position of a stationary flash (Nijhawan 1994, 2002). This ensures that the position of the moving object at one particular instant in time is compared with the probe.

Method

Probe judgments were measured in a group of eight observers. The probe stimuli were drawn during one refresh cycle (visible for about 5 ms, Bridgeman 1998) either at the onset of the sequence, during the sequence at maximum contrast, or at stimulus offset (i.e., 170 ms before max. contrast, at max. contrast, or 170 ms after max. contrast). The probe stimuli were as in Exp. 2 with the exception that the width was increased from 0.03 to 0.15°. Probe offset was 0, ± 0.29 , ± 0.58 , $\pm 0.87^\circ$.

Results

The fit of the psychometric function to the data in the offset condition was not reliable as is evident in the large variation in that condition. The psychometric function was essentially flat for some observers. It may be the case that the flashes masked the patches when presented after patch offset, which rendered the task very difficult. Therefore, this condition will not be considered any further. There were no differences between flash presentation at motion onset and during the motion sequence with respect to motion and foveal displacement, $t_{(7)}=0.5$, $p > .5$. Therefore, the PSEs were averaged across these conditions. Motion-displacement was 0.14° and reliably different from zero, $t_{(7)}=5.7$, $p < .001$. Foveal displacement was away from the fovea (0.25°), $t_{(7)}=2.9$, $p < .05$. The psychometric function was 0.5° wider when the probe was presented at probe onset compared with during stimulus motion, $t_{(7)}=9.4$, $p < .001$.

In a between-subject comparison, the probe judgments from the current experiment were compared with the motor judgments from Exp. 1. One participant was excluded from this comparison because she had participated in both experiments. This left seven independent observations in each group. Motion displacement in the motor condition was significantly larger by 0.13° than in the probe condition, $t_{(12,unpaired)}=3.7$, $p < .01$.

Discussion

Consistent with the results of Yamagishi et al. (2001), perceived motion-displacement with probe judgments was smaller than motion-displacement with motor judgments. It may be that continuation of the motion after the flashed

influenced the perceived position of the flash (i.e., motion may have “dragged” the flash along), such that the perceptual illusion was reduced. Thus, depending on the method used to measure the perceptual error, three different conclusions may be reached: perception shows a larger error than action (Exp. 1), perception and action do not differ (Exp. 2), or action shows a larger error than perception (Exp. 3). The reason for this is that the perceptual illusion decreased as the probes were changed from drifting Gabors, to stationary lines and to flashed lines. As in the previous experiments, motion-displacement in this experiment did not differ as a function of the time of probe presentation. In contrast, it has been shown that the mislocalization of an object moving across space relative to a flash is larger at the onset of motion compared with a position along the trajectory, or motion offset (Müsseler et al. 2002). Finally, the bias to localize the target patches further away from the fovea than the probe lines was replicated.

Experiment 4: open-loop pointing

One may argue against the results of Exp. 1 that motion displacement was so small because participants had visual control over their movements. It may be that the magnitude of motion displacement increases in conditions without visual feedback (“open loop”). To test this idea, we turned off the background illumination of the monitor after stimulus presentation such that the movement was executed in complete darkness (the room lights were also turned off). These methods replicate Yamagishi et al. (2001). Because the latency of movement onset was on the same order as stimulus presentation time, observers never saw their own movement. Further, we dropped the accuracy and fixation constraints in half of the participants to examine whether this would alter the results.

Method

Motor judgments were measured in a group of twelve observers. The target appeared randomly to the left or right of the fixation point, and observers were asked to initiate the movement as soon as they detected the stimulus and to touch the screen at the target’s position. The room was completely dark. After target offset, the screen background changed from gray to black (32 to 0 cd/m²), while the fixation mark changed from a dark filled circle to a white filled circle. Because the manual reaction times (~320 ms) were about the same as the duration of the stimulus sequence (350 ms), the hand movement was executed in darkness without vision of the hand. In a group of six observers, fixation had to be maintained and feedback about the accuracy of the hand movement was given. In another group of six observers, fixation errors were not reported back (free viewing) and no feedback about the accuracy of the hand movement was given.

Results

There was no difference in any of the three dependent variables between the group with and the group without feedback and eye fixation, $ps > .2$. Therefore, the two groups were combined into a single group ($N = 12$). The mean reaction (total) time did not differ across conditions and was 316 ms (657 ms), $F_{(2,22)} < .1$, $p > .6$. Motion-displacement was 0.17° and significantly different from zero, $t_{(11)} = 4.7$, $p < .001$. Foveal displacement was -0.50° and also significantly different from zero, $t_{(11)} = 3.6$, $p < .005$. The mean standard deviation was 0.98 deg^2 . A between-subjects comparison between the motor errors in Exp. 1 and the present experiment showed that there was a non-significant tendency for smaller motion-displacement (0.26 vs. 0.17°), $t_{(18, \text{unpaired})} = 1.8$, $p = 0.09$, and less foveal displacement (-0.90 vs. -0.50°), $t_{(18, \text{unpaired})} = 1.9$, $p = .08$, in the group that pointed without vision of the hand. The standard deviation was smaller in the group that pointed in the light (0.55 vs. 0.98 deg^2), $t_{(18, \text{unpaired})} = 3.3$, $p < .005$.

Discussion

Motion-displacement and foveal displacement were significant when participants pointed without vision of the hand. There was a non-significant tendency for smaller errors in this experiment compared with Exp. 1. Thus, it is unlikely that the motor judgments in Exp. 1 underestimated the illusion because observers saw their hands.

Experiment 5: eye movements

Hand movements are rather slow compared with eye movements. Thus, relatively late visual processes may affect hand movements. In contrast, eye movements may be driven by early, even subcortical information from the superior colliculus (Sparks 2002). Thus, it may be interesting to study whether motion-induced illusory displacement may affect saccadic responses. Saccadic responses are ballistic in nature. That is, once the saccade is initiated, visual feedback is not used until the eye comes to a halt. Of course, visual feedback may be used for corrective saccades after the first saccade (primary saccade) is finished. Therefore, only the primary saccade was considered.

Method

To allow for faster disengagement of eye fixation, the fixation mark was extinguished 50 ms before stimulus onset. Observers were asked to make a saccade to the center of the Gabor patch. The stationary and the moving Gabor patches were shown. No feedback was given. A saccade was detected when the velocity exceeded 22 deg/s and the acceleration was larger than $4,000 \text{ deg/s}^2$.

Results

There was motion-displacement of 0.27° which differed significantly from zero, $t_{(5)} = 7.3$, $p < .001$. Foveal displacement with moving stimuli was toward the fovea (-0.77°) and significantly different from zero, $t_{(5)} = 7.9$, $p < .001$. Foveal displacement was almost of exactly the same magnitude with stationary stimuli (-0.77°), $t_{(5)} = 8.7$, $p < .001$. Mean reaction (total) time was 241 (279) ms and did not differ between conditions, $F_{(2,10)} = 3.2$, $p = .08$. Thus, gaze was brought close to the stimulus position before stimulus offset at 350 ms.

Discussion

Perceived motion-displacement was significant and was of exactly the same size as with manual responses (0.26 vs. 0.27°). Thus, even the fastest responses, eye movements, are affected by the illusion. This result is consistent with the finding that probe stimuli that are presented right at motion onset also show motion-displacement (cf. Exp. 3). Thus, motion-induced illusory displacement may originate very early in the processing stream, possibly in V1 (Whitney et al. 2003), such that no difference between perception and action is expected: when the early visual information that is fed into the dorsal and ventral stream is already distorted, both perception and action will be distorted (Bridgeman 2002; Milner and Dyde 2003). However, because the retinotopic activation in V1 is displaced *opposite* the direction of motion and not in the direction (Whitney et al. 2003), it is not entirely clear where the displacement *in* the direction of motion originates. Foveal displacement was toward the fovea as with manual responses. In contrast to manual responses, foveal displacement was also toward the fovea with stationary stimuli.

General discussion

In the present study, motor and perceptual localization of drifting Gabor patches was investigated. It is well known that the position of a stationary Gaussian window is misperceived in the direction of motion of a sine-wave grating drifting inside the Gaussian window (illusory displacement). In a previous report, it was observed that the deviation of the judged from the true center of the Gabor was larger when motor judgments were used (Yamagishi et al. 2001): when observers pointed to the center of a drifting Gabor, the error in the direction of motion was larger compared with a condition in which observers judged the position of the patch by reading off its position from a ruler. Here, we used smaller stimuli that were better suited for pointing movements and a 2AFC procedure for the probe judgments. The main result was that the size of the illusion depended strongly on the method used: when drifting Gabors were used as probes, the illusion was larger with probe than with motor

judgments. When continuously visible lines were used as probes, the illusion was about the same size as with motor judgments. When briefly flashed lines were used as probes, the illusion was smaller with probe than with motor judgments. Changing the motor task from open-loop (full vision of the hand) to closed-loop (pointing in the dark) did not increase the size of the forward error. Further, the size of the illusion with saccadic responses was about the same as with pointing movements. Overall, the present results do not support the conclusion that the illusion is larger in motor judgments than in perceptual or memory-based probe judgments. The answer to the question of which measure shows the largest error depends strongly on the specific methods. The more general point is that the comparison between perception and action is elusive because of the fundamental problem of choosing an appropriate comparison (probe) stimulus in the perceptual task. This is the case for size judgments (see introduction) and the present study extends this conclusion to judgments of position.

Across experiments, there was a marked difference with respect to the foveal bias: whereas the target tended to be misperceived or misremembered away from the fovea relative to the probes, motor judgments were biased toward the fovea. The bias toward the fovea with motor judgments replicates previous studies: it was shown that there was a tendency to compress space in visual short-term memory (Kerzel 2002; Sheth and Shimojo 2001). Similarly, saccades tend to undershoot the target such that saccadic endpoints are biased toward the source of the saccade (i.e., the fovea, Bischof and Kramer 1968; Lemij and Collewyn 1989).

For probe judgments, there was no time course. That is, judgments were no different with simultaneous and delayed probe presentation (Exps. 1 and 2). It was not the case that visual short-term memory of the target position was further displaced in the direction of motion as research on “representational momentum” would suggest. Also, the size of the illusion did not differ between a condition with a flashed probe at motion onset and a condition with a flash during the motion (Exp. 3). Thus, the illusion arises very early on and does not change over time or in visual short-term memory. The absence of a time course in perception facilitates the comparison with the motor judgment where timing cannot be fully controlled.

Finally, the size of the illusion and the variability were reasonably independent. For instance, motion-displacement did not depend on whether the probe was presented simultaneously with the target or some time later. In contrast, the variability of the judgments was much higher when the probe was presented some time later, showing that the memory trace of the target position degraded quickly. However, it was not the case that observers localized the target further in (or opposite) the direction of motion when they were uncertain about the target location.

Functionally, the motion-induced illusory displacement was thought to compensate for processing delays (Ramachandran and Anstis 1990; Yamagishi et al. 2001):

because of neural delays, the actual position of a moving object changes before it is consciously perceived. In order not to be late, it may be that the position of the moving stimulus is extrapolated into the future (see also Nijhawan 2002) such that the perceived position is seen displaced in the direction of motion. The results of Yamagishi et al. (2001) suggested that extrapolation is stronger in action because motion-induced displacement was larger with motor than with perceptual judgments. In a similar vein, it was noted that goal-directed movements to the endpoint of moving objects overshoot the true final offset while probe judgments of the final position were accurate (Kerzel 2003; Kerzel and Gegenfurtner 2003). Thus, observers point to a position ahead of the currently perceived position of a target in order not to be late (i.e., to compensate for neuronal delays). Although this strategy entails larger errors in action than in perception, it may ensure accurate responses in interceptive action. This distinction supports and refutes Goodale and Milner’s (1992) two visual system’s hypothesis at the same time. On the one hand, action is less accurate than perception which is contrary to their characterization of the two systems. On the other hand, there are clear difference between perception and action which is consistent with their theory. The present results cast doubt on the latter conclusion: depending on the specific methods used, the differences may be replicated (Exp. 3), reversed (Exp. 1) or abolished (Exp. 2). More work is needed to specify what would be the most appropriate comparison between perception and action.

Acknowledgements The author was supported by the Deutsche Forschungsgemeinschaft (DFG KE 825/3-1 and 825/4-1,2). We wish to thank Nina Barthel, Jana Buchmann, Julia Verena Hardt, and Fereshteh Zahir-Fard for helping with data collection.

References

- Aglioti S, DeSouza JF, Goodale MA (1995) Size-contrast illusions deceive the eye but not the hand. *Curr Biol* 5:679–685
- Bischof N, Kramer E (1968) [Investigations and considerations of directional perception during voluntary saccadic eye movements]. *Psychologische Forschung* 32:185–218
- Bock O (1986) Contribution of retinal versus extraretinal signals towards visual localization in goal-directed movements. *Exp Brain Res* 64:476–482
- Bridgeman B (1998) Durations of stimuli displayed on video display terminals: $(n-1)/f + Persistence$. *Psychol Sci* 9:232–233
- Bridgeman B (2002) Attention and visually guided behavior in distinct systems. In: Prinz W, Hommel B (eds) *Common mechanisms in perception and action—attention and performance*, vol. XIX. Oxford University Press, Oxford
- De Valois RL, De Valois KK (1991) Vernier acuity with stationary moving Gabors. *Vis Res* 31:1619–1626
- Franz VH (2001) Action does not resist visual illusions. *Trends in Cognitive Sciences* 5:457–459
- Franz VH, Gegenfurtner KR, Bühlhoff HH, Fahle M (2000) Grasping visual illusions: no evidence for a dissociation between perception and action. *Psychol Sci* 11:20–25
- Goodale MA, Milner AD (1992) Separate visual pathways for perception and action. *Trends Neurosci* 15:20–25

- Henriques DY, Klier EM, Smith MA, Lowy D, Crawford JD (1998) Gaze-centered remapping of remembered visual space in an open-loop pointing task. *J Neurosci* 18:1583–1594
- Hubbard TL (1995) Environmental invariants in the representation of motion: implied dynamics and representational momentum, gravity, friction, and centripetal force. *Psychon Bull Rev* 2:322–338
- Kerzel D (2002) Memory for the position of stationary objects: disentangling foveal bias and memory averaging. *Vis Res* 42:159–167
- Kerzel D (2003) Mental extrapolation of target position is strongest with weak motion signals and motor responses. *Vis Res* 43:2623–2635
- Kerzel D, Gegenfurtner KR (2003) Neuronal processing delays are compensated in the sensorimotor branch of the visual system. *Curr Biol* 13:1975–1978
- Lemij HG, Collewyn H (1989) Differences in accuracy of human saccades between stationary and jumping targets. *Vis Res* 29:1737–1748
- Milner D, Dyde R (2003) Why do some perceptual illusions affect visually guided action, when others don't? *Trends in Cognitive Sciences* 7:10–11
- Müsseler J, Stork S, Kerzel D (2002) Comparing mislocalizations with moving stimuli. The Fröhlich effect, the flash-lag effect and representational momentum. *Vis Cogn* 9:120–138
- Neggers SF, Bekkering H (2000) Ocular gaze is anchored to the target of an ongoing pointing movement. *J Neurophysiol* 83:639–651
- Nijhawan R (1994) Motion extrapolation in catching. *Nature* 370:256–257
- Nijhawan R (2002) Neural delays, visual motion and the flash-lag effect. *Trends in Cognitive Sciences* 6:387
- Ramachandran VS, Anstis SM (1990) Illusory displacement of equiluminous kinetic edges. *Perception* 19:611–616
- Sheth BR, Shimojo S (2001) Compression of space in visual memory. *Vis Res* 41:329–341
- Sheth BR, Shimojo S (2003) Signal strength determines the nature of the relationship between perception and working memory. *J Cogn Neurosci* 15:173–184
- Sparks DL (2002) The brainstem control of saccadic eye movements. *Nature Review Neuroscience* 3:952–964
- Whitney D, Goltz HC, Thomas CG, Gati JS, Menon RS, Goodale MA (2003) Flexible retinotopy: motion-dependent position coding in the visual cortex. *Science* 302:878–881
- Yamagishi N, Anderson SJ, Ashida H (2001) Evidence for dissociation between the perceptual and visuomotor systems in humans. *Proc R Soc Lond B Biol Sci* 268:973–977