

When does action resist visual illusion? The effect of Müller–Lyer stimuli on reflexive and voluntary saccades

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Abstract The primate visual cortex exhibits two anatomically distinct pathways (dorsal and ventral). According to the “two visual systems hypothesis” (TVSH) of Milner and Goodale (The visual brain in action. Oxford University Press, Oxford, 1995), this anatomical distinction corresponds to a functional division of labor between vision-for-action (dorsal) and vision-for-perception (ventral). This proposal is supported by evidence that, in healthy volunteers, perceptual responses are affected by visual illusions, whereas motor responses to the same illusion-inducing stimuli are not. However, previously we have shown that the amplitude of saccadic eye movements is modified by the Müller–Lyer illusion in a similar manner as perceptual responses. Here we extend this finding to reflexive and voluntary (memory-guided) saccades. We show that both types of saccade can be strongly affected by the illusion. In our studies, the effect on reflexive saccades was comparable to that usually observed with verbal reports (an effect size of $22 \pm 8\%$), whereas the effect on voluntary saccades was smaller ($11 \pm 11\%$). In addition, both types of saccade provide evidence for the scaling bias usually observed in perceptual responses. We suggest that previous studies may have employed methods that generally reduced the effect of the illusion. Interpretations of dissociations between reflexive and voluntary saccades in terms of the TVSH appear to be premature.

Keywords Perception · Action · Saccades · Illusions · Müller–Lyer

Introduction

It is widely recognized that in the primate cortical visual system there are two main streams of projections from the primary visual area (Ungerleider and Mishkin 1982). One, the dorsal projection, reaches the posterior parietal cortex. The other, the ventral projection, reaches the inferotemporal cortex. According to Milner and Goodale (1995), the presence of these two streams can be interpreted functionally as a division of labour between subsystems. Specifically, the dorsal subsystem specializes in the visual guidance of actions (vision-for-action), whereas the ventral subsystem specializes in object perception and recognition (vision-for-perception). While in general terms this two-visual-systems hypothesis (TVSH) has proved attractive, the exact mapping of functions to neurobiological structures in the two putative subsystems is controversial (Rizzolatti and Matelli 2003; Musseler et al. 2004; Jeannerod and Jacob 2005).

Support for the TVSH comes from monkey and human studies using a variety of techniques (for a recent review, see Goodale and Westwood 2004). One approach has been to examine the effects of various visual illusions, which by definition induce misperceptions, to determine whether motor responses to such stimuli involve comparable “misactions”. For example, in the Müller–Lyer illusion (Fig. 1) the same segment appears shorter when flanked by outward-pointing arrows ($< >$), and longer when surrounded by inward-pointing ones ($> <$). Within the TVSH framework, the difference could be due to the spatial relations between the judged segment and the arrows, that is, to

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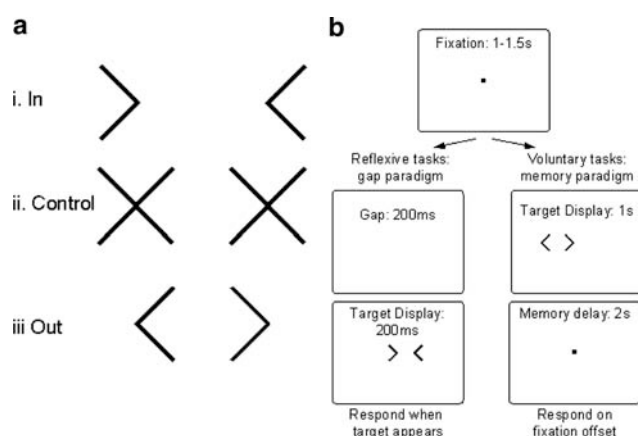


Fig. 1 The stimuli used in these experiments. **a** The “in” (i), “control” (ii) and “out” (iii) configurations. Three amplitudes (separation between vertices) were used (4° , 6° , 8°) and the length of the arms scaled with amplitude (0.9° , 1.4° , 1.9° , respectively). The angle formed by the arms was approximately 90° . The line thickness was 1 mm. **b** Trial structure. Note that configurations were positioned such that the central vertex was at fixation

allocentric (object-relative) coding of spatial extensions used by vision-for-perception. However, actions such as transporting the hand from one end of the segment to the other require egocentric (body- or effector-relative) coding of spatial features by the vision-for-action system. Accordingly, at least in some conditions hand transport should not be influenced by the illusion, a prediction that has been confirmed by some studies (Bruno and Bernardis 2003), although opinions differ on the extent of the observed dissociations, as well as on the conditions that best promote the resistance of actions to illusions (Bruno 2001; Carey 2001; Franz 2001; Milner and Dyde 2003).

In a recent experiment (Bernardis et al. 2005), we compared perception, finger pointing amplitudes, and saccadic amplitudes in response to a version of the Müller-Lyer illusion. We confirmed that the illusion had a negligible effect on pointing, but also demonstrated that the effect of the illusion on saccade amplitude was comparable to the perceptual effect. This result is in agreement with a number of other studies in which the effect of the Müller-Lyer illusion on saccades was investigated (Binsted and Elliot 1999; de Grave et al. 2006). However, they contrast with an earlier study in which the dot-in-frame illusion was used (Wong and Mack 1981), in which reflexive saccades appeared not to be affected by the illusion, while saccades to remembered positions were. Given that saccades are critically dependent on areas classically assigned to the dorsal stream (see Munoz 2002), consistent evidence showing that saccades are influenced by illusions would pose a problem for the TVSH.

A recent study has proposed a potential solution (McCarley et al. 2003). Using a Brentano-style Müller-

Lyer figure, MacCarley and collaborators compared the amplitudes of saccades executed in response to a flash positioned at the vertex on one end of the figure, with saccades executed in response to a verbal command (but with no flashed target). They described the former as reflexive saccades and the latter as voluntary and reported that voluntary saccades were affected by the illusion to a greater extent than reflexive saccades. Goodale and Westwood (2004) suggested that this pattern of results supported the classic TVSH framework. Automatic, reflexive responses, critically dependent on the action pathway, were less likely to be affected by illusions such as the Müller-Lyer than voluntary, perceptually driven responses.

However, in our experiment (Bernardis et al. 2005) in which we measured reflexive saccades, we observed much larger illusory effects on saccade amplitude than those reported by McCarley et al. (2003) for their reflexive condition. The reason for this is unclear, although there were important methodological differences between the two studies. For example, the difference could be due to the methods used to assess the illusion. McCarley et al. (2003) used a Brentano illusion pattern that was approximately equated for *perceived* length based on pilot data from two observers. We used three Müller-Lyer patterns of different lengths, but always compared *equal* physical lengths yielding *different* perceived lengths due to the effect of the illusion. Further, we controlled target display time so that retinal error feedback was never available to subjects; it is unclear whether McCarley et al. (2003) removed the target display once their subjects had executed saccades. And whereas in our experiment subjects saccaded as soon as the target was presented, they provided subjects with a preview period (of approximately 0.5 s) during which the illusory configuration was presented prior to the signal to execute the saccade. Some or all of these differences might have influenced the size of the perceptual effect of the illusion, and the size of the effect on saccade amplitude.

We therefore wished to re-examine the influence of the Müller-Lyer illusion on reflexive saccades and, further, to investigate the effect of the illusion on voluntary saccades. To encourage the execution of fast reflexive saccades, we used a gap paradigm, in which between fixation point removal and target appearance there was a blank period (Fischer and Weber 1993; Pratt et al. 1999). Conversely, to elicit deliberate voluntary movements, the same participants were required to memorize the position of a target, and then, after its removal and a delay period, execute a saccade to the remembered target position. Note, that the requirements of the first of these tasks correspond closely to the types of action that are generally believed to be controlled dorsally (“fast and dumb actions”, see Carey 2001). In contrast, the second task involves processes classically assigned to the ventral stream (see Goodale and

Westwood 2004). To allow a direct comparison with our previous work, the stimuli and all the other features of the experiment were the same as those of Bernardis et al. (2005).

Methods

Participants

Nine healthy adult subjects (including one of the authors, NB) participated in the two main experiments in which reflexive and memory-guided saccades were investigated. Of the eight non-author subjects, three had participated in a previous experiment on the Müller-Lyer illusion and five were naïve. All had normal or corrected-to-normal visual acuity. Some of these subjects, plus additional naïve subjects, participated in two further control experiments. Subjects provided their informed consent and the experiments were performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Displays and apparatus

Stimuli were presented on a 21 inch monitor (1024 × 768 spatial resolution, 100 Hz temporal resolution) driven by a VSG2/5 card (Cambridge Research Systems, Rochester, UK). The monitor was positioned on the fronto-parallel plane 57 cm from the participant's eye. Horizontal eye position of the left eye was recorded using a Skalar Iris IR Eye Tracker. This is a limbus tracker that uses differential infrared light reflection to convert eye position into an analogue voltage; it has a spatial resolution of 0.1°. Eye-tracker output was sampled at 1 kHz and digitized with 16-bit precision using a CED Power 1401 (Cambridge Electronic Design, Cambridge, UK) interface. A chinrest and cheek pads were used to ensure head stabilization. In the main experiment each participant was exposed to four runs of 96 reflexive trials (total: 380 trials) and 4 runs of 96 memory trials over four recording sessions. Each run was composed of 16 tasks presented in a randomized order: 2 illusory configurations × 3 amplitudes (separations between vertices: 4°, 6° or 8°) × 2 directions; 1 control configuration × 2 amplitudes (4° or 8°) × 2 directions. Thus for each condition there was the potential for 24 observations per subject. In each recording session, a five-point calibration was performed. The calibration stimuli were presented six times at each of four positions aligned with the monitor centre, two to the left (5° and 10° from the centre of the display) and two to the right. Participants were instructed to accurately fixate (monocularly with left eye) each stimulus until it disappeared after 1 s.

Each trial began with a random fixation period (1–1.5 s; see Fig. 1b) during which a fixation square (0.3°) was presented in the centre of the display. This was then replaced by a Müller-Lyer (Fig. 1a.i,iii) or a control configuration (Fig. 1a.ii). These were always presented such that one vertex (or centre of an X) appeared at fixation, while the other appeared eccentrically, randomly to either the left or right. In the reflexive trials, a 200 ms blank period (or “gap”) was introduced between the offset of the fixation point and the appearance of the Müller-Lyer or control target configurations. This gap duration was chosen as it is the optimum duration for obtaining the classic gap effect on saccade latency (Fischer and Weber 1993; Krauzlis and Miles 1996). Targets were presented for 200 ms, and subjects were instructed to execute an accurate saccade to the eccentric Müller-Lyer vertex, as soon as it was detected. This target duration was chosen as it ensured that the target was removed before the end of the response saccade, preventing retinal error feedback. Subjects then saccaded back to the centre of the display, to wait for the beginning of the next trial. In memory trials the stimulus was displayed for 1 s, but the subjects were instructed to maintain fixation at the centre of the display (i.e. on the central vertex or centre X); their eye movements were monitored during this period. The stimulus was then replaced by the fixation target for 2 s (the delay period). This delay period was chosen as a compromise; it is long enough to be consistent with requiring non-dorsal processing (Bradshaw and Watt 2002), but short enough not to make each run overly long, causing fatigue or inattention. The signal to execute the saccade was the offset of the central fixation target. Subjects were instructed to saccade to the remembered position of the eccentric Müller-Lyer vertex or centre of the eccentric X. They then saccaded back to the centre of the display for the next trial.

Two further control experiments were also run. Five subjects (three of whom participated in the main experiments, plus two others) completed a memory control experiment in which they executed memory-guided saccades, identical to the main memory-guided saccade experiment. However, the stimulus display time was reduced to 200 ms, identical to that used for the reflexive experiment. The memory delay period remained 2 s. Four subjects (two of whom participated in the main experiments) also completed an experiment in which we sought to remove the effect of transient signals occurring at fixation (the fixation control experiment). One amplitude was used (6°), and there was no gap. During the random fixation period, one of the Müller-Lyer elements (with the vertex positioned in the centre of the display) or an “x” was presented. The stimulus was the appearance of the eccentric element (or x) to complete the configuration. Again, subjects were instructed to saccade to the eccentric

vertex as soon as they detected it. Direction was randomized, as was whether an “in”, “out” or control configuration was presented. The complete configuration was displayed for 200 ms.

Analysis

For each trial, eye position data from approximately 200 ms before to 800 ms after the “go” signal (target appearance in gap trials, fixation offset in memory trials) were written to disk for analysis off-line. Data were analyzed using an interactive program which displayed the eye position data and the time of the go signal. Given that we were analysing large saccades with high accelerations using a high-resolution technique, the primary saccade within each trial was easily identified by eye from the display. For each primary saccade a cursor was placed by eye at the beginning of the saccade to calculate latency and initial eye position, and then at the end of the saccade. The saccade amplitude was calculated as the difference in position between the first and second position measurements. Finally, the calibration data were used to transform the amplitude data from arbitrary system units into units of degrees of eye rotation. Saccades with latencies of <80 ms were regarded as anticipatory and not included in the analysis. Occasionally the response consisted of a sequence of saccades. Data from these trials were not included in the analysis unless the first saccade in the sequence was at least 50% of the required amplitude. In this case the amplitude of that first saccade was included. Some trials were also lost due to blinks or unstable fixation. In total 81% of memory trials, and 85% of gap trials were included in the analysis. Amplitudes and latencies were collated using MS Excel and statistical analysis conducted using SPSS. Saccade amplitudes were plotted against physical distance for the “in”, “out” and control conditions. Repeated

measures analysis of variance (ANOVA) was used to assess the differences between “in” and “out” amplitudes. Linear regression analysis of the amplitude data was also used and regression slopes were inspected for evidence of a scaling bias. A summary percent measure of the effect of the illusion (Bruno and Bernardis 2003) was also computed for the two amplitudes for which we had control data (4° and 8°). This was computed as:

$$[(\text{“in” average} - \text{“out” average}) / \text{control average}] \times 100.$$

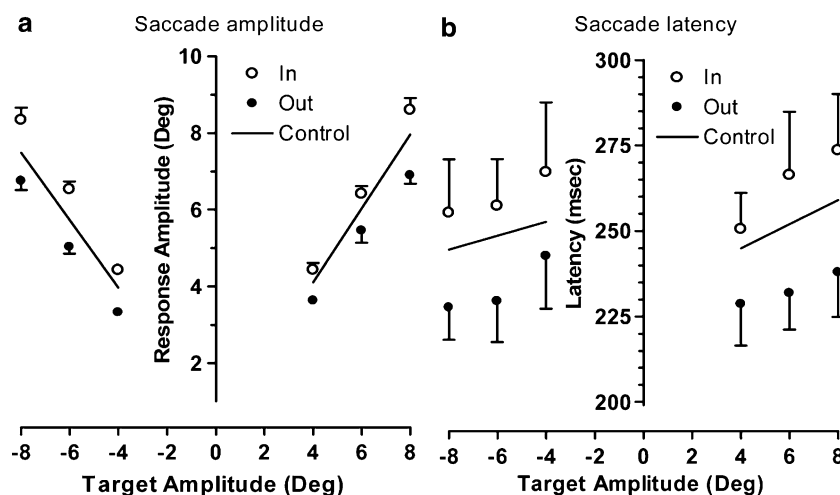
Results

Reflexive task

No subject experienced any difficulty in the reflexive experiments in which they executed a saccade to the eccentric stimulus element as soon as it was detected. In the control condition, in which the target was the centre of an “x”, the mean (here and elsewhere the intersubject mean \pm SD) saccade gain (saccade amplitude/target amplitude) collapsed across subjects, directions and amplitudes was 0.99 ± 0.2 , demonstrating that in the absence of an illusory stimulus, primary saccades were accurate, even with a brief target presentation time (200 ms). Indeed there were relatively few trials where we observed secondary corrective saccades.

In all nine subjects, saccade amplitudes were affected by the Müller-Lyer illusion. Average saccade amplitudes to the vertex of the “in” configuration (Fig. 1a.i) were larger than saccade amplitudes to the vertex of the “out” configuration (Fig. 1a.iii), even although the actual position of the vertices was identical. Figure 2a shows the qualitative pattern of results collapsed across the nine subjects. For clarity the control data is plotted as a line drawn between the two amplitudes for which we collected data (4° and 8°).

Fig. 2 Mean \pm SEM primary saccade amplitude (a) and latency (b) in response to Müller-Lyer and control stimuli for the reflexive (gap) experiment. Data for “in” configuration: open circle; “out” configuration filled circle; control data plotted as line joining points at 4° and 8°. Error bars are plotted in one direction only for the sake of clarity. Negative target amplitudes indicate stimuli were presented to the left of fixation



There is a clear separation between the “in” and “out” data points at each amplitude. We subjected the data to repeated measures ANOVA with amplitude (4° , 6° , 8°), direction (left, right) and configuration (in, out) as within-subjects factors. Not surprisingly amplitude was statistically significant ($F_{2,7} = 572$; $P < 0.001$), as was configuration ($F_{1,8} = 147$; $P < 0.001$). There was also a significant configuration \times amplitude interaction ($F_{2,7} = 8$; $P = 0.001$). Direction did not reach statistical significance ($P = 0.58$).

In order to investigate whether there was any systematic scaling bias in the saccade amplitudes, of the type exhibited by perceptual reports, we subjected the data to linear regression analysis. For each subject we calculated the slope of the least-squares linear regression line for the “in”, “out” and control amplitude data (Table 1). The “in” slope was greater than the “out” slope in six subjects for leftward trials, and eight subjects for rightward trials. We subjected the slopes to repeated measures ANOVA with configuration (in, out, control) and direction (left, right) as within subjects factors. Configuration was significant ($F_{2,7} = 17$; $P < 0.001$), direction was not ($P = 0.643$).

We also investigated whether saccade latency was influenced by the stimulus configuration (Fig. 2b). Latency was highest on “in” trials, lowest on “out” trials, and intermediate on the control trials, although there was considerable variability. For leftward trials, latency across conditions (i.e. in, out and control) was slightly lower in the larger amplitude tasks (i.e. separations of 8° and 6°) compared to the 4° tasks, while the opposite pattern was observed for rightward trials. The difference between “in” and “out” latencies averaged 29 ms. When we subjected the latency data to ANOVA with amplitude (4° , 6° , 8°), direction (left, right) and configuration (in, out) as within-subjects factors, only configuration was statistically significant ($F_{1,8} = 46$; $P < 0.001$), with no statistically

significant interactions between the factors; none of the interactions involving direction reached statistical significance.

The latency difference between the “in”, “out”, and control configurations might constitute a potential confound for the amplitude results. To test this, we subjected the amplitude data to analysis of covariance (ANCOVA) using latency as the quantitative covariate and configuration (in, “out”, or control), amplitude (4° , 6° , or 8°), and direction (left or right) as the qualitative factors. This analysis ruled out any confound: after controlling for the effect of latency, the main effect of configuration remained statistically significant $F_{2,16} = 100$, $P < 0.001$. In addition, Scheffé post-hoc pairwise comparisons confirmed that the “in” configuration yielded larger amplitudes than the “out” ($P < 0.001$). Unsurprisingly, the effect associated with different stimulus separations was again significant ($F_{2,16} = 1309$; $P < 0.001$), whereas direction was not ($F_{1,16} = 1$; $P > 0.05$).

Memory task

In the control condition for the memory task, the mean (\pm SD) saccade gain collapsed across subjects, directions and amplitudes was 0.92 ± 0.3 . The difference between the control gains for the two types of saccade was statistically significant (two sample t test; $t = 5.7$, $P < 0.001$). Once again however, saccade amplitudes to the “in” configuration were larger than amplitudes to the “out” configuration (Fig. 3a). When we tested this with ANOVA we found that as before amplitude was statistically significant ($F_{2,7} = 113$; $P < 0.001$), as was configuration ($F_{1,8} = 65$; $P < 0.001$). There was also a significant configuration \times amplitude interaction ($F_{2,7} = 8$; $P < 0.05$). Direction did not reach statistical significance ($P = 0.22$).

The slopes of the regression lines for individual subjects in the memory task are shown in Table 2. Seven of nine

Table 1 Individual subject regression slopes (\pm SEM) for the amplitude data from the gap task

Subject	Left			Right		
	In	Control	Out	In	Control	Out
HR	0.93 ± 0.06	0.82 ± 0.06	0.73 ± 0.06	1.31 ± 0.12	1.12 ± 0.09	1.03 ± 0.08
RH	0.71 ± 0.06	0.73 ± 0.05	0.60 ± 0.05	1.03 ± 0.07	0.94 ± 0.08	0.93 ± 0.07
CM	0.89 ± 0.09	0.94 ± 0.13	0.89 ± 0.19	1.08 ± 0.08	1.10 ± 0.09	0.95 ± 0.06
HM	1.07 ± 0.08	1.06 ± 0.08	0.84 ± 0.09	0.79 ± 0.07	0.68 ± 0.07	0.67 ± 0.06
JD	1.09 ± 0.04	0.95 ± 0.06	0.85 ± 0.05	1.01 ± 0.04	0.87 ± 0.03	0.7 ± 0.07
IC	1.19 ± 0.06	0.84 ± 0.07	0.98 ± 0.04	1.12 ± 0.06	0.97 ± 0.07	0.77 ± 0.08
DN	0.87 ± 0.05	0.85 ± 0.06	0.87 ± 0.11	1.27 ± 0.09	1.15 ± 0.11	0.72 ± 0.1
NB	0.76 ± 0.11	0.82 ± 0.12	0.87 ± 0.10	0.86 ± 0.10	0.93 ± 0.13	0.74 ± 0.09
FA	1.29 ± 0.16	0.90 ± 0.12	1.04 ± 0.10	0.86 ± 0.13	0.90 ± 0.13	0.81 ± 0.09

Fig. 3 Mean \pm SEM primary saccade amplitude (a) and latency (b) in response to Müller-Lyer and control stimuli for the memory experiment. Same plotting conventions as for Fig. 2

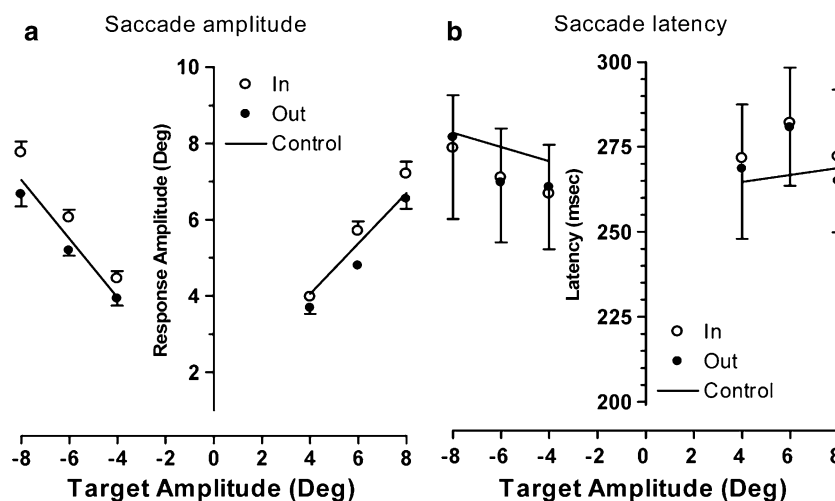


Table 2 Individual subject regression slopes (\pm SEM) for the amplitude data from the memory task

Subject	Left			Right		
	In	Control	Out	In	Control	Out
HR	0.87 ± 0.12	0.95 ± 0.15	1.11 ± 0.11	1.24 ± 0.23	0.99 ± 0.20	1.02 ± 0.16
RH	0.57 ± 0.07	0.52 ± 0.05	0.50 ± 0.05	0.92 ± 0.09	0.78 ± 0.09	0.77 ± 0.08
CM	0.89 ± 0.08	0.67 ± 0.08	0.57 ± 0.08	0.72 ± 0.08	0.58 ± 0.09	0.54 ± 0.06
HM	0.85 ± 0.16	0.70 ± 0.18	0.61 ± 0.20	0.62 ± 0.15	0.60 ± 0.16	0.55 ± 0.12
JD	0.82 ± 0.08	0.80 ± 0.10	0.96 ± 0.08	0.73 ± 0.09	0.72 ± 0.10	0.89 ± 0.10
IC	0.94 ± 0.09	1.00 ± 0.08	0.91 ± 0.09	0.71 ± 0.10	0.79 ± 0.10	0.66 ± 0.10
DN	0.91 ± 0.15	0.83 ± 0.12	0.55 ± 0.10	0.76 ± 0.16	0.60 ± 0.10	0.92 ± 0.12
NB	0.75 ± 0.12	0.62 ± 0.10	0.35 ± 0.09	0.75 ± 0.13	0.89 ± 0.20	0.43 ± 0.11
FA	0.84 ± 0.24	0.95 ± 0.19	0.60 ± 0.20	0.84 ± 0.16	0.58 ± 0.19	0.67 ± 0.22

subjects exhibited steeper slopes for “in” compared to “out” tasks to both the left and the right. However, the differences appeared to be reduced compared to the gap task. When we tested the slopes with the same design of ANOVA as employed for the reflexive task, we found that configuration (in, out, control) remained significant ($F_{2,7} = 5.4$; $P < 0.05$) while again direction was not ($P = 0.72$).

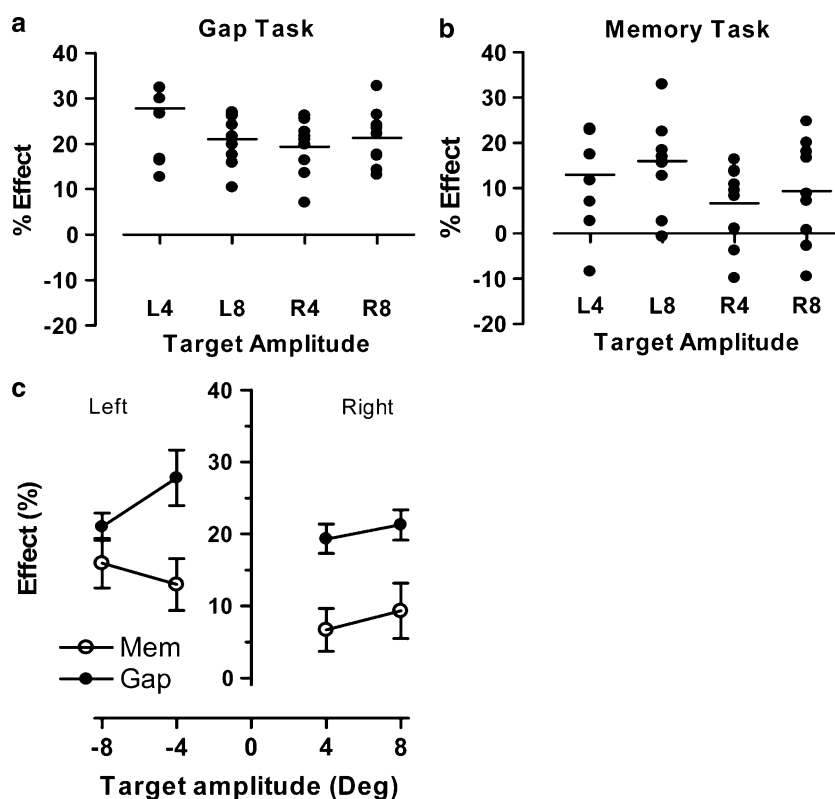
When we examined the influence of the illusion of the latency of memory-guided saccades, we found that in contrast to reflexive saccades, there was little difference between saccades to “in” and “out” configurations (Fig. 3b). However, latency was in general longer for memory-guided saccades compared to gap saccades.

Comparison of the tasks

A direct comparison of the effect size of the illusion on the saccade amplitude in the two main experiments is shown in Fig. 4. Note that as there were only two target amplitudes

at which we collected control data (4° and 8°), this analysis is restricted to these target amplitudes. For the reflexive task, the size of the illusion effect on saccade amplitude ranged from 7 to 31% (Fig. 4a). Collapsed across directions, amplitudes and subjects the mean (\pm SD) effect was $22 \pm 8\%$. The effect of the illusion on saccade amplitude in memory-guided trials was less than that observed for reflexive trials (Fig. 4b). The effect size ranged from -10 to 33% with a mean (\pm SD) of $11 \pm 11\%$. In this context, a negative effect means that the saccade amplitude was larger in the “out” compared to the “in” configuration. Thus the effect of the illusion in the memory condition was also more variable as well as, on average, weaker. Note that we observed no subjects in whom in the reflexive task, the illusion failed to modulate the saccade amplitude in the same way as for perception. As is clear from Fig. 4b, this did occasionally happen with the memory-guided saccade task. The mean effect size for each of the four positions is illustrated in Fig. 4c. When analyzed with a repeated measures ANOVA in which direction (left and right) and

Fig. 4 Size of illusory effect on: **a** reflexive saccade amplitude; **b** memory guided saccade amplitude. Each point represents an individual subject, line shows mean. Note that control data was only collected at amplitudes of 4° and 8°. *L*: left; *R*: right. **c** Comparison of mean \pm SEM effect size between reflexive (Gap filled circle) and memory (Mem open circle) saccade tasks



amplitude (4° and 8°) were treated as within subjects factors and the task type (memory, reflexive) was treated as a between subjects factor, amplitude was not statistically significant ($P = 0.934$), direction was ($F_{1,16} = 7$; $P = 0.02$). The between-subjects factor, task type, was statistically significant ($F_{1,16} = 20$; $P < 0.001$).

We also compared the variability in saccade amplitude between the two conditions by calculating the coefficient of variation ($CV = SD/mean$, expressed as a percentage). Collapsed across directions and amplitudes, CV ranged from 17 to 36% for the memory task with a mean for the nine subjects of $25 \pm 6\%$. For the reflexive task the range was from 10 to 25%, with a mean of $16 \pm 4\%$. To illustrate the difference in variability between the two tasks we plotted the CV in the reflexive condition, against the CV in the memory condition (Fig. 5). Note that for all the subjects the points lie below the line of equality, confirming that saccade amplitude was more variable for the memory condition. Finally the CV data were subjected to ANOVA with direction, amplitude and configuration as within subjects factors and task type as a between subjects factor. Amplitude was the only statistically significant within subjects factor ($F_{2,15} = 13$; $P < 0.001$), and there were no significant interactions. This was because variability for both tasks was higher at 4° than at 8°, independent of direction and configuration. Task type, treated as a between subjects factor was also statistically significant ($F_{1,16} = 12$; $P = 0.003$).

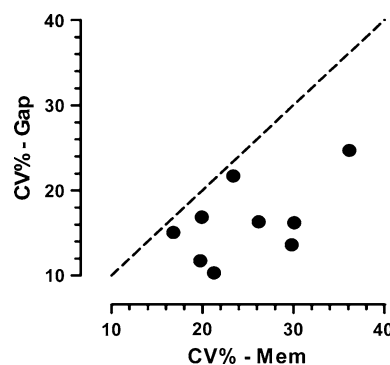


Fig. 5 Coefficient of variation (expressed as a %) for saccade amplitude compared between the reflexive (Gap) and memory (Mem) tasks for each subject. Dashed line is the line of equality. Note that in each subject CV was lower in the reflexive task

Control experiments

There were a number of differences between the memory and reflexive tasks that we wished to specifically investigate in additional experiments. They differed with respect to the display time of the target configuration; in the memory task this was 1 s, in the reflexive task it was 200 ms. Therefore, we collected further data from five subjects who completed a memory control task, in which the target display time was 200 ms. The results were similar to those observed with the 1 s display time.

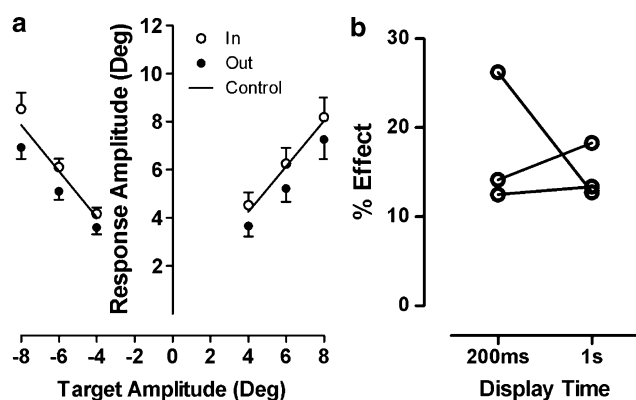


Fig. 6 Data from memory control experiment. **a** Mean \pm SEM primary saccade amplitude for five subjects in response to Müller-Lyer and control stimuli for memory experiment with target display time reduced to 200 ms. Same plotting conventions as for Fig. 2. **b** Comparison of the size of the illusion effect for 200 ms and 1 s display times, collapsed across direction and amplitude, for three subjects who participated both in the main memory experiment and the control experiment

Saccade amplitudes to the “in” configuration were larger than amplitudes to the “out” configuration (Fig. 6a). When tested with ANOVA, we found that as before amplitude was statistically significant ($F_{2,3} = 70$; $P < 0.001$), as was configuration ($F_{1,4} = 15$; $P = 0.001$). Neither the configuration \times amplitude interaction ($F_{2,3} = 4$; $P = 0.073$) or direction ($F_{1,4} = 0.1$; $P = 0.741$) reached statistical significance. For the five subjects, the effect size collapsed across direction and amplitude was $17 \pm 5\%$. We directly compared the effect size for the three subjects who participated in both the main and memory control experiments (Fig. 6b). While in one subject the effect was much larger with the 200 ms display time, for the other two there was little difference.

In the reflexive task, when the saccade target (the eccentric Müller-Lyer element) was presented, the configuration was completed by presenting the other element at fixation. Thus, after the gap, two events occurred, one in the periphery and one at fixation. This “double” event, could have influenced the result we observed. Therefore in the fixation control experiment, we replaced the central fixation target (a small square in the main experiment) during the random fixation period, with a Müller-Lyer element (or “X”). We also removed the gap. Each trial now began with the appearance of the central element (or “X”). The configuration was completed by the appearance of the eccentric element, which was also the instruction to make the saccade. Thus there was no stimulus event at fixation, at the time when the saccade target appeared, when the configuration was completed. However, saccade amplitude was still modulated by the type of configuration presented (Fig. 7a); it was consistently larger with the

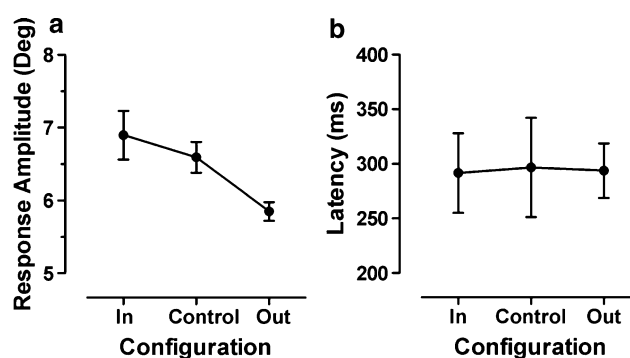


Fig. 7 Data from fixation control experiment. **a** Mean \pm SEM primary saccade amplitude for four subjects in response to Müller-Lyer and control stimuli. **b** Mean \pm SEM primary saccade latency

“in” configuration, and smaller with the “out” configuration, compared to the control configuration. The mean effect size for four subjects was $16 \pm 7\%$. When tested with a repeated measures ANOVA, with direction (left, right) and configuration (in, out) treated as within subjects factors, direction was not significant ($F_{1,3} = 3.70$; $P = 0.15$) configuration was significant ($F_{1,3} = 15.53$; $P = 0.029$), and there was no significant interaction ($F_{1,3} = 0.03$; $P = 0.873$). In contrast, latency was not modulated by the configuration (Fig. 7b; $P > 0.5$ for both factors and the interaction).

Discussion

The purpose of these experiments was to investigate whether there were systematic differences between the effects of the Müller-Lyer illusion on reflexive and voluntary saccades. They were motivated by the claim that reflexive saccades may be influenced by the Müller-Lyer illusion, but voluntary saccades are affected to a far greater extent (McCarley et al. 2003; see also Goodale and Westwood 2004).

Although the usefulness of the “voluntary” and “reflexive” distinction has been challenged in motor control, and there are no standard formal definitions of the terms (see Prochazka 2000, for discussion), at least for saccades some distinctions are broadly accepted. Reflexive saccades are triggered by the target onsets and require no further processing. They have been likened to a visual grasp reflex (Machado and Rafal 2000) and are exogenously controlled. This contrasts with various types of voluntary saccade, which share the characteristic that the saccade is not directed at a target onset. Rather, the target information has to be processed in some way, and then an appropriate saccade executed. Thus in antisaccade tasks (Hallett 1978; Fischer and Weber 1992), a reflexive

saccade has to be inhibited, the target position information has to be extracted from the sensory array and a voluntary saccade executed *away* from the visual onset. Cued saccades require the interpretation of an instruction, and stimuli often avoid visual transients at target positions (Walker et al. 2000). We used memory-guided saccades (Pierrot-Deseilligny et al. 2002) in which a reflexive saccade is inhibited, target position information has to be held in short-term visual working memory, and the saccade executed in response to a second, spatially unrelated, “go” signal. An important difference between reflexive and voluntary saccades is therefore that in the case of voluntary saccades the control is largely endogenous. Note that both reflexive and memory-guided saccades involve a similar, largely dorsal, fronto-parietal cortical network (Munoz 2002; Brown et al. 2004).

We confirmed that, in the conditions used in these experiments, there is a substantial effect of the Müller–Lyer illusion on reflexive saccade amplitude. Both the direction of the effect (amplitude smaller with the vertex out/wings in configuration, larger with the vertex in/wings out configuration compared to a control condition) and its size (22% collapsed across subjects and directions) closely parallels the perceptual effect observed with the same stimuli (Bernardis et al. 2005). In addition we also found evidence of scaling bias (a larger absolute effect for larger stimuli) of a type often observed in perceptual responses. This did not appear in our previous analysis, probably due to the smaller data set we had available. These results suggest a close link between the representations driving both perception and saccades.

The size of effect was larger than that observed by both Binsted and Elliot (1999) and McCarley et al. (2003). As we have discussed previously in detail (Bernadis et al. 2005), Binsted and Elliot (1999) were almost certainly eliciting voluntary rather than reflexive saccades, so the contrast with our reflexive result is not necessarily a surprise. Methodological differences between our experiment and the reflexive condition of McCarley et al. (2003) may also explain the differences between the two sets of results. In addition to those mentioned in the [Introduction](#), one further difference deserves comment. Their method of using the Brentano version of the illusion, with the central element positioned at fixation, with the array extending to the right and left of fixation, could have altered the extent to which the whole array could influence responses, decreasing the effectiveness of the illusion, and thus the effect. The results of de Grave et al. (2006b), who also used the Brentano version, are interesting in this context. They positioned one end of the configuration at fixation, and had subjects saccade to the other end, similar to the method we employed. They reported effect sizes of 30% for horizontal saccades. Thus we have good reason to believe that in both

de Grave et al. (2006) and in our present experiment, the whole stimulus configuration influenced saccade amplitude, and not merely one end of it.

While the illusory stimulus affected the amplitude of memory-guided saccades, in the main experiment the effect was smaller (at 11%) than on reflexive saccades (22%). However, in the reflexive experiment, subjects were exposed to the stimulus for 200 ms, whereas in the memory-guided experiment it was 1 s. In order to investigate whether this difference might account for our failure to find a larger effect on saccade amplitude in the memory experiment we ran a memory control experiment. We found that, for the five subjects tested, the effect size was larger than the overall result for the main experiment. However, at 17% (collapsed across subjects, directions, and amplitudes) it was still smaller than observed in the reflexive condition. In the three subjects who participated in both the main and control experiments, there was only one in whom the shorter display time produced a markedly larger effect. In two others the effect was actually slightly greater with the longer display time.

Although direct comparison is difficult, it appears that we observed smaller effects in the memory-guided condition than McCarley et al. reported for their voluntary condition. They had subjects execute saccades to the vertices of Müller–Lyer figures as directed by a verbal instruction, as opposed to a flash at the target vertex. On the basis of their results they sought to draw conclusions about voluntary saccades in general, and did not distinguish between different types of voluntary saccade. Even if we assume that the results of the memory control experiment indicate that the effect size is more similar between memory and reflexive conditions than we might have expected based on the results of the main experiments, our results remain inconsistent with the conclusions of McCarley et al. While it is possible that there are some conditions (and some illusions) in which reflexive saccades are affected by the illusion less than in a voluntary condition, we have shown that there is at least one set of conditions where the opposite pattern is observed.

In addition to a difference in the size of the effect of the illusion on amplitude between the two main experiments, there were different effects on saccade latency. In the reflexive condition, latency was modulated by the stimulus, whereas in the memory condition it was not. However, in the reflexive condition, the presentation of the target configuration involved two visual transients: one at fixation and one in the periphery. And, by using a gap paradigm, the salience of the central event was probably enhanced. In order to investigate what influence this might have had on the results, we ran a fixation control experiment. The central vertex was present throughout the fixation period and the configuration was completed by the appearance of

the eccentric element. In addition there was no gap. In these circumstances, there was still clearly an amplitude effect; saccade amplitude to the “in” configuration was increased, and amplitude to the “out” configuration was decreased relative to the control condition. However, latency was no longer modulated by the type of configuration. This suggests that in the main experiment the transient at fixation could explain the modulation of latency, but not the modulation of amplitude. Further, in the main reflexive experiment while latency was influenced by configuration (i.e. “in” vs. “out”), the amplitude of the configuration had little influence. Again, this suggests that the latency effect was driven by events at fixation, not the overall configuration.

Both saccade amplitude and saccade latency can be modified by the appearance of more than one object in a display (the global effect; see Walker et al. 1997). If two targets appear in the same hemifield, saccade amplitude is modified, but latency is unaffected. If they are in opposite hemifields, latency is increased, but amplitude is unaffected. In the current experiments, while the “out” configuration was limited to one hemifield, the “in” configuration extended into the opposite hemifield. And indeed, in the reflexive condition, latency was longer for the “in” configuration than the “out”. However, note that in the control configuration, the arms of the “x” extended into the opposite hemifield, and yet clear differences were observed for latency between control and “in” configurations. Therefore while we cannot exclude the possibility that the global effect may have had some influence, particularly on the latencies we observed in the reflexive experiment, it cannot explain all of the results. Indeed, de Grave et al. (2006) demonstrated that vertically oriented Müller-Lyer figures, in which there is no hemifield difference in the displays, also produced large effects on reflexive saccade amplitude.

Finally, there is another saccade specific effect which might have a bearing on our present results. When the saccade target is a shape or a surface, saccades tend to land close to the centre of the shape (e.g. Melcher and Kowler 1999). If the arms of the target Müller-Lyer configuration were taken to imply a triangle, the saccade landing position might be biased in similar direction as the perceptual effect, but by a completely different mechanism. However, this possibility was explicitly investigated by de Grave et al. (2006a), who showed that subjects were indeed able to saccade to the vertices of the figure when instructed to do so (see also Knox 2006).

If it is accepted that it is the illusion that affects saccade amplitude, and not the saccade-specific effects discussed above, then our results are difficult to reconcile with any strong version of the TVSH. At least in the conditions used here, we have shown that a particular class of reflexive

motor actions (i.e. saccades) is consistently influenced by an illusion-inducing stimulus in a manner which closely parallels the perceptual effects that we and others have previously reported. Secondly, we have shown that in similar conditions, memory-guided saccades, while still affected by the illusion, are affected to a lesser extent. Because the dorsal pathway is involved in the online control of action, it has been suggested that information is not retained over time (Milner and Goodale 1995; Hu et al. 1999). Actions executed after a delay therefore have to rely on information derived from the ventral, perceptual pathway (Bradshaw and Watt 2002). In conditions incorporating a delay, memory-guided actions should be influenced by illusions even when the equivalent actions without a delay are immune. This hypothesis however depends on the critical assumption that the stored information (target position in this case) is obtained from the ventral pathway. In fact there is reason to believe that at least for saccades this may not be the case. In a recent fMRI study, Brown et al. (2004) compared reflexive and memory-guided saccades. Greater activation was demonstrated for memory-guided saccades in a number of classic dorsal pathway structures (e.g. rostral and ventral intraparietal sulcus) as well as more frontal saccade-related areas such as frontal and supplementary eye fields. There was relatively little activation in ventral areas.

In conclusion, our results demonstrate that methodological details matter when testing motor responses to illusions. This has been noted previously when comparing different pointing (Bruno and Bernardis 2002, 2003) and grasping (Pavani et al. 1999; Franz et al. 2000) responses. Thus, differences in methods and in the illusions investigated may account for the apparent contradiction between our results and those of Wong and Mack (1981). They used the dot in frame illusion and reported that reflexive saccades were largely unaffected. However, the dot-in-frame and Müller-Lyer illusions are likely to work through different mechanisms, particularly with reference to how saccade programming might be affected. With the Müller-Lyer illusion, the target for the saccade is a component in the illusion-inducing array. In the dot-in-frame illusion the target (the dot) is separate from the illusion-inducing context (the frame). Testing a greater range of illusions may help to establish which properties are critical in determining the presence or absence of an effect on the motor system. Further experiments are certainly required to clarify the influence of illusions on saccades (see Knox 2006) compared to other types of motor behaviour and to their effects on perception. At present, however, claims that the differential effects of the Müller-Lyer illusion on reflexive versus voluntary saccades provides support for the strong version of the TVSH (Goodale and Westwood 2004) remain premature.

References

- Bernardis P, Knox P, Bruno N (2005) How does action resist visual illusion? Uncorrected oculomotor information does not account for accurate pointing in peripersonal space. *Exp Brain Res* 162:133–144
- Binsted G, Elliot D (1999) The Muller–Lyer illusion as a perturbation to the saccadic system. *Hum Movement Sci* 18:103–117
- Bradshaw MF, Watt SJ (2002) A dissociation of perception and action in normal human observers: the effect of temporal delay. *Neuropsychologia* 40:1766–1778
- Brown MRG, DeSouza JFX, Goltz HC, Ford K, Menon RS, Goodale MA, Everling S (2004) Comparison of memory- and visually guided saccades using event-related fMRI. *J Neurophysiol* 91:873–889
- Bruno N (2001) When does action resist visual illusions? *TICS* 5:385–388
- Bruno N, Bernardis P (2002) Dissociating perception and action in Kanizsa's compression illusion. *Psychon Bull Rev* 9:723–730
- Bruno N, Bernardis P (2003) When does action resist visual illusions? Effector position modulates illusory influences on motor responses. *Exp Brain Res* 151:225–237
- Carey DP (2001) Do action systems resist visual illusions? *TICS* 5:109–113
- de Grave D, Smeets J, Brenner E (2006a) Why are saccades influenced by the Brentano illusion? *Exp Brain Res* 175:177–182
- de Grave DDJ, Franz VH, Gegenfurtner KR (2006b) The influence of the Brentano illusion on eye and hand movements. *J Vis* 6:727–738
- Fischer B, Weber H (1992) Characteristics of “anti” saccades in man. *Exp Brain Res* 89:415–424
- Fischer B, Weber H (1993) Express saccades and visual attention. *Behav Brain Sci* 16:553–610
- Franz VH (2001) Action does not resist visual illusions. *TICS* 5:457–459
- Franz VH, Gegenfurtner KR, Bulthoff HH, Fahle M (2000) Grasping visual illusions: no evidence for a dissociation between perception and action. *Psychol Sci* 11:20–25
- Goodale MA, Westwood DA (2004) An evolving view of duplex vision: separate but interacting cortical pathways for perception and action. *Curr Opin Neurobiol* 14:203–211
- Hallett P (1978) Primary and secondary saccades to goals defined by instructions. *Vis Res* 18:1279–1296
- Hu Y, Eagleson R, Goodale MA (1999) The effects of delay on the kinematics of grasping. *Exp Brain Res* 126:109–116
- Jeannerod M, Jacob P (2005) Visual cognition: a new look at the two-visual systems model. *Neuropsychologia* 43:301–312
- Knox PC (2006) The effect of Kanizsa's compression illusion on reflexive saccades. *Exp Brain Res* 175:764–768
- Krauzlis RJ, Miles FA (1996) Release of fixation for pursuit and saccades in humans: evidence for shared inputs acting on different neural substrates. *J Neurophysiol* 76:2822–2833
- Machado L, Rafal R (2000) Control of eye movement reflexes. *Exp Brain Res* 135:73–80
- McCarley JS, Kramer AF, DiGirolamo GJ (2003) Differential effects of the Muller–Lyer illusion on reflexive and voluntary saccades. *J Vis* 3:751–760
- Melcher D, Kowler E (1999) Shapes, surfaces and saccades. *Vis Res* 39:2929–2946
- Milner D, Dyde R (2003) Why do some perceptual illusions affect visually guided action, when others don't? *TICS* 7:10–11
- Milner AD, Goodale MA (1995) *The visual brain in action*. Oxford University Press, Oxford
- Munoz DP (2002) Commentary: saccadic eye movements: overview of neural circuitry. *Prog Brain Res* 140:3–19
- Musseler J, Heijden AHCvd, Kerzel D (2004) Visual space perception and action: introductory remarks. *Vis Cogn* 11:129–136
- Pavani F, Boscagli I, Benvenuti F, Rabuffetti M, Farnà A (1999) Are perception and action affected differently by the Titchener circles illusion? *Exp Brain Res* 127:95–101
- Pierrot-Deseilligny C, Müri RM, Rivaud-Pechoux S, Gaymard B, Ploner CJ (2002) Cortical control of spatial memory in humans: the visuoculomotor model. *Ann Neurol* 52:10–19
- Pratt J, Bekkering H, Abrams RA, Adam J (1999) The gap effect for spatially oriented responses. *Acta Psychol* 102:1–12
- Prochazka A, Clarac F, Loeb GE, Rothwell JC, Wolpaw JR (2000) What do reflex and voluntary mean? Modern views on an ancient debate. *Exp Brain Res* 130:417–432
- Rizzolatti G, Matelli M (2003) Two different streams form the dorsal visual system: anatomy and functions. *Exp Brain Res* 153:146–157
- Ungerleider LG, Mishkin M (1982) Two cortical visual systems. In: Ingle DJ, Goodale MA, Mansfield RJW (eds) *Analysis of visual behaviour*. MIT, Cambridge, pp 549–586
- Walker R, Deubel H, Schneider WX, Findlay JM (1997) Effect of remote distractors on saccade programming: evidence for an extended fixation zone. *J Neurophysiol* 78:1108–1119
- Walker R, Walker DG, Husain M, Kennard C (2000) Control of voluntary and reflexive saccades. *Exp Brain Res* 130:540–544
- Wong E, Mack A (1981) Saccadic programming and perceived location. *Acta Psychol* 48:123–131