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RESEARCH ARTICLE

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How does action resist visual illusion? Uncorrected oculomotor information does not account for accurate pointing in peripersonal space

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Abstract Using spatially identical displays (variants of the Müller–Lyer illusion), we compared the accuracy of spatial verbal judgments with that of saccadic (eye) and pointing (hand) movements. Verbal judgments showed a clear effect of the illusion. The amplitude of the primary saccade from one endpoint of the pattern (at fixation) to the other also showed an effect of the illusion. Conversely, movement amplitudes when pointing from one endpoint (initial finger position) to the other were significantly more accurate than both saccades and verbal responses. In a control experiment in which the viewing conditions between the saccade and pointing experiments were equalized, saccade amplitude was again affected by the illusion. In several studies, systematic biases in conscious spatial judgments have been contrasted with accurate open-loop pointing in peripersonal space. It has been proposed that such seeming dissociations between vision-for-action and vision-for-consciousness might in fact be because of a simple oculomotor strategy: saccade to the target before it disappears, then use the efference copy of the (accurate) saccadic movement to drive pointing. The present data do not support the hypothesis in this simple form.

Keywords Perception · Action · Visuomotor transformations · Saccades · Illusions · Dorsal · Ventral

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Introduction

We can reach for objects at egocentric locations in peripersonal space accurately and efficiently, even in conditions that yield systematic biases when observers verbally describe their percepts (e.g. when seeing geometrical illusions). Consider studies on pointing to the dumbbell illusion (Bruno and Bernardis 2003), a variant of the famous Müller–Lyer arrow illusion (Fig. 1d). A standard matching procedure was used to obtain explicit judgments of segment length for the two versions of the illusion (hoop-in and hoop-out). These judgments yielded a compression/expansion effect of the order of 10–15% of the actual length. However, when participants placed their index finger on one end of the segment, and then pointed to the other end in visually open-loop conditions, these pointing responses failed to show any appreciable illusory effect. Given that explicit judgments and pointing responses were based on the same visual information, the difference is surprising. What is the action system doing to bypass the spatial biases that affect conscious judgments? How does action resist the visual illusion?

In this paper, we seek to evaluate what seems to be the simplest explanation: the *oculomotor* hypothesis of Post and Welch (1996). According to the oculomotor hypothesis, when participants have to point to a location in peripersonal space, they use information provided by the oculomotor system to dynamically control the action and bring the hand to the correct location. Consider again the paradigm described above. According to the oculomotor hypothesis, the participant places his or her index finger on one endpoint of the dumbbell illusion, then makes a saccadic eye movement to the other (target) endpoint. The efference copy of the saccade is passed over to the pointing system and this information is then used to control the action on-line during its execution. In other words, pointing is effectively performed under the control of an internal model (see for instance Miall and Wolpert 1996) rather than primary sensory feedback, allowing for fast and accurate reaching movements (for reviews of

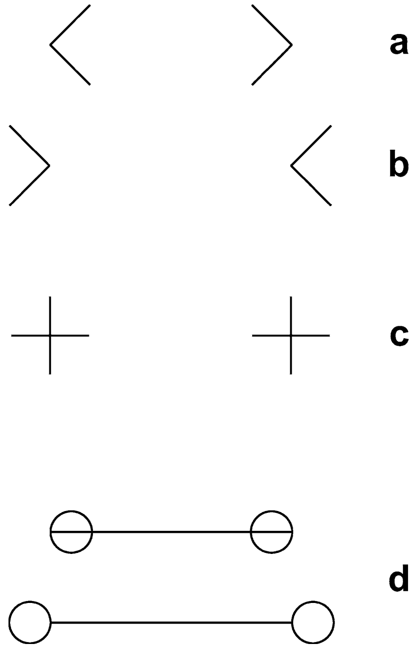

Fig. 1 Geometrical illusions described in the text: (**a**) arrow-outward pattern of a simplified Müller–Lyer illusion; (**b**) arrow-inward pattern; (**c**) baseline "plus" pattern used in the studies; (**d**) dumbbell illusion

hand–eye coordination in reaching see Carey 2000; Desmurget and Grafton 2000).

The oculomotor hypothesis rests critically on two assumptions. The first is that the saccadic efference copy is passed over to the mechanisms that control pointing, but not to those that mediate verbal judgments. If accurate efference copy information were available to both, then both would be accurate. The second assumption is that motor programs for saccadic eye movements are not affected by illusions. If saccades were biased, then it seems implausible that their *biased* efference copy would be used to drive *unbiased* pointing movements.

The first of these assumptions is plausible. It is well known that the accuracy of pointing movements is affected by eye movements in different ways, depending on the type of eye movement (Festinger and Canon 1965; Abrams 1994). Several studies have suggested that eye position information might be used to compute body-centric coordinates in pointing (Hansen 1979; Henriques et al. 1998; Soechting et al. 2001). It has often been reported that adapting saccadic gain produces shifts on pointing responses when these follow saccadic adaptation (Bekkering et al. 1995; de Graaf et al. 1995; Bruno et al. 2003) suggesting common spatial representations driving both types of response. On the other hand, several lines of evidence suggest that spatial maps used in pointing can be dissociated from those used for verbal reports, when eye movements are involved. For example, the compression of visual space that is observed in verbal positional reports for stimuli presented during saccades disappears when pointing to the same positions (Burr et al. 2001).

The second assumption, however, is more problematic. In a direct test of the effect of the Müller–Lyer illusion on eye movements, Binsted and Elliott (1999a) showed that saccades aimed at the vertices of the Müller–Lyer illusion exhibited small undershot and overshot biases consistent with the perceptual illusion. However, they did not provide comparison data on pointing. Another paper (Binsted and Elliott 1999b) included several pointing measures for comparison with primary saccades on Müller–Lyer half patterns. Still the effect that was produced by such displays on verbal judgments was not reported in either of these papers. By computing an average percent illusion effect (see Experiment 1, results section) on saccades from Table 1 in Binsted and Elliott (1999a), we obtained a percent illusory effect of about 13% for targets separated by 15.5°, but only 6% and 3% for 23.3° and 31° targets. The first of these figures is smaller, but still comparable (allowing for procedural differences, see also our Experiment 1) to standard estimates of the perceptual effect of the Müller–Lyer illusion, but the other two are substantially smaller. McCarley et al (2003) also reported a biasing of saccade endpoints using the Brentano version of the Müller–Lyer illusion and reported that the size of the illusory effect was larger for voluntary than for reflexive saccades. We calculated the illusory effect obtaining data from their figures; it was around 4% for reflexive saccades and around 20% for voluntary saccades. However, neither perceptual nor pointing data were provided for the same stimuli. Finally, Meegan et al (2004) recently reported that the accuracy of points of subjective equality and of pointing responses on the segments in the Müller–Lyer illusion showed a similar (weak) illusory bias. However, their data were not affected by a manipulation of stimulus duration. The same weak bias held for both 10 ms and 3000 ms. Given that the first of these is incompatible with a saccadic movement, this result suggests that pointing accuracy is not affected by the presence or absence of a preliminary saccade. In addition, their pointing task involved a go signal that was provided by the experimental program rather than allowing participants to start when they decided to do so, as we did in our previous studies (Bruno and Bernardis 2003). For all these reasons, it is difficult to decide whether these data demonstrate clear illusion effects on saccades, providing definitive evidence against the oculomotor hypothesis.

To resolve the issue, we compared the effect of the Müller–Lyer illusion on performance in three tasks: a verbal report of perceived length, a saccadic eye movement from one endpoint of the illusion to the other endpoint, and a pointing movement from one endpoint to the other endpoint. We used the same displays and identical temporal regimes in all three tasks, and selected our participants in order to perform both between and within-participant comparisons. Given the earlier results of Bruno and Bernardis (2003), we expected pointing to show either no effect or a very weak effect of the Müller–Lyer illusion. If the oculomotor hypothesis is correct, then the first (i.e. primary) saccade from one to the other endpoint of the illusory pattern should also show little or no effect, or at least a substantially smaller effect than is observed in verbal estimates.

Experiment 1: verbal estimations

To obtain a baseline estimate of the strength of the Müller–Lyer illusion in the present conditions, we collected verbal estimates of apparent width for three physical widths in our displays. Observers provided a numerical estimate relative to an arbitrary standard that was always visible. Conditions of presentation were exactly the same as were later used in the visuo-motor experiments.

Methods

Participants

Three members of the University of Trieste community (including the first author) and one member of the University of Liverpool (the second author) participated. All had normal or corrected-to-normal visual acuity. Observers provided their informed consent and the experiment was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Displays and apparatus.

The stimuli were simplified versions of the Müller–Lyer illusion and resembled those used by Binsted and Elliot (1999a). They were composed of "inward" or "outward" arrow patterns, with no segment connecting them (Figs. 1a and 1b). Performance on these stimuli was compared with a baseline condition made with "plus" patterns (Fig. 1c). Distances between the two vertices of the arrows or the two centers of the plus patterns were 4, 6, and 8 cm, corresponding to 4, 6, and 8 degrees of visual angle at a distance of 57 cm. Each pattern extended either to the left or the right of the monitor centre; one endpoint was always placed exactly at the centre of the monitor. The stimulus patterns were drawn in medium grey (approximately 6 cd m^{-2}) against a white background (60 cd m^{-2}) on a 19-inch ELO-Entuitive touchmonitor controlled by a Macintosh PowerMac G4 computer. The monitor was set at a 1024×768 spatial resolution and at a 80 Hz temporal resolution.

Conditions and procedure

After presentation of the pattern participants estimated the distance between the two vertices (or centers) of the pattern elements against a standard (a thin segment) that was conventionally assigned a magnitude of 100. The standard appeared in the upper left corner of the display, and its length was always 100 pixels. Displays were presented tachistoscopically (200 ms) after a brief presentation (400 ms) of a fixation point. The standard remained on the monitor until response. Responses were called out by observers verbally and entered on the keyboard of the computer by the experimenter. Each observer contributed 180 trials, resulting from 10 presentations of each of the 3 patterns×3 distances×2 directions, in a completely randomized order.

Data analysis

In all reported experiments, we summarized the data by computing the average verbal estimates (converted to degrees of visual angle) for each display type (arrow-in, out, or plus) and each distance (4, 6, or 8 deg). To obtain a qualitative assessment of the results, we then computed linear regressions fits of these averages against physical distance. In the baseline data verbal estimations are expected to fit a line with unitary slope and zero intercept. A constant bias is expected to produce and a non-zero intercept, whereas a scaling bias is expected to change the slope. Relative to these baseline data, the "inward" (expanding) patterns (Fig. 1b) are expected to lie on top of the baseline data (bigger slope or intercept, or both); whereas the "outward" (contracting) patterns (Fig. 1a) are expected lie below the baseline data. Next, to test the significance of the qualitative pattern, we subjected all the individual verbally judged amplitudes by the four participants to a repeated-measures analysis of variance. The independent variables were as follows:

- the actual distance between the arrows in the stimulus pattern (4, 6, or 8 deg),
- the direction of the arrows in the pattern (inward or outward—we did not use the baseline data here), and
- the position of the pattern relative to the central fixation point (left or right).

Assuming an effect of the illusion, we expect this analysis to reveal a significant effect of the distance between the arrows, and significant effects of arrow direction and of the interaction between distance and direction (corresponding to non-parallel lines in the qualitative pattern), or simply a significant effect of arrow direction (corresponding to separate, but parallel lines in the qualitative pattern). Finally, to obtain a summary percent measure of the effect we averaged the amplitude data and computed the quantity [(arrows outward− arrows inward)/baseline]×100 for each distance, direction, and observer. This percent measure provides a metric for comparing the present effects with those already in the literature (see Bruno and Bernardis 2003).

Results

Figure 2 presents the qualitative pattern of the results as averages collapsed across the four participants. As expected from the literature, verbal estimations showed a clear effect of the illusion. In the baseline condition, linear fit parameters were very close to the no-bias expectations (slopes equal to 0.86 and 0.90 for the leftward and rightward displays, respectively, and intercepts equal to

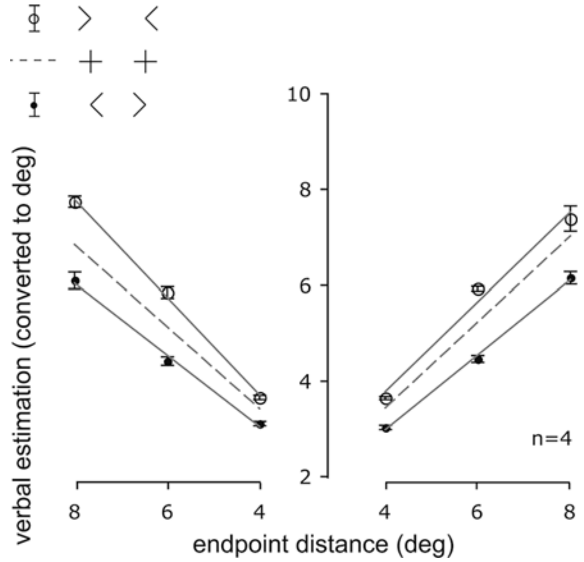

Fig. 2 Verbal estimation experiment. *Left*, patterns extending from central fixation to the left of the screen. *Right*, patterns extending to the right. *Dashed lines*, linear fits to baseline data (not shown). *Continuous lines*, linear fits to the arrow-inward and arrow-outward data. *Filled disks*, average estimations with the arrow-outward patterns. *Open disks*, average estimations with the arrow-inward patterns. *Error bars* are 1 SEM, computed by averaging the individual SEM of each observer

−0.01 and −0.16). However, relative to the baseline data we observed smaller slopes in the "outward" condition (left=0.75; right=0.78) and bigger slopes in the "inward" condition (left=1.02; right=0.94), as is clearly visible from the plot. Table 1 presents individual regression parameters for each of the four observers who were averaged in Fig. 2. As shown in the table, the qualitative pattern that is apparent in Fig. 2 is also visible in all four observers, who all show nicely separated fitted lines due to ordered differences in the estimated slopes or, in one case (P.B.), the intercepts. In accord with this characterization of the pattern, the analysis of variance revealed a significant effect of arrow direction, $F_{(1,47)}=42.6$, $P<0.007$, and of arrow distance, $F_{(2,47)}=97.9$, $P<0.0001$, and of the interaction between direction and distance, $F_{(2,47)}=7.5$, $P<0.023$. To obtain a percent measure of this illusory effect, for each width, direction, and observer we averaged the amplitude data and computed the quantity [(arrows out −arrows in)/baseline]×100. Combining the resulting 24 measures yielded an overall percent measure of 22.3 ±2.2%. A *t*-test on these individual sample means demonstrated that a sample percent measure=22.3% is highly unlikely if the population percent illusory effect=0%, $t_{(23)}=10$, $P<0.0001$.

Experiment 2: saccades

To test the oculomotor hypothesis, verbal estimates of widths in the Müller–Lyer illusion must be compared with two types of motor response—eye movements and pointing movements. As a first step in this direction, we

Table 1 Experiment 1, verbal estimation. Slopes and intercepts ±1SE

Subject	Condition	Stimulus on left side		Stimulus on right side	
		Slope	Intercept	Slope	Intercept
pb	Outward	0.90±0.04	−0.86±0.28	0.90±0.04	−0.89±0.26
	Control	0.80±0.01	0.32±0.06	0.93±0.11	−0.34±0.70
	Inward	0.91±0.03	0.06±0.23	0.91±0.16	0.002±1.03
ac	Outward	0.56±0.12	0.78±0.78	0.80±0.21	−0.32±1.30
	Control	0.86±0.20	−0.21±1.30	0.88±0.21	−0.31±1.28
	Inward	1.20±0.15	−1.25±0.95	1.02±0.09	−0.23±0.55
pk	Outward	0.59±0.06	0.58±0.40	0.57±0.01	0.47±0.04
	Control	0.69±0.04	0.66±0.30	0.75±0.19	0.41±1.21
	Inward	0.78±0.04	0.63±0.25	0.74±0.01	0.84±0.03
ag	Outward	0.94±0.02	−0.36±0.14	0.84±0.10	0.09±0.62
	Control	1.07±0.07	−0.80±0.44	1.03±0.22	−0.43±1.39
	Inward	1.18±0.25	−0.99±1.54	1.07±0.23	−0.52±1.41

recorded eye movements in observers that were requested to fixate one Müller–Lyer vertex presented in the centre of the monitor at fixation (or the centre of the plus), and then to saccade to the other endpoint. We then analyzed the amplitudes of the primary saccade for comparison with data from the other experiments.

Methods

Participants

Three members of the University of Liverpool community (including the second author) and one member of the University of Trieste (the first author) participated. All had normal or corrected-to-normal visual acuity. Observers provided their informed consent and the experiments was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Displays and apparatus

The stimuli were visually identical to those of the first experiment (Figs. 1a–c). The only difference was that they were presented on a 21" monitor (1024×768 spatial resolution, 100 Hz temporal resolution) driven by an IBM compatible computer. 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 deg. Eye-tracker output was sampled at 1 kHz and digitized with 16-bit precision using a CED Power 1401 interface. A combination of chinrest and cheek pads was used to ensure head stabilization.

Conditions and procedure

Each participant viewed all types of display (inward and outward-arrows, pluses). A total of 270 trials (3 patterns×3 distances×2 directions×15 repetitions) were divided into 3 blocks in a pseudo random order to avoid excessively long sessions. In the middle of each block participants were given 5 min to rest their eyes. At the beginning of each set of measurements, a five-point calibration task was performed. Participants were seated in front of the monitor and their head was stabilized. The calibration stimuli were then presented six times at each of four positions aligned with the monitor centre, two to the left (5° and 10° distance from centre) and two to the right. Participants were instructed to accurately fixate (monocularly with left eye) each stimulus until it disappeared after 1 s. After calibration was completed, the experimental trials commenced. At the beginning of each trial, subjects fixated a central fixation point which was displayed for a variable fixation period ranging from 1–1.5 s. Next, the stimulus was presented for 200 ms. Participants were instructed to execute a saccade to the other vertex or intersection (in the control displays), as quickly and accurately as possible. They then had 800 ms to perform the saccade before trial ended. The stimulus patterns had always one vertex (or intersection in the plus pattern) exactly at the central fixation point, and the other appeared randomly to its left or right. After having performed the saccade, the participant again fixated the central point, and the next stimulus appeared after the variable fixation time. The experimenter monitored the participants' eye movements on a trial-by-trial basis to ensure that they maintained their performance. Verbal feedback was given as necessary.

Data reduction, validation, and analysis

For each trial, eye position data from approximately 200 ms before to 800 ms after target appearance were written to disk for analysis off-line. Data were analyzed using an interactive program which displayed the eye position data and the time at which the target appeared. Given that we were analyzing large saccades with high accelerations by a high-resolution technique, primary saccades within each trial could be easily identified by simply looking at this display. Thus, 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.

Occasionally, we observed saccades with latencies <90 ms. Typically, these saccades were very hypometric, that is, they were less than 50% of the required amplitude. Accordingly, such saccades were classified as anticipatory and trials containing them were rejected. In addition, trials were also occasionally rejected because of blinks. In total, however, less than 3.5% of the trials were rejected for these reasons. Inspecting the distribution of saccadic latencies demonstrated that most saccades were fully open-loop, that is, the target disappeared before the start of the saccade and there was no availability of visual feedback during the execution. Only in 627 saccades out of 1898 (about 33%), movement started before the stimulus was turned off (i.e. before 200 ms). To fully exclude contamination from visual feedback, these 627 saccades were also excluded from our analysis. The accuracy of primary saccades was analyzed by a similar method to that used to analyze verbal responses. We plotted saccadic amplitudes against physical distance for the "inward", "outward", and baseline "plus" conditions. Linear regressions were fitted to the data, and regression slopes were inspected to evaluate the illusory effect. Next, the amplitudes were subjected to analysis of variance. Finally, a summary percent measure of the effect was computed.

Results

Participants had no difficulty performing the saccade task. The appearance of one set of arrows with the vertex at fixation did not lead to systematic alterations of the initial fixation position. In addition, in the great majority of trials there was a single, clear primary saccade. Only rarely did we observe subsequent corrective saccades. Figure 3 presents the qualitative pattern of the results, using the same plotting conventions as those used for the first experiment. In the baseline data, the slopes relating saccadic amplitude to actual width were again similar to the no-bias expectations (slopes equal to 0.90 and 0.79 for the rightward and leftward displays, respectively). Relative to this baseline, there was a clear difference in saccadic amplitude in the arrow-inward and arrow-

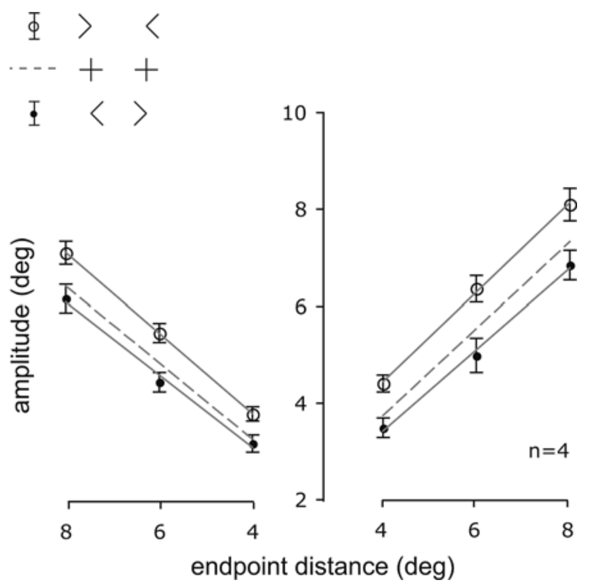

Fig. 3 Saccade experiment. Primary saccade amplitudes. Plotting conventions are the same as for Fig. 2

Table 2 Experiment 2, saccadic task. Slopes and intercepts±1 SE

Subject	Condition	Stimulus on left side		Stimulus on right side	
		Slope	Intercept	Slope	Intercept
pb	Outward	0.88±0.04	−0.16±0.25	1.01±0.18	−0.03±1.09
	Control	0.86±0.06	0.15±0.40	1.04±0.02	0.18±0.15
	Inward	0.75±0.03	1.27±0.16	0.90±0.09	1.69±0.55
ic	Outward	0.88±0.10	−0.29±0.61	0.83±0.09	−0.21±0.58
	Control	0.96±0.07	−0.12±0.43	0.83±0.06	0.03±0.39
	Inward	0.83±0.03	1.13±0.16	1.00±0.02	−0.39±0.12
pk	Outward	0.57±0.14	0.18±0.88	0.87±0.08	0.17±0.50
	Control	0.60±0.03	0.17±0.23	0.90±0.10	0.52±0.64
	Inward	0.71±0.06	0.26±0.41	1.02±0.08	0.85±0.49
jd	Outward	0.61±0.01	0.79±0.03	0.66±0.21	0.28±1.30
	Control	0.74±0.01	0.04±0.03	0.82±0.01	−0.15±0.02
	Inward	1.03±0.02	−0.92±0.15	0.77±0.06	0.77±0.38

outward patterns. However, this difference showed up mainly as a constant error (regression intercepts) and less strongly in the linear slopes. When saccading to the left, these slopes were 0.75 and 0.83 for the arrow-outward and arrow-inward data, respectively; when saccading to the right, 0.84 and 0.92, in the same order. Intercepts, on the other hand, were equal to 0.06 (leftward) and 0.14 (rightwards) in the baseline displays, but equal to 0.44 (leftward) and 0.73 (rightwards) in the arrow-inward displays and equal to 0.07 (leftward) and 0.05 (rightward) in the arrow-outward displays. Thus, the qualitative pattern of the saccade data was somewhat different from that of the perceptual data (Experiment 1). We note, however, that in subsequent measures (see Experiment 4) we found again a pattern very similar to that observed in Experiment 1, suggesting that the similarity in the slopes of Fig. 2 is not systematic. For this reason, we will not discuss it further. As for the previous experiment, Table 2 presents the individual linear parameters. As in the first experiment, inspecting the individual linear fit parameters demonstrated that all four observers showed the effect, yielding clearly separated lines because of ordered differences in the slopes or the intercepts. In accord with this characterization of the pattern, the analysis of variance revealed a significant effect of arrow direction, $F_{(2,47)}=20.0$, $P<0.021$, and of distance $F_{(1,47)}=188.2$, $P<0.0001$, whereas the interaction between direction and distance did not reveal a significant effect, $F_{(2,47)}=0.4$. Finally, we summarized the saccade results by the percent measure of the illusion effect, which was 24.8±3.8%. Again, a *t*-test on the individual sample means demonstrated that an average measure=24.8% is highly unlikely if the population percent illusory effect=0%, $t_{(23)}=6.45$, $P<0.0001$. We conclude that the effect of the illusion on saccades is comparable with the effect on verbal judgments.

Experiment 3: pointing

As the second step in our test of the oculomotor hypothesis, we measured the accuracy of open-loop pointing on the same displays used for the verbal estimate and saccade experiments. The pointing task was identical with the saccadic task, except that now participants had to place their index finger on an initial position, and then move their hand sideways to point to the target rather than making a saccadic eye movement toward it.

Methods

Participants

Three members of the University of Trieste community (including the first author) and one member of the University of Liverpool (the second author) participated. All had normal or corrected-to-normal vision. Observers provided their informed consent and the experiments was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Displays and apparatus

The displays and the apparatus used to present them and record the pointing responses were the same as those of Experiment 1. Thus, the stimulus patterns were drawn in medium grey (approximately 6 cd m^{-2}) against a white background (60 cd m^{-2}) on a 19-inch ELO-Entuitive touchmonitor controlled by a Macintosh PowerMac G4 computer. The ELO-Entuitive is a touch-on-tube monitor which uses wave technology to record touched locations directly through the glass surface of the CRT screen, eliminating the overlay surface that is needed in standard touchmonitors. This provides optical quality comparable with that of a high-quality standard CRT. The technology also provides superior precision in measurements of touched locations (standard deviation of error less than 2 mm, for details on the technology see http://www.elotouch.com/products/inteltec/intelspec.asp). The monitor was set at a 1024×768 spatial resolution and 80 Hz temporal resolution. The locations where the index fingers of the participants contacted the touch monitor were read by the experimental program and recorded for subsequent analysis.

Conditions and procedure

The procedure was similar to that used by Bruno and Bernardis (2003). Trials began upon successful calibration of the touchmonitor. The starting point was always positioned at the central fixation mark. Participants were requested to foveate this mark and to put their right index finger (all were right handed) on it. As soon as the participants placed their finger on the mark, the stimulus was presented tachistoscopically (200 ms). Each participant viewed all three types of pattern (arrows inward, outward, and pluses) and was seated 57 cm in front of the fronto-parallel touch monitor where the stimuli appeared. Participants pointed from one arrow vertex to the other vertex (or from the plus centre to the other). Each participant completed 180 trials, resulting from 10 presentations of each of the 3 patterns×3 distances (4, 6, 8 cm)×2 directions (left, right), in a completely randomized order.

Data validation and analysis

Pointing amplitudes were recorded directly by the stimulus presentation software by subtracting the *x* coordinate of the first point from the *x* coordinate of the second point. The accuracy of the response was analyzed as already described in the previous experiments. The stimulus presentation software also recorded the latency of each pointing action. As in the previous experiment, to ensure that each analyzed movement was performed in fully open-loop conditions, we inspected these pointing latencies and removed from the analysis responses that begun before the stimulus were turned off. From a total amount of 720 trials only 45 (6.2%) had a latency period that was shorter than 200 ms.

Results

Figure 4 presents the qualitative results as averages computed across all four participants The pattern of the baseline data suggested that participants were very accurate (slopes equal to 0.97 and 0.99 for the leftward and rightward displays, respectively; intercepts equal to −0.01 and 0.16). In the arrow-inward patterns, performance was very similar to baseline (slopes equal to 1.00 and 1.01 for the leftward and rightward displays, respectively; intercepts equal to 0.04 and 0.17), as was the case for the arrow-outward patterns, (slopes equal to 0.91 and 1.01 for the leftward and rightward displays, respectively; intercepts equal to 0.12 and −0.08). Table 3 presents individual linear regression parameters. As can be seen by inspecting these parameters, two participants showed essentially no illusory effect, whereas the other two participants showed a slight separation between the linear fits for the inward and outward arrow pattern, suggesting a weak effect of the illusion, when moving to the left but not when moving to the right. Accordingly, the analysis of variance revealed a significant effect of the distance between the arrows, $F_{(2,47)}$=1227.7, P<0.0001, but not of arrow direction or of the interaction between direction and distance, $F_{(1,47)}$=5.2, P<0.1 and $F_{(2,47)}$=1.1, P<0.3, respectively. Although the difference between the inward and outward pattern did not reach statistical significance in this study, computing the percent illusory effect yielded a value of 7.1±1.3%. A *t*-test on the individual sample mean suggested that this measure was again unlikely if the sample came from a population with mean=0%, $t_{(23)}$=5.51, P<0.0001. It is possible therefore that the lack of significance of the inward-outward comparison in the analysis of variance is, in fact, merely because of insufficient statistical power. However, comparing the percent illusion effect in pointing with the expectations based on the average effects in other two studies demonstrated that pointing produced a statistically smaller bias, $t_{(23)}$=−11.89, P=0.0001 and –13.76, P<0.0001. We conclude that, unlike saccades, pointing is only marginally affected by the illusion.

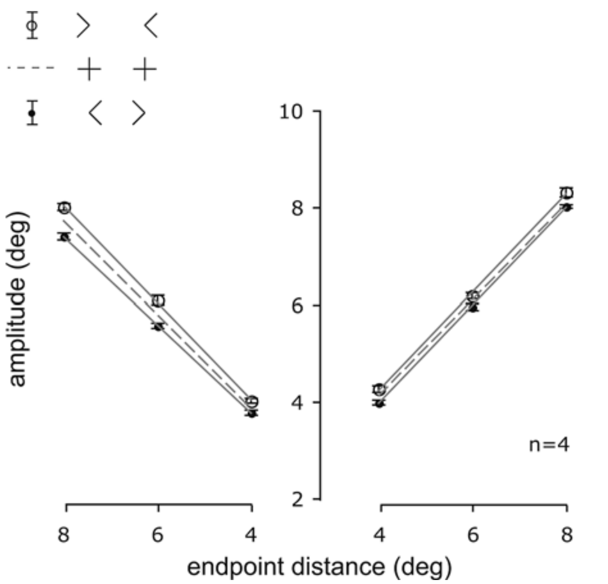

Fig. 4 Pointing experiment. Plotting conventions are the same as for Fig. 2

Table 3 Experiment 3, pointing. Slopes and intercepts±1 SE

Subject	Condition	Stimulus on left side		Stimulus on right side	
		Slope	Intercept	Slope	Intercept
pb	Outward	1.05±0.02	−0.37±0.13	1.04±0.02	−0.23±0.14
	Control	1.00±0.06	−0.06±0.36	1.01±0.01	−0.01±0.10
	Inward	1.06±0.03	−0.22±0.19	1.00±0.01	0.16±0.09
ab	Outward	0.98±0.01	−0.33±0.07	1.00±0.03	0.29±0.21
	Control	0.99±0.06	0.39±0.39	0.93±0.01	0.66±0.08
	Inward	1.00±0.01	0.36±0.08	0.92±0.10	0.70±0.63
pk	Outward	0.86±0.04	0.02±0.28	1.03±0.01	−0.30±0.03
	Control	1.00±0.07	−0.47±0.42	1.05±0.13	−0.33±0.81
	Inward	1.00±0.05	0.22±0.33	1.12±0.07	−0.13±0.45
aj	Outward	0.74±0.04	0.40±0.24	0.96±0.01	−0.08±0.05
	Control	0.88±0.03	−0.04±0.17	0.98±0.03	0.12±0.21
	Inward	0.93±0.05	−0.07±0.32	1.03±0.03	−0.12±0.17

Experiment 4: saccades with finger at fixation

There was a potentially important difference between the procedures of the second and the third experiments. In the second experiment the stimulus was always fully visible. In contrast, in the third experiment one endpoint was sometimes partially occluded by the subject's finger when placed at fixation on the central target. Partial occlusion was more conspicuous when the stimulus appeared on the right side of the monitor and when the dimensions of the arrow were small. If partial occlusion of the stimulus reduces the effect of the illusion by effectively removing one of the arrows from the field of view, this might explain the strong decrease in the effectiveness of the illusion that we observed in the third experiment. As a test of this alternative explanation, we replicated the second (saccade) experiment with one simple but crucial difference. Observers were asked to place their finger over the fixation point throughout each run of trials. Thus, their finger always partially occluded one of the arrows while they executed saccades from one vertex to the other. If partial occlusion reduces the effect of the illusion, the results should now become more similar to those of Experiment 3. If, conversely, occlusion does not reduce the effect of the illusion, they should remain similar to those of Experiment 2.

Methods

Participants

Three members of the University of Liverpool community (including the second author) and one member of the University of Trieste (the third author) participated. All had normal or corrected-to-normal visual acuity. Observers provided their informed consent and the experiments was performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

Displays, apparatus, conditions, and procedure

The stimuli, apparatus and conditions were completely identical with those of the second experiment (Figs. 1a–c). The only difference was in the procedure. Now the participants were asked to place their right index finger on the fixation point at beginning of each trial, and to remain with the index in the same position for all the duration of each trial. The finger was placed exactly over the fixation point, with the cross aligned with the nail centre.

Data reduction, validation, and analysis

Each trial was analyzed in the same way and with the same constraints of the second experiment. Also in this experiment, we removed anticipatory saccades and trials with blinks. In total, however, less than 18% of the trials were rejected for these reasons. Only in 319 saccades out of 1531 (about 21%), movement started before the stimulus was turned off (i.e. before 200 ms), these saccades were also excluded from our analysis. The accuracy of primary saccades was analyzed by the same method to that used in the second experiment.

Results

Qualitatively, subjects had no difficulty performing the saccade task. Holding their index finger over the fixation did not create any difficult in the ability to fixate steadily before the appearance of the stimulus. Figure 5 presents the qualitative pattern of results. Plotting conventions are the same as those used for the other experiments. In the baseline data, the slopes relating saccadic amplitude to actual width were equal to 0.93 and 0.86 for the rightward and leftward displays, respectively. However, as can be seen from the graph, there was a clear difference between the arrow-inward and arrow-outward patterns, relative to baseline. Contrary to Experiment 2 and similarly to Experiment 1, however, this difference showed up again in the linear slopes. When saccading to the left, the slopes were 0.81 and 0.94 for the arrow-outward and arrow-inward data, respectively; when saccading to the right, the

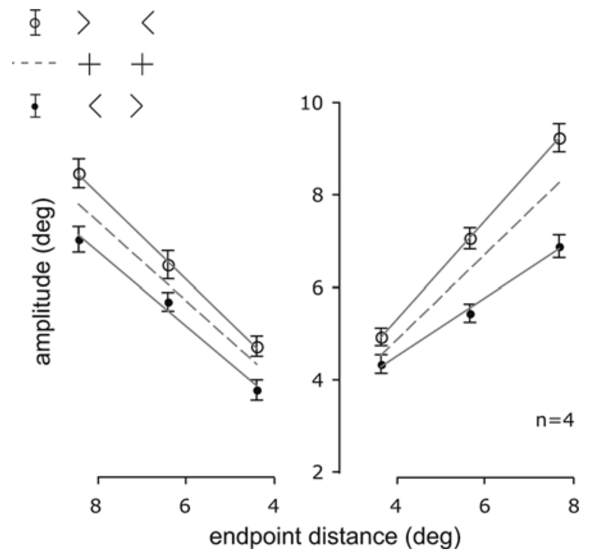

Fig. 5 Eye movement with finger at fixation, control experiment. Plotting conventions are the same as for Fig. 2

Table 4 Experiment 4, saccadic control task. Slopes and intercepts ±1 SE

Subject	Condition	Stimulus on left side		Stimulus on right side	
		Slope	Intercept	Slope	Intercept
nb	Outward	0.83±0.08	−0.02±0.50	0.76±0.02	1.47±0.13
	Control	0.92±0.01	0.26±0.01	0.96±0.01	1.24±0.01
	Inward	0.97±0.01	0.20±0.02	1.02±0.09	1.13±0.57
ic	Outward	0.86±0.03	1.76±0.19	0.92±0.03	0.53±0.17
	Control	0.97±0.01	1.21±0.01	1.10±0.01	0.25±0.01
	Inward	1.00±0.02	1.70±0.13	1.27±0.07	0.02±0.43
pk	Outward	0.79±0.12	0.82±0.76	0.17±0.18	4.86±1.11
	Control	0.72±0.01	1.86±0.01	0.87±0.01	1.59±0.01
	Inward	0.82±0.10	1.81±0.64	1.07±0.16	1.42±0.99
jd	Outward	0.77±0.09	0.18±0.57	0.69±0.01	0.34±0.08
	Control	0.83±0.01	0.44±0.01	0.79±0.01	0.40±0.01
	Inward	0.95±0.01	0.33±0.02	0.95±0.03	0.10±0.16

slopes were 0.64 and 1.08. Intercepts, on the other hand, were equal to 0.94 (leftward) and 0.87 (rightwards) in the baseline displays, but to 1.01 (leftward) and 0.67 (rightwards) in the arrow-inward displays and to 0.69 (leftward) and 1.80 (rightward) in the arrow-outward displays. Table 4 presents regression parameters computed on the individual data, showing that all observers showed the pattern in both directions Accordingly, and as in Experiment 1, the analysis of variance revealed a significant effect of arrow direction, $F_{(1,47)}$=186.7, P=0.0008, and of arrow distance, $F_{(2,47)}$=187.1, P<0.0001 and of the interaction between direction and distance, $F_{(2,47)}$=16.9, P<0.003. The percent measure of the illusion effect was 20.2±1.9%, an effect size again highly unlikely if the population percent illusory effect=0%, $t_{(23)}$=10.53, P<0.0001. We conclude that partial occlusion does not reduce the effect of the illusion in the present conditions.

General discussion and conclusion

The results of our experiments suggest that the spatial representation driving saccadic eye movements is different from the representation used to drive open-loop pointing. In short, saccades are strongly affected by the orientation of the fins in the Müller–Lyer illusion, whereas pointing is much less sensitive to the illusion. These results hold for both between-group comparisons (averages of all participants in each experiment) and when comparing the data within the participants that served in all studies. Thus, these data confirm the conclusion of Binsted and Elliot (despite procedural differences and corresponding quantitative differences in the results). We also demonstrated that when the viewing conditions in the pointing and saccade experiments were equalized, by having the subjects position their finger at the fixation point throughout the saccade experiment, the illusion continued to have a substantial effect on saccade amplitude.

Two differences between our methods and those of Binsted and Elliot (1999a) might explain why their reported illusory effects on saccade amplitude were much smaller than ours. First, they used very much larger stimuli (vertex separations of 15.5°–31° of visual angle compared with 4°–8°). Our choice of separations was in part determined by the mode of stimulus delivery (a monitor). However, most naturally occurring saccades are small; from the data of Bahill et al (1975) it is clear that 85% of natural saccades have amplitudes of less than 15°. Thus, to present stimuli where the minimum required saccade was 15° might be regarded as ecologically problematical. Such large gaze shifts would normally involve both the head and eyes. Second, the stimuli used by Binsted and Elliot consisted of large painted figures that were continuously visible. Their participants were requested to execute paced saccades between the vertices of the Müller–Lyer figures in synchrony with a metronome. When saccades are performed in this way, there is clearly ample scope for adaptation due to retinal errors (see McLaughlin 1967; Deubel 1995).

Assuming an illusion magnitude of the size we observed, at the end of each primary saccade a large retinal error would be generated because the eye would not have landed at the desired position (i.e. on the appropriate vertex). Such a retinal error might be expected to induce adaptation of saccade gain. Binsted and Elliot recorded the occurrence of corrective saccades but did not report whether during the execution of a series of saccades the primary saccade amplitude changed. Thus, there is the possibility that illusion effects of the size that we have reported here were adapted out. To prevent this possibility, in the present studies we deliberately exposed subjects to briefly presented targets (display time 200 ms). As a result, we observed very few corrective saccades.

McCarley et al (2003) compared the effect of the Brentano version of the Müller–Lyer illusion on voluntary and reflexive saccades. In their "reflexive" condition, subjects previewed the Müller–Lyer stimulus for 506 ms before a go signal was flashed at one of the vertices. In the "voluntary" condition, the go signal was a spoken word. While direct comparison without results is difficult, clearly we were eliciting saccades in response to transient stimuli, a response that would most appropriately defined as reflexive. Yet we observed illusion effects of 24.8% (Experiment 2) and 20.2% (Experiment 4) compared with approximately 4% in McCarley's reflexive condition. There was, however, an important difference between our procedure and that of McCarley: we did not have a preview period. It remains to be seen whether the size of the illusory effect would be reduced if we introduced a preview period in our paradigm. In principle, we could also try to make the response more "voluntary" as opposed to "reflexive" (e.g. by introducing a memory delay or by requiring subjects to make an antisaccade response). However, it seems unlikely that this would enhance the effect of the illusion given that effect we observed on saccades was already comparable with that observed in the perceptual matching experiment.

Implications for the oculomotor hypothesis

The present results provide strong evidence against the oculomotor hypothesis in the form that was presented in the introduction. If participants were using uncorrected efference copies of their first saccades to drive pointing, then the accuracies of these two motor responses should have been comparable. Instead, performance in the saccadic task was markedly different from performance in the pointing task. In fact, the percent effect of the illusion on saccadic eye movements was approximately three times larger than its effect on pointing (20–24% vs. about 7%). Conversely, the saccadic effect was comparable with that on verbal estimates (which was about 22%).

Even though the current results argue against the use of uncorrected efference copies of first saccades to drive open-loop pointing, positional information from saccades might still interact with pointing in more complex ways. One might argue that the oculomotor system could execute additional "corrective" saccades to compensate for its own constant biases, even in the absence of visual feedback, and that the efference copies of these additional saccades could be used by pointing. This however seems implausible, and is contradicted by our observation of few corrective saccades in Experiment 2 in the absence of retinal errors. Recall also that we used the same displays and stimulus durations (200 ms) in both Experiments 2 and 4 (saccades) and in Experiment 3 (pointing). Thus although we did not measure eye movements in Experiment 3, it is likely that corrective saccades were equally rare in Experiments 3, 4, and 2. Thus it is unlikely that efference copies from subsequent corrective saccades can account for accurate pointing in our experiment. A second possibility might be that the pointing system is capable of taking into account constant biases exhibited by saccades when formulating motor plans in some other, unknown way. A test of this possibility would consist of measuring saccades and pointing within the same trials, and investigating whether saccades and pointing consistently show similar scaling biases while saccades also show constant undershot and overshot biases. Experiments aimed at performing such measurements are currently being designed in our laboratories and will be the object of a future report.

Our present claim that uncorrected oculomotor information cannot account for accurate pointing might seem at odds with numerous findings that have been interpreted as suggesting that eye and arm movements can share spatial information. For instance, several results demonstrated transfer of saccadic adaptation to hand pointing (Bekkering et al. 1995; de Graaf et al. 1995; Bruno et al. 2003) and there is evidence that saccade trajectories can be affected by those of concomitant closed-loop reaches (Tipper et al. 2001). Our claim, however, is not that the saccadic and the pointing systems cannot share spatial information, but that in the conditions we have used here accurate information is not available for sharing. The space-related internal modifications (gain settings) that are induced by saccadic adaptation procedures (via retinal error signals) might well be shared with the pointing system. At the same time, it could still remain true that the initial representation used to plan a saccade is affected by the orientation of the fins relative to each other, whereas the representation used by pointing is not. Direct tests of this possibility are also possible. Using saccadic or pointing adaptation procedures on the Müller–Lyer stimuli, we should expect to observe that adaptation transfers from one motor response to the other, while each continues to show its idiosyncratic biases. Again, our laboratories are currently planning experiments aimed at testing this possibility.

Finally, it also remains to be seen whether the present conclusion, which properly applies only to the conditions of the current measures, can be generalized to eye and pointing movements in more natural conditions. One obvious difference is that in natural perception–action cycles stimuli are not turned off after a few hundred milliseconds, but remain continuously visible for additional acquisition of visual information. In these conditions, it seems much more plausible that additional corrective saccades quickly correct biases and reach accurate egocentric positions. Thus, a record of these could in principle be used to drive accurate pointing. The relative timings of pointing, the primary saccade, and these putative corrective saccades would be a critical issue in this case. Assuming an average latency of about 200 ms for the primary saccade, and an additional 150 ms for the first corrective saccade, this implies that accurate positional information would not be available in the oculomotor system until after 350 ms. This type of information might be useful when performing relatively slower pointing gestures, but not when pointing is performed very rapidly.

Implications for models of perception and action

The present results have several implications for models of perception, action, and visuomotor transformations. Since the publication of Milner and Goodale's seminal monograph (1995), several authors have proposed interpretations of functional dissociations between vision-for-action and vision-for-consciousness. In our view, these interpretations can be divided into three classes. The implications of the current results will be accordingly discussed in relation to each.

According to a first interpretation, what seem like dissociations between separate functions is in fact just experimental artifact (Franz et al. 2000, 2001; Franz 2001), due to inadequate matching of the perceptual and motor responses. According to this view, if the experimental tasks are designed to ensure fully comparable conditions, then both vision-for-action and vision-for-consciousness show similar biases. Thus, apparent functional dissociations are not due to different internal representations used by separate visual mechanisms, but simply to task demands that differentiate motor outputs from verbal reports in certain conditions. We discuss this view first as it seem to us that our data are clearly not in accord with it. In the present paper, we demonstrated a functional difference between one action (pointing) and one perceptual response, in fully matched conditions. In this, the present results resembled observations that some of us have reported before (Bruno and Bernardis 2002, 2003). Thus, we believe that the present data confirm that perception–action dissociations are a genuine theoretical problem and not a mere methodological artifact.

According to a second interpretation, results dissociating between vision-for-action and vision-for-consciousness are the signature of two functionally and anatomically distinct modules—a context-sensitive "perceptual" module, which is subject to the illusion, and a context-insensitive "visuomotor" module, which is not. The perceptual module is identified with the ventral stream of projections from the primary visual area (V1) to the inferotemporal cortex (IT), whereas the visuomotor module is identified with the dorsal stream to posterior parietal cortex (PPC—Milner and Goodale 1995). The current data demonstrate that some types of action response (saccades) are affected by the illusion. The underlying neuroanatomy of the saccade system is relatively well understood, and involves a number of cortical areas (see Munoz 2002 for a recent review). Saccades are critically dependent on areas classically assigned to the dorsal/visuomotor stream such as posterior parietal cortex. Thus, the present data run counter to a "strong" version of the perception-action model of Milner and Goodale. Clearly, at least some types of action can be affected by illusions as much as verbal responses. However, this result could in principle be reconciled with the perception–action model, either by hypothesizing that the dorsal stream is influenced by ventral processes when generating saccades, whereas egocentric pointing is entirely dorsal (Carey 2001), or by suggesting that the illusory effect is generated before the ventral-dorsal split (Milner and Dyde 2003) when planning saccades, but not when planning pointing.

Finally, according to a third, "compromise" interpretation, perception–action dissociations are due to functional constraints on the verbal–perceptual and visuomotor tasks, but without necessarily entailing anatomically separate modules. Thus, the crucial distinction lies not in the mode of response, perceptual vs. motor, or in the visual pathway involved, dorsal vs. ventral, but in functional differences such as coding for (allocentric) length vs. coding for (egocentric) position (Mack et al. 1985; Smeets and Brenner 1995) or privileging allocentric or egocentric spatial frames of reference in different tasks or during different phases of the action (Gentilucci et al. 1996, 1997; Vishton et al. 1999; Wraga et al. 2000; Bruno 2001; Glover and Dixon 2001, 2002). Given that this interpretation explicitly predicts that some actions will be immune from illusions, whereas others will not, it seems to us that this interpretation provides the best general framework for the present data. Additional work is needed to distinguish between different versions of this general idea. It could be, for instance, that functional constraints tend to favor allocentric coding in motor plans for saccades, but egocentric coding in those for pointing. Alternatively, it might be that the current difference between saccades and pointing is due to different spatial frames in ballistic movements, which are entirely under the control of spatial representations used by planning processes, and in movements that can exploit on-line control at least in the final phase of the action. Given that our pointing movements were of this second kind, but on-line control could be done in principle only on the basis of nonvisual feedback, this proposal opens up an additional research question concerning the integration of vision, proprioception, and kinesthesia in the control of fast hand responses.

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