

The influence of the Brentano illusion on eye and hand movements

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When making an eye movement and a hand movement toward a visual target, the movements could be guided by visual judgments of direction and distance (or length) of the required displacement (vector coding), estimates of the final position (position coding), or both. Using the same information for the eyes and the hand is efficient; however, if this information contains an error, this causes both the eye and the hand to be incorrect. In this study, we tried to find out whether saccades and pointing movements use the same source of information when eye and hand movements are performed either concurrently or separately. Four experiments have been performed using the Brentano illusion, which primarily influences judgments of length but not those of position. This illusion only influences movements if the illusory length is relevant for the task, demonstrating that vector coding is involved. Subjects made saccades, pointing movements, or both between vertices of the Brentano illusion. The illusion influenced saccades and pointing movements when these movements were performed concurrently and separately, showing that the eye and the hand use vector coding. However, depending on the task, eye and hand movements were influenced to a different extent. This favors the interpretation that the eyes and the hand use a common motor command but each with a different relative contribution of vector coding.

Keywords: illusion, saccades, pointing, eye movements, hand movements, perception, action

Introduction

Several researchers have attempted to determine the manner in which actions are susceptible to illusions. Studies on saccadic eye movements showed an effect of the Müller-Lyer illusion on the amplitude of the (first) saccades (Binsted & Elliott, 1999a; Festinger, White, & Allyn, 1968; Yarbus, 1967), whereas Wong and Mack (1981) reported that saccadic eye movements were not affected by an illusion of displacement. Dassonville and Bala (2004) found a similar result, which, however, showed that the absence of an illusion effect is likely due to cancellation by a second effect. In addition, studies of illusory effects on arm movements have produced inconsistent results. Mack, Heuer, Villardi, and Chambers (1985) and Post and Welch (1996) found no effect of the Müller-Lyer illusion on pointing movements, whereas Elliott and Lee (1995), Gentilucci, Chieffi, Daprati, Saetti, and Toni (1996), and Meegan et al. (2003) did find an effect on aiming movements using the same illusion. Binsted and Elliott (1999b) suggested that the difference in illusion effect on arm movements could be caused by the time of extinction of the target. The illusion caused a

manual bias only when the target was removed at movement onset. Also, in the study of de Grave, Brenner, and Smeets (2004), removal of the target at movement onset resulted in an effect of the illusion. However, a larger effect was found when the stimulus and the hand were removed from vision during the movement.

Mack et al. (1985) and Smeets, Brenner, de Grave, and Cuijpers (2002) have suggested that these inconsistent results can be understood in terms of inconsistently processed spatial attributes. Physically related spatial attributes are not necessarily perceived in a consistent manner, presumably because they are processed independently. For example, in Euclidean space, motion is equivalent to a change in position. However, when seeing a motion aftereffect, like the waterfall illusion, we only perceive motion but not a change in position. A similar dissociation between spatial attributes has been found in the Müller-Lyer illusion (Gillam, 1998; Gillam & Chambers, 1985; Mack et al., 1985). When the length of a control line has to be adjusted to match the length of the Müller-Lyer illusion, errors are made. However, hardly any errors are made in the perception of vertex position (Gillam & Chambers, 1985; Mack et al., 1985). Thus, the illusion affects information about the length/distance

between the endpoints but not information about the absolute position of the endpoints.

Hand and eye movements have been studied using this illusion to find out what attributes are used in these movements. When a pointing movement is made along the shaft of the illusion (i.e., moving from one endpoint to the other), either information about the position of the endpoint (position coding: Bizzi, Hogan, Mussa-Ivaldi, & Giszter, 1992; Carrazzo, McIntyre, Zago, & Lacquaniti, 1999; Feldman & Levin, 1995; McIntyre, Stratta, & Lacquaniti, 1997, 1998; van den Dobbela, Brenner, & Smeets, 2001) or length information about the distance to be moved (vector coding: Bock & Eckmiller, 1986; Desmurget, Pélisson, Rossetti, & Prablanc, 1998; Messier & Kalaska, 1997; Rossetti, Desmurget, & Prablanc, 1995; Vindras & Viviani, 1998) can be used to plan the movement. If a subject fixates the target position, he or she is more likely to use vector coding due to availability of egocentric target information. Therefore, a large effect of the illusion is expected for movements along the shaft. This has indeed been found in the studies of de Grave et al. (2004) and Gentilucci et al. (1996). However, if movements are made from an outside position toward one of the endpoints of the shaft (such that the movements are more or less perpendicular to the shaft), then the shaft's length is irrelevant. Therefore, these movements are not influenced by the illusion (de Grave et al., 2004; Mack et al., 1985; Post & Welch, 1996; but see Glazebrook et al., 2005).

Studies on the control of saccades generally have shown that saccades are entirely vector coded (Becker & Jürgens, 1979; McIlwain, 1991; Robinson, 1972), which suggests that saccades will be influenced by the Müller-Lyer illusion (de Grave, Brenner, & Smeets, 2006). Thus, whether the illusion influences a movement depends on whether the illusion affects the attribute that is used for that movement. Movements that are based on the distance of the target relative to the starting position (vector coded) will be influenced by the illusion but not the ones based on the position of the endpoint (position coded). Depending on the task demands, different relative combinations of vector coding and position coding can be found (de Grave et al., 2004).

The former studies looked at eye and hand movements when they were performed separately. In this study, we try to determine which attributes are used in pointing and saccadic eye movements when they are performed concurrently. We used the Brentano version of the Müller-Lyer illusion, which combines the wings-in and wings-out configurations in one figure. Subjects performed pointing movements and saccades to the endpoints of the shaft. If saccades and pointing movements are based on the same visual information and use a common motor command (Bekkering, Abram, & Pratt, 1995; Biguer, Jeannerod, & Prablanc, 1982; Biguer, Prablanc, & Jeannerod, 1984; Bizzi, Kalil, & Tagliasco, 1971; Bock, 1986; Reina & Schwartz, 2003), we would predict that the endpoint of the first saccade and the endpoint of the

pointing movement will be equally affected by the Brentano illusion. When the eyes and the hand are guided by different information (Binsted & Elliott, 1999b) or if a different combination of vector and position coding is used for both movements, a difference in illusion effect is expected between the end positions of saccades and those of the pointing movements.

Experiment 1: Combined task—Saccadic eye movements and pointing

In the first experiment, the Brentano illusion was used to identify the visual information that guides saccades and pointing movements when they are performed concurrently.

Method

Subjects

Ten right-handed psychology students of the Justus-Liebig-University Giessen took part in this experiment for which they received payment. None of the subjects participated in any of the other experiments. All were naive with respect to the aim of the study.

Apparatus and stimulus

A chin rest was placed in front of a touch screen (40 × 30 cm, 1280 × 960 pixels, 100 Hz) to keep the subject's head fixed at a viewing distance of 45 cm. At this distance, 1 pixel corresponds to 0.04 deg. Before each trial, a black fixation point was presented in the middle of the screen. The diameter of this fixation point was 0.28 deg/0.22 cm. The stimulus, drawn in black on a white background, consisted either of one of two Brentano configurations or a control configuration (Figure 1a). For all configurations, the length of each of the two shafts was 6.77 deg/5.29 cm. The inclination of the wings with respect to the shafts was 30 deg in the Brentano configurations and 90 deg in the control configuration. The length of the wings was 2.30 deg/1.80 cm for the Brentano configurations and 1.91 deg/1.50 cm for the control configuration. The stimulus was always presented with one of the outer arrows on the fixation point and could be in four directions relative to the fixation point: above, below, left, or right. (see Figure 1b for all possible combinations).

Eye movements were registered using an Eyelink II eye tracker (SR Research Ltd.) with a temporal resolution of 250 Hz and a spatial resolution of 0.2 deg. The end positions of the hand movements were registered with the touch screen.

Procedure

All subjects performed six blocks of 36 trials. Each block contained three repetitions of all possible combinations of

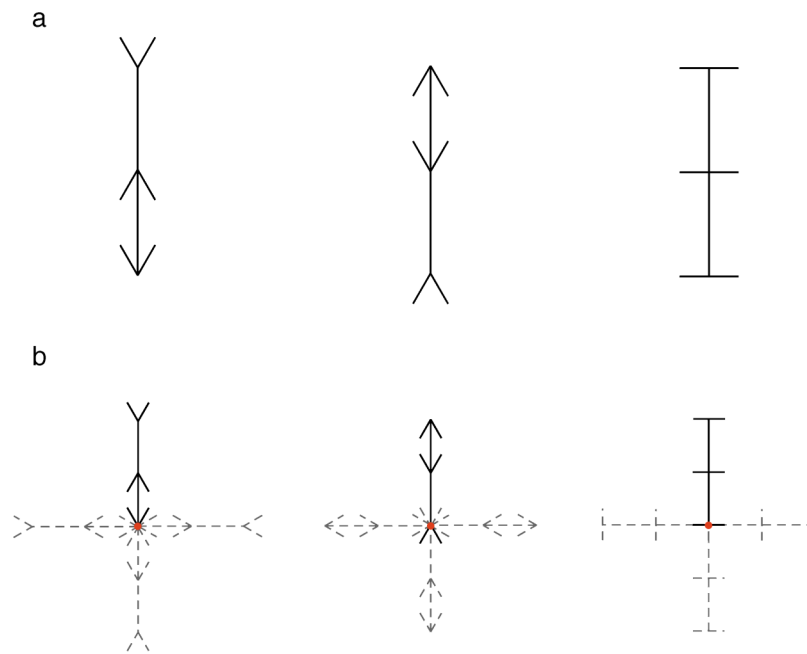


Figure 1. (a) Three configurations were used: the Brentano illusion with the wings-in and the wings-out configurations and a control configuration with wings that are perpendicular to the shaft. (b) Each configuration could be presented in one of four directions: up, down, left, or right.

stimulus configuration and movement direction. The order of trials within a block was completely randomized. Before each trial, a fixation point was presented in the middle of the screen. Subjects were required to fixate this point and then press a button to perform drift correction. When drift correction was successful, the fixation point turned green and the subjects had to point to this green fixation point while keeping fixation. After a touch was registered, the stimulus was presented for 200 ms. Subjects were asked to look and point at the middle vertex of the presented stimulus configuration. They were encouraged to reach the desired end position in one saccade. After each block, subjects could take a break. The total duration of the experiment was about 45 min.

Data analysis

For eye movements, only the first saccades after stimulus presentation were analyzed. Trials on which no saccades were made or when saccades started during stimulus presentation were deleted from analysis. This resulted in a loss of 5% of all trials.

In general, subjects tend to misjudge the distance that is to be moved when viewing of the stimulus is prevented. Estimates of these distances differ between subjects and between different spatial positions. Therefore, for both saccades and pointing movements, a measure of the magnitude of the illusion was computed for each subject and movement direction, which is independent of the amplitude of the movement. We calculated the mean difference in distance between movements along the “wings-out” (long looking) and the “wings-in” (short

looking) configuration. This difference in distance was divided by the mean distance in the control configuration. The result is the size of the illusion expressed as a percentage of the length of the movement in the control stimulus.

A repeated measures ANOVA with the factors direction (up, down, left, or right) and type of movement (saccade or pointing) was performed on the illusion effects to examine whether the performed movements toward the middle vertex were influenced differently by the illusion. Furthermore, with this ANOVA, it was checked whether the grand mean of the illusion effects in saccades and pointing differed from zero (to check whether there was any effect of the illusion). Repeated measures ANOVAs with the factors direction and stimulus configuration (short, control, or long) were performed on the reaction times (RTs) and movement times (MTs) of the eye and on the total response times (TRTs) of the hand ($TRT = RT + MT$). Note that only the touch on the screen was registered and not the release of the hand from the screen; therefore, we could not distinguish the RT from the MT of the hand (the TRT of the hand includes the RT + MT). In case of a main effect, Tukey post hoc tests were performed to see which levels of a factor differed. In all experiments, we used a significance level of $\alpha = .05$ for the statistical analyses. *p* values above .01 are given as exact values. If not stated otherwise, we performed a repeated measures ANOVA using the Greenhouse–Geisser correction if a factor had more than two levels. This corrects for possible violations of the sphericity assumption in repeated measures data. For the Greenhouse–Geisser correction, the parameter ϵ is

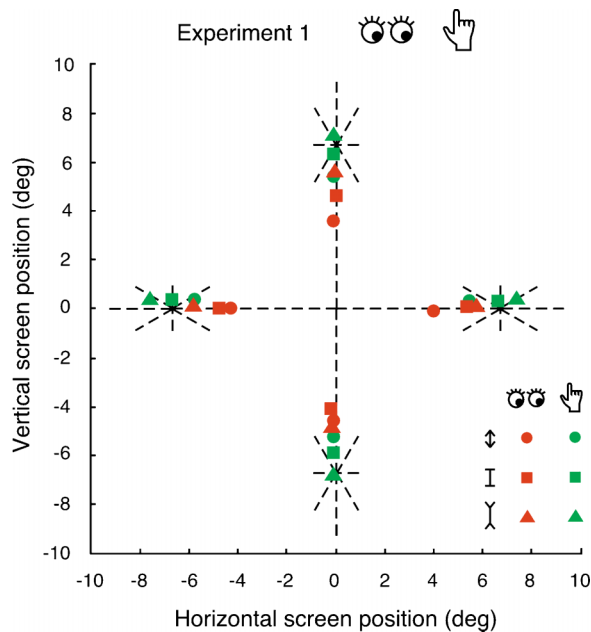


Figure 2. **Experiment 1:** Average end positions of saccades (red symbols) and pointing movements (green symbols) for the different stimulus configuration in all movement directions. Triangles represent data for the wings-out configuration of the Brentano illusion, squares for the control configuration, and circles for the wings-in configuration. The dashed lines represent the positions at which the stimuli were presented.

estimated as $0 < \varepsilon \min \leq \varepsilon \leq 1$, which is used to adjust the degrees of freedom of the F distribution. If $\varepsilon = 1$, no violation of sphericity was detected and the Greenhouse–Geisser correction has no effect. If $\varepsilon < 1$, the resulting test is more conservative than if no correction was performed (Greenhouse & Geisser, 1959; Jennings, 1987; Vasey & Thayer, 1987).

Results and discussion

We only looked at the first saccades after stimulus presentation. However, in 15% of the trials, a corrective saccade was made. Because these saccades only occurred in a small number of trials, we did not analyze corrective saccades. Figure 2 shows the average end positions of the first saccades (red symbols) and pointing movements (green symbols) for each stimulus figure in each direction with respect to the stimulus configuration. The ANOVA showed an overall effect of the illusion, $F(1,9) = 69.45$, $p < .01$, which means that both saccades and pointing movements toward the wings-in configuration (circles) undershot the target position with respect to the control configuration (squares). Movements of the eye and the hand toward the wings-out configuration (triangles) overshot. This was the case in all four movement directions.

Figure 3a shows the size of the effect of the illusion on saccades toward the middle arrowhead. In Figure 3b, the illusion effects on pointing are shown. Upward saccades and saccades to the left and right showed a significant effect of the illusion ($37.91 \pm 4.49\%$ for upward saccades,

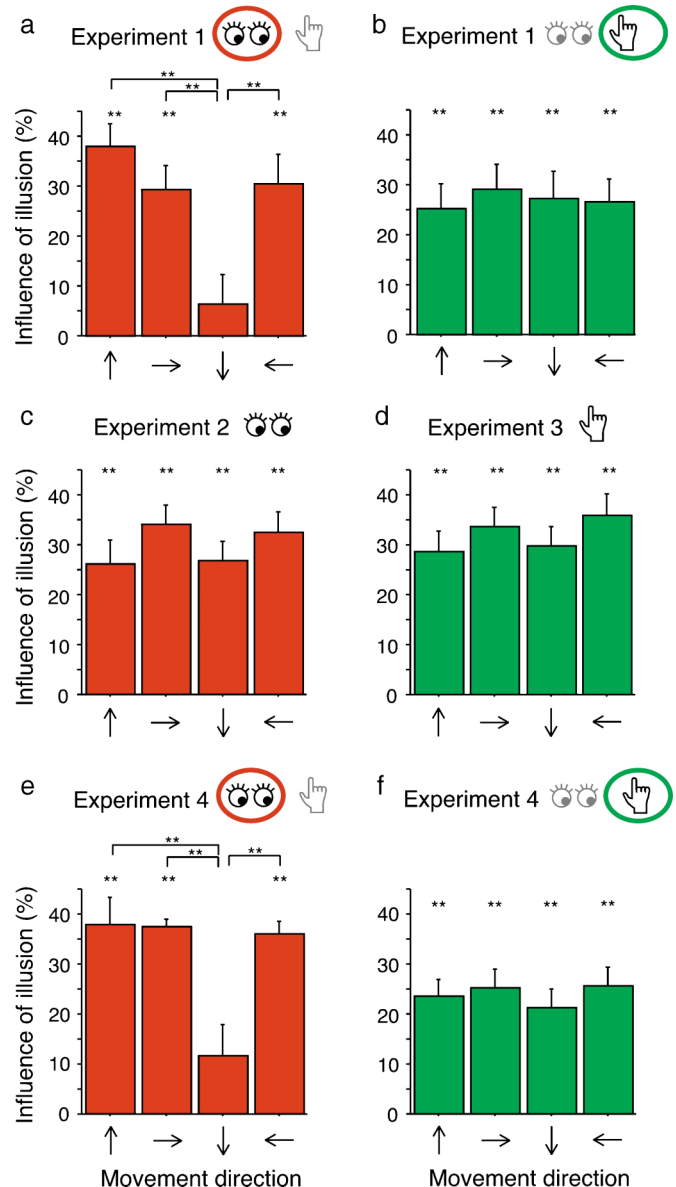


Figure 3. Magnitudes of the illusion in all four movement directions for (a) saccadic eye movements when performed concurrently with pointing movements; (b) pointing movements when performed with saccades; (c) saccades performed separately; (d) pointing movements performed separately; (e) saccades when performed concurrently with pointing movements, without an instruction on eye movements; and (f) pointing movements when performed without eye movement instruction. Symbols indicate a significant effect of the illusion and significant differences between the directions of movement (** $p < .01$). Error bars represent standard errors between subjects.

$30.41 \pm 5.96\%$ for saccades to the left, and $29.35 \pm 4.68\%$ for saccades to the right). A nonsignificant effect of the illusion ($6.45 \pm 5.79\%$) was found for downward saccades. Pointing movements showed a significant effect of the illusion in all four directions (up, 25.86 ± 4.98 ; down, $27.25 \pm 5.56\%$; left, $26.58 \pm 4.6\%$; right, $29.18 \pm 4.97\%$). These results indicate that the coding of both saccades and pointing movements is based on an estimate of distance, which, in turn, is based on the judged length of the shaft. The ANOVA on the calculated illusion effects showed no significant difference between the types of movement (eye or hand), $F(1,9) = 0.05$, $p = .83$, which favors the interpretation that similar information is used to guide eye and hand movements. However, we did find a significant difference between the directions of movement, $(3,27) = 5.01$, $\varepsilon = .94$, $p < .01$, and an interaction between the direction and the type of movement, $F(3,27) = 8.39$, $\varepsilon = .86$, $p < .01$.

Post hoc analysis (Tukey's Honestly Significant Difference [HSD], $p < .05$) showed that the illusion effect on downward saccades differed from the other directions. The smaller effect of the illusion on downward saccades could be explained by the fact that subjects occluded the illusion with their hand. Before the stimulus was presented, subjects had to place their finger on the fixation point with their hand blocking the view of the downward-presented stimuli. However, in the same trials, the effect of the illusion on pointing did not decline in the downward condition. This cannot easily be explained if partial occlusion of the stimulus is the reason for the declined effect on downward saccades. To be able to compare and interpret the results of the different experiments better, we calculated illusion effects on the horizontal movement directions separately. As expected, the main effect of direction, $F(1,19) = 0.06$, $p = .81$, and the interaction, $F(1,19) = 0.51$, $p = .48$, disappeared in that case. The absence of a main effect of movement type persisted, $F(1,19) = 0.31$, $p = .59$. Thus, our interpretation that similar information is used to guide eye and hand movements still holds.

On the RT of the eye, a main effect of direction was found, $F(3,27) = 17.88$, $\varepsilon = .52$, $p < .01$. Post hoc analysis (Tukey's HSD, $p < .01$) showed that only the RT for the downward eye movement direction (232 ± 11 ms) differed significantly from all other directions (up, 191 ± 6 ms; right, 189 ± 7 ms; left, 194 ± 8 ms). Also, a main effect was found for the stimulus configuration, $F(2,18) = 20.31$, $\varepsilon = .75$, $p < .01$. All stimulus configurations differed significantly from each other (short, 189 ± 7 ms; control, 201 ± 8 ms; long, 216 ± 9 ms). Furthermore, an interaction was found between direction and stimulus configuration, $F(6,54) = 5.53$, $\varepsilon = .46$, $p < .01$. In the studies of Binsted and Elliott (1999b; the "full" condition in Experiments 1 and 2) and Binsted, Chua, Helsen, and Elliott (2001; conditions in which the eyes and the hand started at the same location), RTs of the eye were somewhat higher (around 300 ms). This difference can be understood in

terms of a distinction in types of saccades. Although the saccadic eye movements in the aforementioned studies are made several seconds after stimulus onset, these saccades can be considered voluntary. The saccades in our experiment are made in response to the peripheral onset of the stimulus and, therefore, regarded as reflexive. McCarley, Kramer, and DiGirolamo (2003) showed that voluntary saccades (about 360 ms) have longer saccadic latencies than reflexive saccades (180–200 ms).

On the MT of the eye, a main effect of stimulus configuration was found, $F(2,18) = 11.85$, $\varepsilon = .85$, $p < .01$. Again, all stimulus configurations differed significantly (short, 50 ± 2 ms; control, 54 ± 2 ms; long, 57 ± 2 ms). No main effect of direction, $F(3,27) = 3.32$, $\varepsilon = .46$, $p = .08$, or an interaction between direction and stimulus configuration was found, $F(6,54) = 0.75$, $\varepsilon = .41$, $p = .51$. These data correspond nicely to the endpoint data. If the distance to be moved looks longer (shorter), the end position of the movement is further away (closer), resulting in a longer (shorter) MT.

TRTs of the hand showed a main effect of direction, $F(3,27) = 8.59$, $\varepsilon = .60$, $p < .01$, and stimulus configuration, $F(2,18) = 8.06$, $\varepsilon = .98$, $p < .01$, with no interaction, $F(6,54) = 1.95$, $\varepsilon = .23$, $p = .19$. Post hoc analysis (Tukey's HSD, $p < .01$) showed that the TRT of the downward hand movement (823 ± 58 ms) differed significantly from all other directions (up, 737 ± 47 ms; right, 709 ± 44 ms; left, 746 ± 46 ms).

Overall, this experiment shows that both the eyes and the hand use illusory length information to the same extent when they are performed concurrently, which suggests that both movements are vector coded. An earlier study using the Brentano illusion (de Grave et al., 2006) also showed that both pointing movements and saccades use vector coding but not to the same extent. The saccades relied more strongly on vector coding than the hand (pointing), leading to the conclusion that the eyes (saccades) and the hand (pointing) use different information for their movement. These conclusions were based on experiments in which saccadic eye movements and pointing movements were tested separately. It might be possible that concurrently performed eye and hand movements use different information than when they are performed separately. Therefore, we tested saccades and pointing movements separately in Experiments 2 and 3.

Experiment 2: Saccadic eye movements

In this experiment, we used the same stimuli and setup as in the first experiment to find out whether the information used to perform saccades concurrently with pointing movements is different from the information to guide

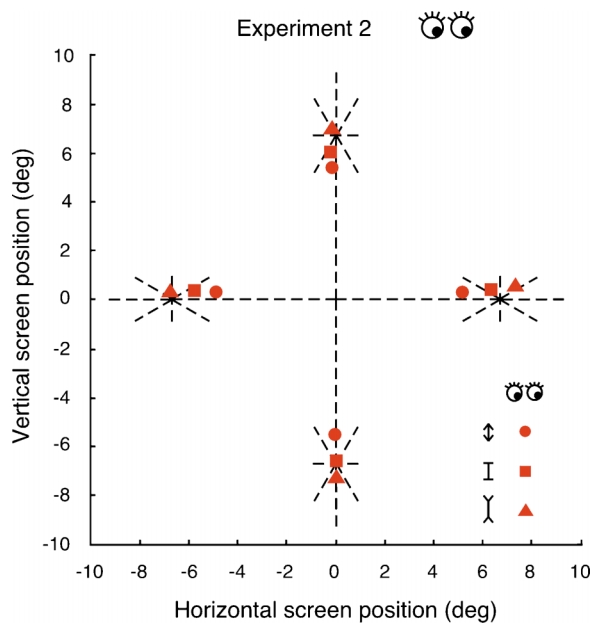


Figure 4. **Experiment 2:** Average end positions of saccades for the different stimulus configuration in all movement directions. Triangles represent data for the wings-out configuration of the Brentano illusion, squares for the control configuration, and circles for the wings-in configuration. The dashed lines represent the positions at which the stimuli were presented.

separately performed saccades. As mentioned earlier, studies on saccadic eye movements show that saccades are entirely vector coded (Becker & Jürgens, 1979; McIlwain, 1991; Robinson, 1972). Therefore, we expect to find the same effect of the Brentano illusion as in the first experiment.

Method

Subjects

Ten right-handed psychology students of the Justus-Liebig-University Giessen took part in this experiment for which they received payment. None of the subjects participated in any of the other experiments. All were naive with respect to the aim of the study.

Apparatus and stimulus

The same apparatus and stimuli were used as in the first experiment.

Procedure

The procedure was the same as in the previous experiment with the following exception. After successful drift correction, subjects did not have to touch the fixation point on the screen. However, the stimulus was then presented (150 ms after the fixation point turned green) and subjects made a saccadic eye movement toward the middle arrowhead. No pointing movement was made. Trials on which

the first saccade was made in an incorrect direction or trials on which saccades started during stimulus presentation were repeated randomly inside a block of trials.

Data analysis

Statistical tests were similar to the tests for saccadic eye movements in **Experiment 1**. A repeated measures ANOVA was used to check whether the overall illusion effect in saccades differed from zero (to check whether there was any effect of the illusion). On the calculated illusion effects, a repeated measures ANOVA was performed with the factor direction of movement to examine whether the performed movements toward the middle vertex were influenced differently by the illusion. Repeated measures ANOVAs with the factors direction and stimulus configuration were performed on the RTs and MTs of the eye.

Results and discussion

Only the first saccades after the stimulus was presented were taken into account. In 9% of all trials, a corrective saccade was made. The ANOVA showed a significant overall effect of the illusion on saccades, $F(1,9) = 204.36$, $p < .01$. **Figure 4** shows the average end positions of the first saccades for each stimulus figure in each direction. In all four directions, saccades toward the wings-in (wings-out) configuration undershot (overshot) with respect to the control configuration.

Figure 3c shows the effect of the illusion on saccades toward the middle arrowhead when saccades are performed separately. Saccades in all directions showed a significant effect of the illusion (upward, $26.24 \pm 4.75\%$; downward, $26.71 \pm 4.08\%$; leftward, $32.60 \pm 3.94\%$; rightward, $34.05 \pm 3.87\%$). This shows that when saccades are performed separately, illusory length information is used. The ANOVA did not show a significant difference between the directions of movement, $F(3,27) = 0.92$, $\varepsilon = .70$, $p = .42$. Also, when only the horizontal directions were taken into account, no effect of direction was found, $F(1,9) = 0.44$, $p = .52$.

The effect of the illusion on separately performed saccades (**Experiment 2**, only horizontal directions, $29.97 \pm 2.56\%$) did not differ from the illusion effect on concurrently performed saccades (**Experiment 1**, only horizontal directions, $29.88 \pm 2.58\%$), suggesting that in both saccadic eye movement tasks, vector coding is used to guide the movement (**Figure 5**).

The RT of the eye showed no main effects of direction or stimulus configuration. Also, no interaction was present. Average RT was 321 ± 8 ms. On the eye MT, we did find a main effect of direction, $F(3,27) = 10.47$, $\varepsilon = .58$, $p < .01$, and stimulus configuration, $F(2,18) = 27.64$, $p < .01$. The downward direction (62 ± 15 ms) differed significantly from all other directions (up, 54 ± 13 ms; right, 51 ± 11 ; left, 47 ± 9 ms; Tukey's HSD, $p < .01$). All stimulus configurations differed significantly from each other (short, 49 ± 2 ms; control, 54 ± 2 ms; long, 58 ± 2 ms;

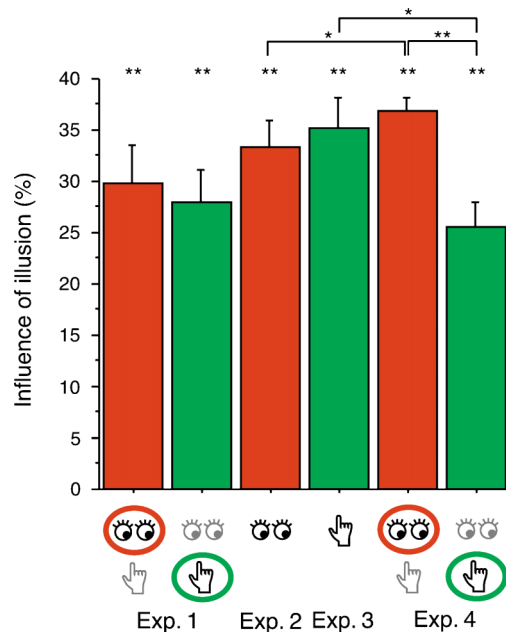


Figure 5. Average influence of the Brentano illusion on horizontal saccades and pointing movements when performed concurrently and separately. Also, the illusion effect on saccades and pointing movements is shown when no instruction was given regarding eye movements during pointing. Symbols indicate a significant effect of the illusion (* $p < .05$; ** $p < .01$). Error bars represent standard errors between subjects.

Tukey's HSD, $p < .01$). No interaction was found between direction and stimulus configuration, $F(6,54) = 0.42$, $\epsilon = .40$, $p = .70$. The MTs of the eye did not differ from the MTs of the eye in the first experiment.

Experiment 3: Pointing movements while keeping fixation

To test whether the influence of the Brentano illusion on separately performed pointing movements differs from pointing movements combined with eye movements, we required subjects to make pointing movements while keeping fixation.

Method

Subjects

Ten right-handed psychology students of the Justus-Liebig-University Giessen took part in this experiment for which they received payment. None of the subjects participated in any of the other experiments. All were naive with respect to the aim of the study.

Apparatus and stimulus

The same apparatus and stimuli were used as in the first experiment. Eye movements were monitored to ensure that fixation was kept during the experiment.

Procedure

The procedure was the same as in the first experiment with the following exception. Subjects were required to keep fixating the fixation point throughout a trial. This was monitored using the Eyelink. Trials on which eye movements were made counted as errors and were repeated randomly inside the block.

Data analysis

As in the other experiments, a repeated measures ANOVA was performed to check whether the illusion effects in pointing differed from zero in any direction (to check whether there was any effect of the illusion). On the calculated illusion effects, a repeated measures ANOVA was performed with the factor direction of movement to examine whether the performed movements toward the middle vertex were influenced differently by the illusion. Another repeated measures ANOVA with the factors direction and stimulus configuration was performed on the TRTs of the hand.

Results and discussion

Figure 6 shows the average end positions of the pointing movements (green symbols) for each stimulus figure in each direction. Eye positions are depicted in this figure as the red symbols in the middle. As requested, subjects kept

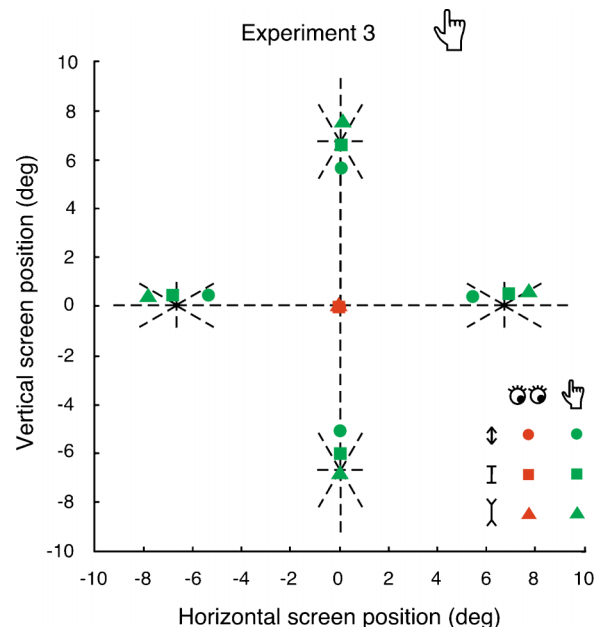


Figure 6. Experiment 3: Average end positions of pointing movements (green symbols) for the different stimulus configuration in all movement directions. Eye positions are depicted as the red symbols in the middle. Triangles represent data for the wings-out configuration of the Brentano illusion, squares for the control configuration, and circles for the wings-in configuration. The dashed lines represent the positions at which the stimuli were presented.

their fixation at the fixation point during a trial while pointing. Pointing movements toward the wings-in (wings-out) configuration were undershot (overshot) with respect to the control configuration in all four directions. The ANOVA showed a significant overall effect of the illusion on pointing movements, $F(1,9) = 781.71$, $p < .01$.

Figure 3d shows the effect of the illusion on pointing movements toward the middle arrowhead when pointing has to be performed without eye movements. Pointing movements in all directions showed a significant effect of the illusion (upward, $28.57 \pm 4.15\%$; downward, $29.73 \pm 3.85\%$, leftward, $35.84 \pm 4.32\%$; rightward, $33.69 \pm 3.88\%$). This shows that when pointing is performed without eye movements, illusory length information is used. The ANOVA on four directions, $F(3,27) = 0.67$, $\epsilon = .55$, $p = .56$, as well as the one on the horizontal movement directions, $F(1,9) = 0.19$, $p = .68$, did not show a significant difference between the directions of movement.

The effect of the illusion on separately performed pointing movements (only horizontal movements, $34.77 \pm 2.84\%$) did not differ from the illusion effect on concurrently performed pointing movements (only horizontal movements, $27.88 \pm 2.31\%$), suggesting that vector coding is used in both pointing tasks.

The TRTs of the hand showed a main effect of direction, $F(3,27) = 20.41$, $\epsilon = .85$, $p < .01$. The post hoc test (Tukey's HSD, $p < .05$) showed that the TRT for the upward movement (604 ± 35 ms) differed significantly from the rightward one (555 ± 34 ms), which, in turn, differed from the downward movement (583 ± 33 ms). The leftward (626 ± 32 ms) movement differed from the downward and rightward ones. Also, a main effect was found for the stimulus configuration, $F(2,18) = 28.00$, $\epsilon = .81$, $p < .01$. All stimulus configurations differed significantly from each other (short, 570 ± 28 ms; control, 586 ± 29 ms; long, 620 ± 30 ms; Tukey's HSD, $p < .01$). No interaction was found, $F(6,54) = 0.95$, $\epsilon = .50$, $p = .43$. The TRTs in this experiment were significantly shorter than the TRTs of the hand in the first experiment. This could have been caused by the fact that in the first experiment, the hand is waiting for information coming from the eye before starting the movement, resulting in a higher RT (which is included in our TRT measure).

So far, we found very similar effects of the Brentano illusion on saccades and pointing movements (Figure 5, horizontal movements), which suggests that both the eyes and the hand use length information (vector coding). In contrast, when performing saccadic eye movements and pointing movements toward the Müller-Lyer illusion, Bernardis, Knox, and Bruno (2005) found different effects of the illusion for the eyes and the hand, concluding that different representations are used to drive the eye and the hand. These contradictory findings can be understood if the relative contributions of vector and position coding are different depending on small differences in task demands. In the pointing experiment of Bernardis et al., the effect of the illusion on pointing movements was much smaller

(7.1%) than that in our pointing task (Experiment 3: 31.1%). This discrepancy could be caused by a difference in eye movement instruction while pointing. In our pointing experiment, subjects were required to keep fixation throughout a trial, whereas Bernardis et al. did not give their subjects any instruction regarding eye movements in their pointing task. Whether this could explain the difference in illusion effect was investigated in a fourth experiment.

Experiment 4: Pointing movements without eye movement instruction

In this control experiment, we examined the influence of the Brentano illusion on pointing movements when no instruction about eye movements was given.

Method

Subjects

Ten right-handed psychology students of the Justus-Liebig-University Giessen took part in this experiment for which they received payment. None of them participated in any of the other experiments. All were naive with respect to the aim of the study.

Apparatus and stimulus

The same apparatus and stimuli were used as in the other experiments. Eye movements were monitored to determine where subjects looked at when no specification about eye movements was given.

Procedure

The procedure was the same as in the third experiment with the exception that no instruction about eye movements was given.

Data analysis

Data analysis is similar to that of Experiment 1. For the calculations on eye movements, trials on which no saccades were made or when saccades started during stimulus presentation were deleted from analysis. This resulted in a loss of 13% of all trials. To compare the effect of the illusion in all experiments, we performed an ANOVA on the average illusion effects of all movement types in the experiments.

Results and discussion

Although we did not give any instruction on eye movements, subjects made a saccade in the direction where the

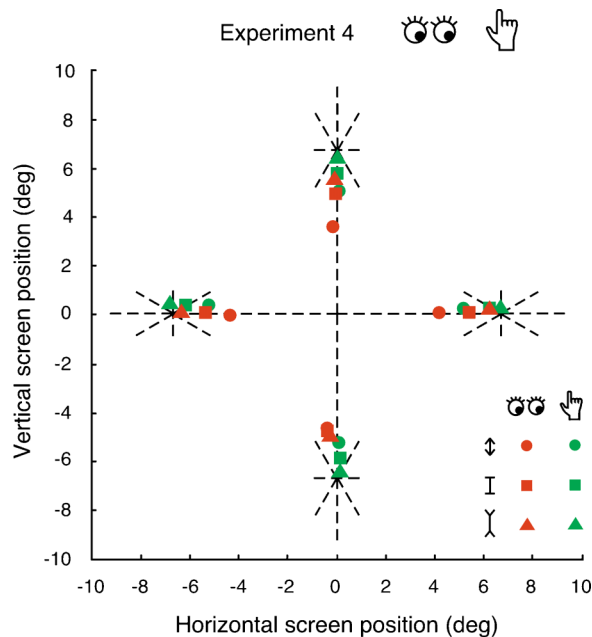


Figure 7. **Experiment 4:** Average end positions of saccades (red symbols) and pointing movements (green symbols) when no instruction was given for eye movements. Triangles represent data for the wings-out configuration of the Brentano illusion, squares for the control configuration, and circles for the wings-in configuration. The dashed lines represent the positions at which the stimuli were presented.

stimulus appeared in 97% of the trials. In 14% of the trials, a corrective saccade was made. For calculations, we only considered the first saccades after stimulus onset. **Figure 7** shows the average end positions of the first saccades (red symbols) and pointing movements (green symbols) for each stimulus figure in each direction. Saccades and pointing movements toward the wings-in configuration undershot the target position with respect to the control configuration. Movements of the eyes and the hand toward the wings-out configuration overshoot. This was the case for all movement directions. The ANOVA showed a significant overall effect of the illusion, $F(1,9) = 117.21$, $p < .01$.

Figure 3e shows the size of the effect of the illusion on saccades toward the middle arrowhead. In **Figure 3f**, the illusion effects on pointing are shown. Upward saccades and saccades to the left and right showed a significant effect of the illusion ($37.81 \pm 5.60\%$ for upward saccades, $35.98 \pm 2.63\%$ for saccades to the left, and $37.54 \pm 1.32\%$ for saccades to the right). As in the first experiment, a nonsignificant effect of the illusion ($11.61 \pm 6.24\%$) was found for downward saccades. Pointing movements showed a significant effect of the illusion in all four directions (up, $23.63 \pm 3.18\%$; down, $21.30 \pm 3.65\%$; left, $25.63 \pm 3.82\%$; right, $25.30 \pm 3.70\%$). The repeated measures ANOVA showed a significant difference between the four directions of movement, $F(3,27) = 11.11$, $\epsilon = .76$, $p < .01$, but not between the types of

movement (eye or hand), $F(1,9) = 3.8$, $p = .09$. As in the first experiment, an interaction was found between direction and type of movement, $F(3,27) = 6.92$, $\epsilon = .86$, $p < .01$, which was caused by a significant smaller effect of the illusion on eye movements in the downward direction (Tukey's HSD, $p < .01$). When only the horizontal directions were taken into account, the main effect of direction and the interaction disappeared. However, we did find an effect on the task, $F(1,9) = 6.60$, $p < .05$. For the horizontal movements, the effect of the illusion on eye movements was significantly larger than its effect on hand movements. Thus, although both types of movements are influenced by the illusion, the eyes and the hand do not use length information to the same extent when no explicit instruction is given on eye movements.

Figure 5 shows that the effect of the illusion on the horizontal saccades in this experiment differed from the illusion effect in **Experiment 2** in which only eye movements had to be made. Also, the effect on the horizontal pointing movements in this experiment differed from the illusion effects in **Experiment 3** (only hand movements, horizontal). This shows that the effect of the Brentano illusion and, with that, the relative contribution of vector coding can differ due to a very small change in the instruction. Although the effect of the illusion on horizontal hand movements was significantly smaller in this experiment with respect to the other experiments containing hand movements, the effect did not drop to the level of the study of Bernardis et al. (2005) in which an effect of 7.1% was found. This suggests that the fixation instruction is not the only critical difference between the small pointing effect in the study of Bernardis et al. and the much bigger effect on pointing movements in our experiments.

On the RT of the eye, a main effect of direction was found, $F(3,27) = 7.17$, $\epsilon = .68$, $p < .01$. Post hoc analysis (Tukey's HSD, $p < .05$) showed that only the RT for the downward eye movement direction (249 ± 14 ms) differed significantly from all other directions (up, 211 ± 10 ms; right, 197 ± 8 ms; left, 213 ± 14 ms). Also, a main effect was found for the stimulus configuration, $F(2,18) = 5.57$, $\epsilon = .57$, $p = .01$. Only the short stimulus configuration (207 ± 9 ms) differed significantly from the long one (231 ± 13 ms; Tukey's HSD, $p < .05$). The RT to the control stimulus was 215 ± 9 ms. No interaction was found between direction and stimulus configuration, $F(6,54) = 1.74$, $\epsilon = .31$, $p = .21$.

On the MT of the eye, only a main effect of stimulus configuration was found, $F(2,18) = 14.06$, $\epsilon = .71$, $p < .01$. All stimulus configurations differed from each other (short, 56 ± 2 ms; control, 60 ± 2 ms; long, 63 ± 3 ms; Tukey's HSD, $p < .05$). No main effect of direction, $F(3,27) = 3.09$, $\epsilon = .62$, $p = .08$, was present, although it approached significance (average MT, 60 ± 2 ms). We found no interaction, $F(6,54) = 0.66$, $\epsilon = .30$, $p = .52$. MTs of the eye did not differ from the ones in the first or the second experiment.

TRTs of the hand showed a main effect of stimulus configuration, $F(2,18) = 4.41$, $\varepsilon = .66$, $p < .05$; the only significant difference (Tukey's HSD, $p < .05$) was between the short (675 ± 24 ms) and the long configuration (735 ± 24 ms). The TRT in the control condition was 710 ± 30 ms. No main effect of direction, $F(3,27) = 1.56$, $\varepsilon = .54$, $p = .24$, or an interaction, $F(6,54) = 1.06$, $\varepsilon = .28$, $p = .36$, was found. As in the first experiment, the hand moved significantly slower than in [Experiment 3](#) where only pointing movements had to be made.

General discussion

In all experiments, the Brentano illusion affected the movements to be made, which suggests that eye and hand movements are based on vector coding. This is consistent with other studies that have shown that length information is used when performing saccadic eye movements (Becker & Jürgens, 1979; McIlwain, 1991; Robinson, 1972) and pointing movements (Bock & Eckmiller, 1986; Desmurget et al., 1998; Messier & Kalaska, 1997; Rossetti et al., 1995; Vindras & Viviani, 1998).

In the study of Bernardis et al. (2005), saccades and pointing movements toward the Müller-Lyer illusion were tested in separate trials. For saccadic eye movements, they found a similar effect (24.8%) to our separate saccadic eye movement experiment (29.9%; only horizontal movements). However, their pointing movements showed a much smaller effect (7.1% vs. separate pointing movements in [Experiment 3](#): 34.8% [only horizontal movements]). The difference in illusion effect between their pointing experiment and our separate pointing experiment could have been caused by whether or not fixation had to be kept during the pointing movement. Therefore, we performed a control experiment in which subjects had to point without the need to fixate the fixation point. We did find a difference between the effect of the illusion on pointing movements with or without eye movement instruction. However, the illusion effect on pointing movements in [Experiment 4](#) was still much larger than in the study of Bernardis et al. Thus, keeping fixation can only be one of the causes of the difference in illusion effect on pointing.

When saccades and pointing movements were performed concurrently in the same trial ([Experiments 1 and 4](#)), a significantly smaller effect of the illusion was found for downward eye movements. An obvious explanation would be that the downward illusion was (partially) occluded by the pointing hand, thus, reducing an effect of the illusion on eye movements. However, the reduced illusion effect was not present in the hand movements that were made in the same trials. Furthermore, downward eye movements made without hand movements ([Experiment 2](#)) did not show a reduction in illusion effect. We cannot explain this discrepancy, but it suggests that some factor other than the hand covering the illusion suppresses the influence of the

illusion on saccades. To be able to compare the different experiments, we only looked at movements made in the horizontal direction.

Other studies using the Brentano illusion (de Grave et al., 2004; 2006) also showed that both pointing movements and saccades use vector coding but not to the same extent. Pointing relied less on vector coding than on saccades; therefore, they concluded that the eyes (saccades) and the hand (pointing) use different information in their movements. However, in those studies, eye and hand movements were tested in different setups and conditions, which made a direct comparison between eye and hand movements impossible.

Conclusion

In this study, we were able to compare eye and hand movements directly and found relatively large illusion effects on both (concurrently and separately performed). Furthermore, significant differences in effects of the illusion were found when the instruction was slightly changed. On the basis of these data, we conclude that the eyes and the hand can use a common motor command; however, depending on the task demands, the eyes and the hand can use this information each with its own relative contribution of vector and position coding.

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References

- Becker, W., & Jürgens, R. (1979). An analysis of the saccadic system by means of double step stimuli. *Vision Research*, 19, 967–983. [[PubMed](#)]
- Bekkering, H., Abram, R. A., & Pratt, J. (1995). Transfer of saccadic adaptation to the manual motor system. *Human Movement Science*, 14, 155–164.
- Bernardis, P., Knox, P., & Bruno, N. (2005). How does action resist visual illusions? Uncorrected oculomotor information does not account for accurate pointing in

- peripersonal space. *Experimental Brain Research*, 162, 133–144. [PubMed]
- Biguer, B., Jeannerod, M., & Prablanc, C. (1982). The coordination of eye, head, and arm movements during reaching at a single visual target. *Experimental Brain Research*, 46, 301–304. [PubMed]
- Biguer, B., Prablanc, C., & Jeannerod, M. (1984). The contribution of coordinated eye and head movements in hand pointing accuracy. *Experimental Brain Research*, 55, 462–469. [PubMed]
- Binsted, G., Chua, R., Helsen, W., & Elliott, D. (2001). Eye–hand coordination in goal-directed aiming. *Human Movement Science*, 20, 563–585. [PubMed]
- Binsted, G., & Elliott, D. (1999a). Ocular perturbations and retinal/extraretinal information: The coordination of saccadic and manual movements. *Experimental Brain Research*, 127, 193–206. [PubMed]
- Binsted, G., & Elliott, D. (1999b). The Müller–Lyer illusion as a perturbation to the saccadic system. *Human Movement Science*, 18, 103–117.
- Bizzi, E., Hogan, N., Mussa-Ivaldi, F. A., & Giszter, S. (1992). Does the nervous system use equilibrium point control to guide single and multiple joint movements? *Behavioral and Brain Sciences*, 15, 603–613.
- Bizzi, E., Kalil, R. E., & Tagliasco, V. (1971). Eye–head coordination in monkeys: Evidence for centrally patterned organization. *Science*, 173, 452–454.
- Bock, O. (1986). Contribution of retinal versus extra-retinal signals towards visual localization in goal-directed movements. *Experimental Brain Research*, 64, 476–482. [PubMed]
- Bock, O., & Eckmiller, R. (1986). Goal-directed arm movements in absence of visual guidance: Evidence for amplitude rather than position control. *Experimental Brain Research*, 62, 451–458. [PubMed]
- Carrozzo, M., McIntyre, J., Zago, M., & Lacquaniti, F. (1999). Viewer-centered and body centered frames of reference in direct visuomotor transformations. *Experimental Brain Research*, 129, 201–210. [PubMed]
- Dassonville, P., & Bala, J. K. (2004). Perception, action, and Roelofs effect: A mere illusion of dissociation. *PLoS Biology*, 2, e364. [PubMed]
- de Grave, D. D., Brenner, E., & Smeets, J. B. (2004). Illusions as a tool to study the coding of pointing movements. *Experimental Brain Research*, 155, 56–62. [PubMed]
- de Grave, D. D., Smeets, J. B., & Brenner, E. (2006). Why are saccades influenced by the Brentano illusion? *Experimental Brain Research*. [PubMed]
- Desmurget, M., Pélisson, D., Rossetti, Y., & Prablanc, C. (1998). From eye to hand: Planning goal-directed movements. *Neuroscience and Biobehavioral Reviews*, 22, 761–788. [PubMed]
- Elliott, D., & Lee, T. (1995). The role of target information on manual aiming bias. *Psychological Research*, 58, 2–9.
- Feldman, A. G., & Levin, M. F. (1995). The origin and use of positional frames of reference in motor control. *Behavioral and Brain Sciences*, 18, 723–806.
- Festinger, L., White, C. W., & Allyn, M. R. (1968). Eye movements and decrement in the Müller–Lyer illusion. *Perception & Psychophysics*, 3, 376–382.
- Gentilucci, M., Chieffi, S., Deprati, E., Saetti, M. C., & Toni, I. (1996). Visual illusion and action. *Neuropsychologia*, 34, 369–376. [PubMed]
- Gillam, B. (1998). Illusions at century's end. In J. Hochberg (Ed.), *Perception and cognition at century's end* (pp. 95–136). London: Academic Press.
- Gillam, B., & Chambers, D. (1985). Size and position are incongruous: Measurements on the Müller–Lyer figure. *Perception & Psychophysics*, 37, 549–556. [PubMed]
- Glazebrook, C. M., Dhillon, V. P., Keetch, K. M., Lyons, J., Amazeen, E., Weeks, D. J., et al. (2005). Perception–action and the Muller–Lyer illusion: Amplitude or endpoint bias? *Experimental Brain Research*, 160, 71–78. [PubMed]
- Greenhouse, S. W., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika*, 24, 95–112.
- Jennings, J. R. (1987). Editorial policy on analyses of variance with repeated measures. *Journal of Motor Behavior*, 16, 235–254.
- Mack, A., Heuer, F., Villardi, K., & Chambers, D. (1985). The dissociation of position and extent in Muller–Lyer figures. *Perception & Psychophysics*, 37, 335–344. [PubMed]
- McCarley, J. S., Kramer, A. F., & DiGirolamo, G. J. (2003). Differential effects of the Müller–Lyer illusion on reflexive and voluntary saccades. *Journal of Vision*, 3(11), 751–760, <http://journalofvision.org/3/11/9/>, doi:10.1167/3.11.9. [PubMed] [Article]
- McIlwain, J. T. (1991). Distributed spatial coding in the superior colliculus: A review. *Visual Neuroscience*, 6, 3–13. [PubMed]
- McIntyre, J., Stratta, F., & Lacquaniti, F. (1997). Viewer-centered frame of reference for pointing to memorized targets in three-dimensional space. *Journal of Neurophysiology*, 78, 1601–1618. [PubMed] [Article]
- McIntyre, J., Stratta, F., & Lacquaniti, F. (1998). Short-term memory for reaching to visual targets: Psychophysical evidence for body-centered reference frames. *The Journal of Neuroscience*, 18, 8423–8435. [PubMed] [Article]

- Meegan, D. V., Glazebrook, C. M., Dhillon, V. P., Tremblay, L., Welsh, T. N., & Elliott, D. (2003). The Muller–Lyer illusion affects the planning and control of manual aiming movements. *Experimental Brain Research*, 155, 37–47. [[PubMed](#)]
- Messier, J., & Kalaska, J. F. (1997). Differential effect of task conditions on errors of direction and extent of reaching movements. *Experimental Brain Research*, 115, 469–478. [[PubMed](#)]
- Post, R. B., & Welch, R. B. (1996). Is there dissociation of perceptual and motor responses to figural illusions? *Perception*, 25, 569–581. [[PubMed](#)]
- Reina, G. A., & Schwartz, A. B. (2003). Eye–hand coupling during closed-loop drawing: Evidence of shared motor planning? *Human Movement Science*, 22, 137–152. [[PubMed](#)]
- Robinson, D. A. (1972). Eye movements evoked by collicular stimulation in the alert monkey. *Vision Research*, 12, 1795–1808. [[PubMed](#)]
- Rossetti, Y., Desmurget, M., & Prablanc, C. (1995). Vectorial coding of movement: Vision, kinaesthesia, or both? *Journal of Neurophysiology*, 74, 457–463. [[PubMed](#)]
- Smeets, J. B., Brenner, E., de Grave, D. D., & Cuijpers, R. H. (2002). Illusions in action: Consequences of inconsistent processing of spatial attributes. *Experimental Brain Research*, 147, 135–144. [[PubMed](#)]
- van den Dobbelaars, J. J., Brenner, E., & Smeets, J. B. (2001). Endpoints of arm movements to visual targets. *Experimental Brain Research*, 138, 279–287. [[PubMed](#)]
- Vasey, M. W., & Thayer, J. F. (1987). The continuing problem of false positives in repeated measures ANOVA in psychophysiology: A multivariate solution. *Psychophysiology*, 24, 479–486. [[PubMed](#)]
- Vindras, P., & Viviani, P. (1998). Frames of reference and control parameters in visuomanual pointing. *Journal of Experimental Psychology: Human Perception and Performance*, 24, 569–591. [[PubMed](#)]
- Wong, E., & Mack, A. (1981). Saccadic programming and perceived location. *Acta Psychologica*, 48, 123–131. [[PubMed](#)]
- Yarbus, A. L. (1967). *Eye movements and vision*. New York: Plenum press.