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RESEARCH ARTICLE

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Why are saccades influenced by the Brentano illusion?

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Abstract In the Brentano version of the Müller-Lyer illusion one part looks longer and the other looks shorter than it really is. We asked participants to make saccadic eye movements along these parts of the figure and between positions on the figure and a position outside the illusion. By showing that saccades from outside the figure are not influenced by the illusion, we demonstrate that the reason that saccades along the figure are influenced is that the incorrectly judged length is used to plan the amplitude of the saccade. This finding contradicts several current views on the use of visual information for action. We conclude that actions are influenced by visual illusions, but that such influences are only apparent if the action is guided by the attribute that is fooled by the illusion.

Keywords Perception · Action · Eye movements · Saccades · Illusion

Introduction

Saccades are very fast eye movements that bring an object of interest onto the part of the retina with the highest acuity. They are ballistic in the sense that once a saccade has started its trajectory cannot easily be modified by updated visual information (Carpenter 1988; Findlay and Walker 1999). They are coded in terms of a planned amplitude and direction (Robinson 1972; Becker and Jürgens 1979; McIlwain 1991). Saccades between the endpoints of the central shaft of the Müller-Lyer figure have been shown to differ for the two configurations (<—> and >—<) (Bernardis et al. 2005; Binsted and Elliott 1999; Festinger et al. 1968; Yarbus 1967). Does this mean that saccades are always fooled by this illusion?

It is evident that illusions do not always influence our actions to the extent that one would expect on the basis of their influences on perception (Milner and Goodale 1995). However, the reasons for this are not evident. One view is that there are two visual systems (Goodale and Milner 1992; Milner and Goodale 1995), one for perception and another for action. According to this "two visual systems hypothesis" the primary function of the visual system for perception (the ventral stream) is identifying and recognizing objects in the visual environment. The information in this stream is therefore processed in a manner that is independent of the viewing conditions: information is encoded in an allocentric frame of reference. Such encoding considers all sorts of complex, contextual relationships within the image making it sensitive to visual illusions. The visual system for action (dorsal stream) is specialized in the visual information needed for the control one's limbs, which means that the spatial positions of objects need to be determined with respect to the body (in an egocentric frame of reference). Largely ignoring the context is believed to make the dorsal stream insensitive to visual illusions.

The fact that illusions do influence actions to some extent can be explained in several ways within the "two visual systems hypothesis". The effects on action might be attributed to the illusions arising at early stages of visual processing, before the separation into a dorsal (action) and a ventral (perceptual) stream of visual processing (Dyde and Milner 2001). Another possible explanation for illusions influencing action is that surrounding context elements are treated as potential obstacles and therefore influence the movement (Haffenden and Goodale 2000; De Grave et al. 2005). For example grip orientation (De Grave et al. 2005) and maximum grip aperture (Haffenden and Goodale 2000) change due to the location of the

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surrounding circles in the Ebbinghaus illusion. The effect could be in the same direction as the perceptual illusion, but this is considered to be a coincidence.

Beside the "two visual systems hypothesis" are two alternative views that are based on the assumption of common processing for perception and action. Both claim that perception and action are equally susceptible to illusions. According to the "single representation model" of Franz et al. (2000), there is a single representation underlying perception and action. The (apparent) discrepancy between the susceptibility of perception and action to visual illusions is a result of incorrectly matching the perceptual and motor tasks. If the tasks are matched appropriately the effect of the illusion on perception and action will be the same. This view was supported by showing that taking such precautions does indeed make the effects on perception and action indistinguishable.

Another view that is based on the assumption of common processing for perception and action is the "inconsistent attributes hypothesis". According to this hypothesis many attributes are processed independently, without ensuring consistency between related attributes (Smeets et al. 2002). For example, motion is physically equivalent to a change in position. However, when seeing a motion after-effect, like the waterfall illusion, we only perceive motion but not a change in position. A similar dissociation has been found between the spatial attributes of length and position in the Müller-Lyer illusion (Gillam and Chambers 1985; Gillam 1998; Mack et al. 1985). The perceived length of the shaft is changed, without changing the perceived positions of the ends. Due to the use of different spatial attributes in perceptual tasks than in action, a difference between the effects of the illusion can be found (Smeets and Brenner 1995). Thus illusions can influence any (perceptual or motor) task, but only if performing the task relies on the attribute that is influenced by the illusion.

Most previous studies about the discrepancy between visual information processing for perception and action have concentrated on arm movements, in particular grasping. Saccadic eye movements have two properties that make them particularly suitable for discriminating between the three above-mentioned views: they are too fast to be corrected by updated visual information that is acquired as the eyes approach the target (taking less than 50 ms for saccades of up to 10°), and they are known to be planned in terms of a direction and an amplitude of displacement.

Saccadic eye movements are already known to be influenced by illusions such as the Müller-Lyer illusion (Bernardis et al. 2005; Binsted and Elliott 1999; Festinger et al. 1968; Yarbus 1967). This finding may appear to refute the "two visual systems hypothesis" because an action should not be influenced by an illusion. However, the illusion may affect early processes (before the pathways split). Moreover, the saccade may be influenced by the wings of the Müller-Lyer figure for reasons that have nothing to do with the perceived length of the shaft. Saccades towards complex stimuli are known to be pulled towards the "centre of gravity" of the stimulus configuration (Findlay 1982; He and Kowler 1989). In that case saccades towards a wings-in vertex might end too close to the centre of the figure because the saccade is made to the centre of the arrowhead rather than to the tip of the shaft. Saccades towards a wings-out vertex might end outside the figure for the same reason.

It has been argued that physically related spatial attributes are not always perceived in a consistent manner: the arrowheads of the Müller-Lyer illusion influence the perceived lengths of the shafts, without influencing the perceived positions of the shafts' endpoints (Smeets et al. 2002; Gillam and Chambers 1985; Mack et al. 1985). Therefore, the "inconsistent attributes hypothesis" makes a specific prediction for an experiment in which saccades to a vertex of the Müller-Lyer figure are made from different starting positions. This prediction differs clearly from that of the other views. According to the "inconsistent attributes hypothesis" the length of the central shaft of the illusion is misperceived, so that the amplitudes of saccades between the vertices of the illusion (i.e. along this shaft) will be influenced to the same extent as the percept. For saccades from the side there should be no effect at all, because the length of the shaft is irrelevant.

In the present study, we use the Brentano version of the Müller-Lyer figure. Neither the "two visual systems hypothesis" (Goodale and Milner 1992; Milner and Goodale 1995) nor the "single representation model" (Franz et al. 2000) present any reason to predict that the influence of the illusion will depend on the starting position of the saccades, because they both rely on consistent representations of space. The "single representation model" predicts that the effect of the Müller-Lyer illusion should be the same for saccades as for perceptual judgments (with equivalent tasks) regardless of the starting position, as does the "two visual systems hypothesis" if the illusion's effect originates before the two visual streams separate. If saccades are pulled towards the "centre of gravity", then the influence of the illusion on the saccadic endpoints should not depend on where the eye movement started.

Method

Participants

This study is part of an ongoing research program that has been approved by the ethical committee of the Erasmus MC. Twelve participants volunteered to take part in the study after being informed about what they would be required to do. All had normal or corrected-to-normal vision.

Stimuli and apparatus

A bite-board was placed in front of a computer screen (38.4×28.8 cm, 1,024×768 pixels, 75 Hz) to keep the participant's head fixed at a viewing distance of 85 cm. At this distance, one pixel corresponds to 0.025°. The stimulus consisted of a vertical black Brentano figure and a red target dot on a white background (Fig. 1). The length of each of the figure's vertical shafts was 5.4°. The length of the wings was 1.5°. The inclination of the wings with respect to the shafts was 30°. Two configurations were used (see schematics in Fig. 1). The 0.13° diameter target dot could either appear on one of the three vertices of the Brentano illusion or 5.4° to the right of the middle vertex. Eye movements were recorded with an Eyelink eye tracker (SR Research Ltd.) with a temporal resolution of 250 Hz and a spatial resolution of 0.2°.

Procedure

Participants performed two blocks of 400 trials, one for each configuration of the Brentano figure. The order of the two blocks was counterbalanced across participants. The participants were instructed to shift their gaze to follow the red target dot as it jumped between the four positions (Fig. 1). The Brentano figure was visible at the same location throughout a block of trials. When the red target dot jumped to a new position, participants made a saccade to that position. The target jumped to a new position as soon as the participant kept his or her eyes within a radius of 20 pixels around the target dot for 100 ms. The target of each saccade was the starting position of the saccade to the next target.

Ten of the 12 participants (two had moved to another country at the time of the experiment) also performed a perceptual judgment task. At the start of each trial a fixation point, a similar red dot to the one in the saccadic eye movement task, was presented at the centre of the screen. A Brentano figure was presented simultaneously with the middle vertex on the fixation point. One second later a second red dot appeared on the upper or lower vertex to indicate which shaft length had to be judged. Half a second later the stimulus with the two red dots disappeared and a test line was presented for 500 ms. The test line was presented at the former position of the indicated shaft, but was shifted by one third of its length in the direction of the former position of the middle vertex to prevent participants from comparing the endpoints. Participants pressed one of two arrow buttons to indicate whether they thought that the test line was longer or shorter than the shaft between the two red dots. Half a second after they pressed a button a new stimulus appeared. Four staircases of 50 trials (two shafts; two configurations) were randomly interleaved. If the test line was judged to be shorter (longer) than the shaft, its length was increased (decreased) by 0.05° on the next presentation for that shaft and configuration.

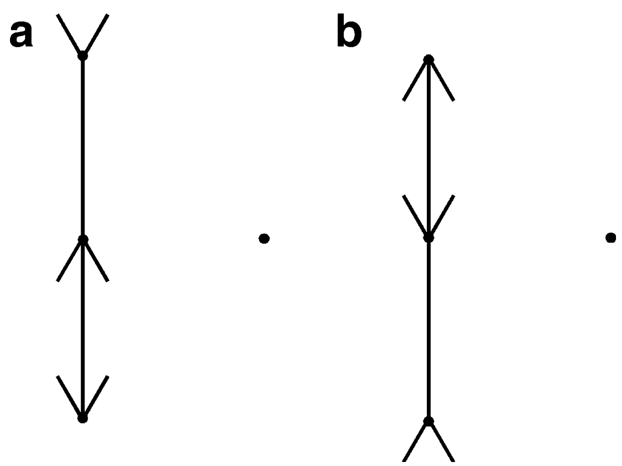

Fig. 1 The two Brentano configurations; one with the wings-in part at the top (**a**) and one with the wings-out part at the top (**b**). Each participant performed one block of trials for each configuration. The *dots* indicate the positions at which a target could appear (on one of the vertices or outside the illusion). Only one configuration was visible at a time

Data analysis

For the eye movement task only the first saccades after the target jumped to the middle vertex were analyzed. Trials on which the saccade was not in the required direction or in which gaze shifted within 50 ms after the target jumped were excluded from analysis. This resulted in a loss of 8% of all trials.

The quantitative evaluation of the influence of the illusion was based on the three types of saccades toward the target dot on the middle vertex (upward, downward or leftward). We obviously concentrated on the vertical position of the saccadic endpoints because the illusion was presented in the vertical direction. In order not to confound general errors in estimates of the distance to be moved with errors induced by the illusion, we always compared movements for the two configurations. Moreover, since the general estimates of the distance to be moved differed between subjects and between different spatial positions, a scaled measure of the magnitude of the illusion was computed for each participant and each type of saccades. To do so we determined the median difference in vertical distance between the endpoints of movements along the "wings-out" and the "wings-in" configuration. This difference is divided by the participant's median saccadic length (considering both configurations). The result is the influence of the illusion expressed as a percentage of the length of the saccadic eye movement. Note that for the saccades from outside the figure the influence is measured in the direction orthogonal to the saccade. Statistical tests were all conducted across participants. A repeated measures ANOVA was performed on the size of the illusion, to examine whether the three types of saccades towards the middle vertex were influenced differently by the illusion. Post-hoc paired t tests were used to determine which types of saccades differed. One sample t tests were performed to check whether the illusion magnitude in each of the three types of movements differed from zero (to check whether there was any effect of the illusion).

For the perceptual judgment task we also calculated the average difference in perceived length between the wings-in and the wings-out part (expressed as a percentage of the length of the shaft) for each participant. To do so we determined the average difference between the test line lengths for the wings-in and the wings-out configuration during the last 40 trials of each staircase and divided this value by two to get an estimate of the influence of a single configuration. We did so for both the upper shafts and for the lower shafts and averaged them. The result is the size of the illusion expressed as a percentage of the length of the shaft of the Brentano figure. A one sample t test was performed to check whether the illusion magnitude differed from zero (to check whether there was any effect of the illusion). Paired t tests were used to determine whether the illusion's effect on perception differed from its effect on saccades.

Results

The two panels of Fig. 2 each show the vertical component of five arbitrary saccades made by one participant to the middle target from each of the other three target positions. For both configurations of the Brentano figure this participant's saccades undershot the target when moving along the wings-in part of the figure, and overshot the target when moving along the wings-out part. In both cases corrective saccades were made after about 200 ms, indicating that the initial endpoints were not the parts of the figure towards which the participants intended to direct their gaze. When saccades were made from outside the figure they ended at the target position (thin traces) without a systematic vertical error. Note that such saccades have similar amplitudes as the other two kinds of saccades, but this is not visible in Fig. 2 because only the vertical component of the horizontal saccade is shown. The critical finding is that the vertical error that is visible for the other two kinds of saccades is absent for saccades from outside the Brentano figure.

The traces shown in Fig. 2 are representative of saccades toward the middle target dot (see Fig. 3). Saccades perpendicular to the shaft were not influenced by the illusion, whereas saccadic eye movements along the shaft (from the bottom to the middle target and from the top to the middle target) did show a significant effect of the illusion.

The two left-most columns in Fig. 3 show the size of the effect of the illusion on saccades towards the middle target dot. The ANOVA showed a significant difference between the types of saccades [$F(2)=3.95$, $P<0.05$]. Saccades between the vertices (along the shaft) showed a significant effect of the illusion (13% for saccades from the bottom to the middle target and 8% for ones from the top to the middle target). No significant effect of the illusion (−1%) was found for saccades perpendicular to the shaft. These results are consistent with saccades being based on an estimate of distance (rather than of position), which in turn is based on the judged length of the shaft if the movement is along the shaft.

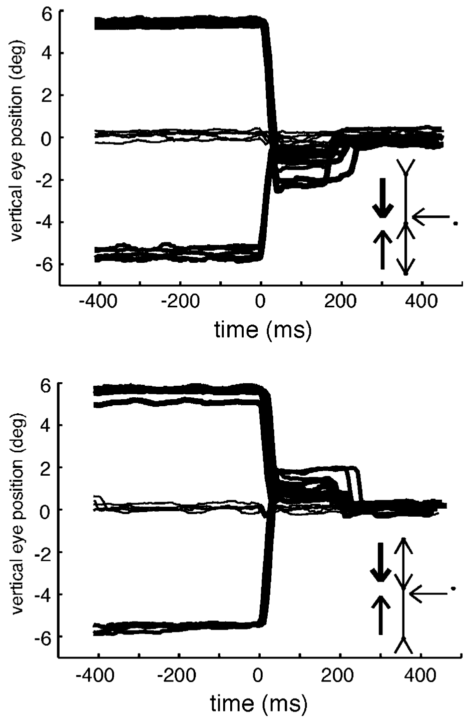

Fig. 2 Examples of the vertical components of the saccades for the two configurations of the Brentano illusion. *Each panel* shows 15 raw traces of one participant's eye movements towards the middle target dot (five from each starting position: top, bottom and outside). Zero on the horizontal axis is the moment of saccade onset. Note the corrective saccades after about 200 ms. The *arrows* indicate the directions of the analyzed saccades

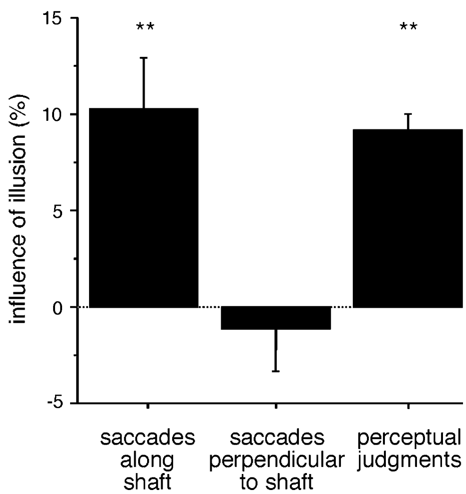

Fig. 3 Magnitude of the influence of the illusion on saccades toward the middle target dot and on perceptual judgments. *Error bars* represent standard errors between participants and *asterisks* indicate a significant effect of the illusion (**$P<0.01$)

The magnitude of the effect of the illusion remained constant throughout the experiment and was similar for the two configurations. The influence of the illusion on the amplitude of the saccades was not accompanied by systematic vergence errors. Saccades away from the middle target dot showed a similar pattern to those towards the middle target dot, whereas saccades between the upper or lower target and the dot outside the figure (and vice versa) were influenced by the illusion to a smaller extent.

For the perceptual judgments we found an illusion magnitude of 9% (right-most column in Fig. 3, $t=10.80$, $P<0.01$), which is similar to the magnitude of the effect on the amplitude of saccades along the shaft ($t=-0.75$, $P=0.46$) but significantly different from saccades from outside the illusion ($t=4.87$, $P<0.01$). This too is consistent with saccades being based on an estimate of the judged length of the shaft as long as the movement is along the shaft.

Discussion

Saccadic eye movements along the shaft were influenced by the illusion. Saccades perpendicular to the shaft were not. This is exactly as predicted by the inconsistent attributes hypothesis (Smeets et al. 2002). The Brentano figure influenced saccades along the shaft to the same extent as it influenced the perceived shaft length, but since only the length was misperceived saccades in the orthogonal direction were unaffected by the illusion (Fig. 3).

According to the "centre of gravity" theory (Findlay 1982; He and Kowler 1989) the illusory effect is caused by saccades being directed to the centre of the pattern near the vertex. This theory would predict the same error in saccadic end position for saccades perpendicular to the shaft (the centre of gravity does not change with starting position), which is inconsistent with our data. None of the other hypothesis can account for our data either, because none of them consider the direction of the eye movement to be important.

The magnitude of the illusion on saccades did not differ from the magnitude of the perceptual illusion, which is consistent with participants using length information to determine the saccade amplitude. McCarley et al. (2003) also found that saccades can be influenced by the Müller-Lyer illusion to a similar extent as perceptual judgments, but they found that this was only so for voluntary saccades. Reflexive saccades were only modestly affected by the illusion. Our procedure was similar to the one that they used to elicit reflexive saccades. We cannot explain this discrepancy, but it suggests that some other factor than whether the saccade is reflexive or voluntary can influence the extent to which the illusion affects saccades. However this does not interfere with our conclusion that the illusion influences saccades along the shaft but not ones orthogonal to the shaft. Whether the effect on saccades along the shaft is really identical to the perceptual effect under all conditions remains to be seen.

In a study by Bernardis et al. (2005, experiment 2) participants made saccadic eye movements along the Müller-Lyer illusion. They found an illusion effect of 24.8%, which is much larger than the effect of the illusion on the saccades in this study. This could have been caused by the direction of presentation of the illusion. In the Bernardis et al. (2005) study the illusion was presented horizontally whereas in our study the illusion was presented vertically. Whether horizontal and vertical saccades are affected differently by the illusion has been tested by de Grave et al. (2006). In their experiment 2 they showed that, although the influence of the illusion was a little less in the vertical than in the horizontal direction, the illusion effects on horizontal and vertical saccades did not differ significantly. Thus, the orientation of the stimulus alone cannot explain the large difference in effect.

We conclude that the Brentano figure only influences saccades when the length that is misjudged in the figure is relevant for planning the amplitude of the saccade. This supports our view that illusions influence actions, but only to the extent that the attribute that is affected by the illusion (in this case the judged shaft length) is used to perform the task.

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