Time course of the effect of the Müller-Lyer illusion on saccades and perceptual judgments

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The amplitude of saccadic eye movements is affected by size illusions such as the Müller-Lyer illusion, but this effect varies highly between studies. Here we examine the origin of this variability by testing the influence of three temporal factors on the effect of the Müller-Lyer illusion: presentation time, response delay, and saccade latency. Subjects performed reflexive saccades, deferred saccades, and memory-guided saccades along the shaft of the illusion. We evaluated the time course of the saccadic illusion effects. We compared it to the influence of presentation time on the illusion effect in a perceptual judgment task. According to the "two visual systems hypothesis", visual perception and visual memory rely on a perceptual representation coded along the ventral "perception" pathway, which is affected by visual contextual illusions. Visuomotor actions, such as saccades, depend on the dorsal "action" pathway that is largely immune to illusions. In contrast with this hypothesis, our results **show that the illusion affected both saccade amplitude and perceptual judgments with a similar time course. Presentation time of the Müller-Lyer illusion, not response delay or saccade latency, was the major factor in determining the size of the illusion effect. Longer presentation times resulted in smaller effects, suggesting that our visual representation is dynamic and becomes more accurate when we look at an object for a longer time before we act on it.**

Introduction

An influential theory of visual processing is the two visual systems hypothesis, which posits a functional distinction between vision for perception and vision for action (Goodale & Milner, 1992; Milner & Goodale, 2006, 2008). In this framework, visual perception and visual memory rely on processing in the ventral stream of the brain. Here, object characteristics (such as shape, size and color) and locations are transformed into an allocentric representation that allows for long-term storage (Milner & Goodale, 2006). Because such a representation takes the context into account, both perception and memory-guided actions are assumed to be highly sensitive to visual contextual illusions. For visuomotor control, on the other hand, the location of an object needs to be specified relative to the observer and irrespective of the context (i.e., in egocentric coordinates), on a moment-to-moment basis (Goodale, Westwood, & Milner, 2004; Milner & Goodale, 2006; Westwood & Goodale, 2003). The visuomotor system, which resides in the dorsal stream, is therefore assumed to be largely immune to contextual illusions.

While several studies on grasping of and pointing to visual contextual illusions support the two visual systems hypothesis (e.g., Aglioti, DeSouza, & Goodale, 1995; Bridgeman, Peery, & Anand, 1997; Westwood, Heath, & Roy, 2000), others have reported that these

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actions do not resist visual contextual illusions (e.g., Brenner & Smeets, 1996; Elliott & Lee, 1995; Franz, Gegenfurtner, Bulthoff, & Fahle, 2000; Smeets & Brenner, 1995). Illusions are also found to affect saccadic eye movements (but see Wong & Mack, 1981), which critically involve dorsal stream areas (Munoz, 2002). For example, the Müller-Lyer illusion (MLI), which changes the perceived length of a line segment through its inward or outward flanking fins, also affects the amplitude of saccades along the shaft of the illusion (e.g., Binsted & Elliott, 1999; de Grave, Smeets, & Brenner, 2006). The magnitude of this effect varies largely between studies, ranging from virtually none to about 30%, depending on experimental conditions.

Which experimental parameters influence the magnitude of the saccadic illusion effect? Besides the predictability of the location of the MLI (Bruno, Knox, & de Grave, 2010; de Grave & Bruno, 2010), and the availability of visual error feedback available after the saccade (Bruno et al., 2010), the latency of the saccade seems to play a role. Larger illusion effects were found for saccades with shorter latencies (de Grave & Bruno, 2010; van Zoest & Hunt, 2011, using a directional version of the MLI), as if the representation that drives the saccade becomes more veridical with the passing of time. Van Zoest and Hunt (2011) also found that perceptual judgments become less biased with longer presentation of the MLI, and therefore suggested that both perception and action might be controlled by a common visual representation (see also Franz, 2001).

Careful inspection of the literature reveals additional evidence for a decrease of the saccadic illusion effect over time. For example, deferring the instructed saccade by imposing a preview of the MLI before a target appeared at its vertex (DiGirolamo, McCarley, Kramer, & Griffin, 2008; McCarley & Grant, 2008; McCarley, Kramer, & DiGirolamo, 2003) resulted in rather small effects on saccade amplitude (6%–7%, when calculated as described in the Methods). In addition, illusion effects for memory-guided saccades were twice as small as for reflexive saccades (Knox & Bruno, 2007), with longer presentation times for memory-guided saccades than for reflexive saccades. Taken together, these results suggest that the size of the illusion effect depends on the time available for visual processing before the start of the saccade.

Can these observations be interpreted in terms of the two hypotheses outlined above? The two visual systems hypothesis predicts that the MLI will hardly affect reflexive and deferred saccades, but will strongly affect memory-guided saccades and perceptual judgments, irrespective of processing time. Alternatively, if there is a single visual representation that becomes more accurate over time, both saccades and perceptual judgments will be less influenced by the illusion as subjects are provided with more time to process the information.

As explained above, a comparison across studies supports the latter option. To test this prediction in more detail, the present study examined three temporal factors that could influence the magnitude of the MLI effect on saccade amplitude: response delay (i.e., the time between the appearance of the MLI and the signal to make a saccade), latency (i.e., the time between the signal to make a saccade and saccade onset), and presentation time (i.e., the time that the MLI is visible before the response). Subjects had to perform reflexive saccades, deferred saccades, and memory-guided saccades along the shaft of the MLI. The stimulus always disappeared shortly after the signal to make a saccade, so that visual error feedback is not available. To test whether the influence of time is specific to saccades, a second group of subjects performed a perceptual task in which they judged the length of the illusion with different presentation times. We did not try to match the perceptual task to the saccade tasks, but we aimed to investigate whether the influence of presentation time is similar.

Methods

Two experiments were performed. In Experiment 1, subjects performed reflexive, deferred, and memory-guided saccades. Experiment 2 consisted of a perceptual task in which the length of the Müller-Lyer illusion had to be estimated. The study was part of a research program that was approved by the ethics committee of the Faculty of Human Movement Sciences of the VU University, Amsterdam.

Experiment 1: Reflexive, deferred and memory-guided saccades

The first experiment consists of three sub-studies. In Experiment 1A, subjects performed reflexive, deferred, and memory-guided saccades in separate blocks of trials. Reflexive saccades with and without gap were used to investigate whether there is an effect of latency on the illusion effect. By using deferred and memory-guided saccades, we could modulate response delay and presentation time. Illusion effects were compared within and across saccade types. In response to the results, two additional experiments were performed to obtain a thorough overview of the effect of presentation time. In Experiment 1B, subjects performed reflexive saccades, whereas in Experiment 1C deferred saccades were performed.

Subjects

Twelve volunteers took part in Experiment 1, nine of whom successfully performed this experiment (aged 24–34 years, three men). One subject did not complete the experiment because of having difficulty suppressing a direct response in the memory-guided saccade task. Two other subjects had the same problem, making a saccade before or within 100 ms after the go signal in more than 25% of the trials (compared to 2%–19% for the included subjects) and were removed from the analysis because they performed too few correct trials to get a reliable measure of saccade parameters. All subjects had normal or corrected-to-normal vision.

Setup

Subjects were seated in a dimly lit room, with their head stabilized by a chin rest positioned about 52 cm from a computer screen (36 × 27 cm, 1024 × 768 pixels, 85 Hz). At this distance, 1.0 cm on the screen corresponds to approximately 1.1° of visual angle. Eye movements of both eyes were recorded with an Eyelink II Eye Tracker (SR Research Ltd., Canada), with a temporal resolution of 500 Hz and a spatial resolution of 0.2°.

Stimuli

The stimulus was a horizontal MLI with a shaft length of 6.0 cm or 7.0 cm, and a fin length of 1.8 cm, all in 1 mm thick lines. Two shaft lengths were used to prevent subjects from planning a standardized saccadic response. The angle of each fin with respect to the shaft was 30° (inward) or 150° (outward). The MLI was presented in black on a light gray background. It was presented so that one end of the shaft was at the blue fixation dot in the center of the screen, and the other end to the left or right, marked with a red target dot (both dots had a diameter of 0.35 cm). In all conditions, a 50 ms beep was presented at the moment a response was required (at the moment the MLI appeared for reflexive saccades, or at the moment the fixation dot disappeared for deferred and memory-guided saccades).

Procedure

A schematic overview of the timing of trials for reflexive, deferred, and memory-guided saccades of Experiment 1 is shown in Figure 1. In all blocks, MLIs with different fin configurations, shaft lengths, directions, and presentation times were presented in random order. Block duration was maximal 10 min, with short breaks between blocks.

Experiment 1A

Subjects performed two sessions on separate days, with each session consisting of one block of reflexive saccades, one block of deferred saccades, and one block of memory-guided saccades. The order of blocks was counterbalanced across subjects. In the first session, subjects performed 16 practice trials before each block, to get familiar with the procedure.

Reflexive saccades: Each trial started with a central fixation dot that was presented for a random time period (500–1000 ms). After this period, the fixation dot disappeared and the MLI with the target dot was presented for 153 ms. Subjects were instructed to move their eyes to the target dot as quickly as possible in response to the onset of the stimulus and the tone. In either the first or the second block of reflexive saccades, a 200 ms gap was added between the disappearance of the fixation dot and the onset of the stimulus and the tone. Such a gap can evoke express saccades with latencies as short as 100 ms (Fischer & Ramsperger, 1984). Each block contained 160 trials (2 fin configurations × 2 shaft lengths × 2 directions × 20 repetitions).

Deferred saccades: After the 500–1000 ms fixation period, the stimulus appeared for 506 or 1000 ms (the response delay) while the fixation dot remained visible. Subjects were instructed to keep fixation until the tone was presented, at which moment the fixation dot disappeared (go signal). The stimulus remained visible for another 153 ms (resulting in a presentation time of 659 or 1153 ms). If the subject made a saccade towards the target before the go signal, he/she was notified by a red bar that appeared at the location of the stimulus. Each of the two blocks consisted of 160 trials (2 fin configurations × 2 shaft lengths × 2 directions × 2 presentation times × 10 repetitions).

Memory-guided saccades: After the 500–1000 ms fixation period, the stimulus was presented for 153 or 659 ms with the fixation dot visible. Then the stimulus disappeared, but the fixation dot remained visible for another 847 ms (the memory period). Then the go signal was presented, instructing the subject to move his/her eyes to the remembered location of the target dot as quickly as possible. As for deferred saccades, the subject was notified if he/she made a saccade toward the target before the go signal. Each of the two blocks consisted of 160 trials (2 fin configurations × 2 shaft lengths × 2 directions × 2 presentation times × 10 repetitions).

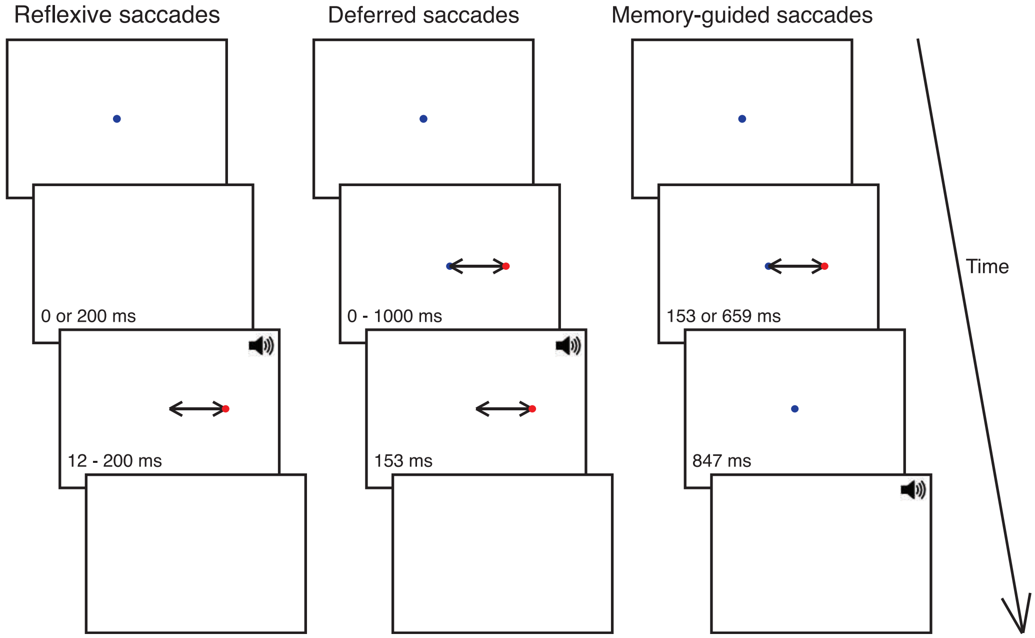

Figure 1. Timing of trials for reflexive saccades (Experiment 1A and 1B), deferred saccades (Experiment 1A and 1C) and memory-guided saccades (Experiment 1A). The left column includes reflexive-gap saccades (Experiment 1A), which only differed from reflexive saccades by a 200 ms gap between the disappearance of the fixation dot and the appearance of the MLI with the target. Subjects were instructed to move their eyes to the (remembered) position of the red target dot at the end of the MLI. In addition to a visual cue (the appearance of the MLI or the disappearance of the fixation dot), a brief tone was presented at the moment a saccadic response was required. After the cue, the MLI never remained on the screen long enough for subjects to obtain a visual error signal.

Experiment 1B

In response to the results of Experiment 1A, an additional reflexive saccade experiment was performed to study the illusion effect for presentation times up to 200 ms in more detail. The procedure was the same as for reflexive saccades without gap in Experiment 1A, but six different presentation times were used: 12, 24, 47, 94, 153, and 200 ms (i.e., 1, 2, 4, 8, 13, and 17 frames at 85 Hz). Subjects performed one session with three blocks of 192 trials (2 fin configurations × 2 shaft lengths × 2 directions × 6 presentation times × 4 repetitions). To optimize experimental duration and because the subjects had already practiced the task in Experiment 1A, we used fewer repetitions than in Experiment 1A (12 instead of 20).

Experiment 1C

We also performed an additional experiment using deferred saccades to obtain saccadic results over a broader range of presentation times. The procedure was the same as for deferred saccades in Experiment 1A, but with delays of 0 ms (i.e., reflexive saccades), 153 ms, and 306 ms (resulting in presentation times of 153 ms, 306 ms, and 459 ms, respectively). Trials in which the subject made a saccade towards the target before the go signal were aborted and repeated at the end of the block. Subjects performed one session with two blocks of 168 trials (2 fin configurations × 2 shaft lengths × 2 directions × 3 delays × 7 repetitions). In this experiment, one of the original subjects was unavailable and therefore replaced.

Data analysis

From the saccade data, we first removed trials with blinks and trials without stable fixation at the time of stimulus onset. Horizontal eye velocity, calculated from the eye positions given by the Eyelink and then upsampled to 1000 Hz by linear interpolation, was used to define saccade onset and offset. Saccade onset was defined as the last sample before eye velocity reached a $30° s^{-1}$ threshold, searching back in time from the moment at which eye velocity crossed a $100° s^{-1}$ threshold. Saccade offset was defined as the first of two consecutive samples (2 ms) below the $30° s^{-1}$ threshold, searching forward in time from peak eye velocity. We removed trails in which saccade latency (defined as the time between the go signal and saccade onset) was shorter than 100 ms or longer than 500 ms, and trials in which the saccade ended in the hemifield opposite to the target. Next, saccades were discarded from the analysis if the amplitude was shorter than 50% of the target distance, vertical eye position deviated more than

1.5° from a straight line between fixation and target position, saccade duration was longer than 80 ms, or if amplitude, peak velocity, or duration differed by more than three standard deviations from the mean for that stimulus (i.e., each combination of fin configuration, shaft length, and direction).

The remaining trials were analyzed separately for each experiment and saccade type. For each subject we determined the median saccade amplitude and latency for each stimulus and presentation time. The saccade rejection procedure left us with an average of 19 and 18 trials per stimulus for reflexive saccades (with and without gap, respectively), 17 trials per stimulus and presentation time for deferred saccades, and 16 trials per stimulus and presentation time for memory-guided saccades. In both Experiment 1B and 1C, on average 11 trials per stimulus and presentation time were used for determining median saccade amplitude and latency. Next, the illusion effect was calculated as the difference between the median amplitude of saccades along the inward and outward fin configuration, divided by the average of the medians for both fin configurations (de Grave et al., 2006). The result is the influence of the illusion as a percentage of saccade amplitude. Finally, illusion effects were averaged across shaft lengths and directions.

For Experiment 1A, a repeated measures ANOVA was performed on the mean illusion effects with condition (reflexive, reflexive-gap, deferred 659 ms presentation, deferred 1153 ms presentation, memory-guided 153 ms presentation, memory-guided 659 ms presentation) as the within-subjects factor. For Experiment 1B and 1C, we performed repeated measures ANOVAs with presentation time as within-subjects factor. Post-hoc paired t tests were performed after obtaining a significant main effect. A significance level of 0.05 was used.

Since these analyses suggested that presentation time determined the magnitude of the illusion effect, we further examined the relationship between presentation time and illusion effect over all saccadic conditions, taking the data of Experiments 1A, 1B, and 1C together. In this way, we could test the hypothesis that our visual representation of the target becomes more accurate over time.

Experiment 2: Perceptual judgments

In this experiment, subjects estimated the length of the shaft of the MLI. We varied presentation time to investigate the time course of the illusion effect on these perceptual judgments. Our aim was to compare this time course to the time course of the illusion effect on saccades. We thus did not attempt to match the saccadic and perceptual tasks, which is hardly possible to do adequately, and we will not compare the absolute illusion effects.

Subjects

A group of nineteen volunteers that did not take part in the saccade experiment took part in the perceptual experiment (aged 19–25 years, 10 men). All subjects had normal or corrected-to-normal vision.

Setup

The setup was the same as in Experiment 1, but without the use of the Eyelink system. Perceptual responses were called out verbally by the subject and entered into a computer by the experimenter.

Stimuli

The stimulus was again a horizontal MLI, with inward or outward fin configuration. We used shaft lengths of 4.8, 6.0, and 7.2 cm with corresponding fin lengths of 1.4, 1.8, and 2.2 cm, respectively. A broader range of shaft lengths than in the saccade experiment was used to ensure that subjects would not give a stereotypical response. The MLI was presented near the center of the screen, with a random horizontal offset of 0 to 2.0 cm from the center.

Procedure

The subject initiated each trial with a key press. After 500 ms, the MLI was presented for 200, 306, 706, or 2000 ms. When the MLI disappeared, the subject had to give a verbal estimate of the length of the shaft with a precision of 0.5 centimeter, and then press a key to start the next trial. Subjects performed three blocks of 144 trials (2 fin configurations $\times$ 3 shaft lengths $\times$ 4 presentation times $\times$ 6 repetitions). Free viewing of the MLI was allowed. No time limit was given for the response.

Data analysis

For the perceptual judgments, we calculated the average estimated length for each stimulus and presentation time. We fitted the estimated lengths per subject and presentation time as a linear function of the true shaft lengths. Because the slopes of these functions differed significantly from 1.0, (mean $\pm$ SEM: 0.68 $\pm$ 0.06, $t(18) = 5.26$, $p < 0.001$), we calculated corrected illusion effects. Illusion effects were calculated by taking the difference in estimated length for the fins-in and fins-out MLI and dividing this by the average slope of the functions per subject multiplied by the true shaft length (Bruno et al., 2010). Next, illusion effects were averaged across shaft lengths. A repeated-measures ANOVA was performed on the mean illusion effects with presentation time as the within-subjects factor.

Results

We tested whether the size of the effect of the MLI depends on the time available for visual processing. In Experiment 1, we examined the MLI effect on reflexive, deferred and memory-guided saccades. In Experiment 2, we performed a perceptual judgment task in which presentation time was varied. We compared the time course of the MLI effect on saccades and perception.

Experiment 1: Reflexive, deferred and memory-guided saccades

Experiment 1A

As can be seen in Figure 2, relatively large illusion effects were found for reflexive saccades (with and without a gap) and memory-guided saccades with short presentation of the MLI (blue bars and darker green bar), whereas smaller effects were found for deferred saccades and memory-guided saccades with longer presentation times (red bars and lighter green bar). The ANOVA showed a significant main effect of condition, $F(5, 40) = 4.12$, $p = 0.004$. These results support the hypothesis that there is a single target representation that becomes more veridical over time (van Zoest & Hunt, 2011), in this case presentation time. We will now outline our observations in further detail.

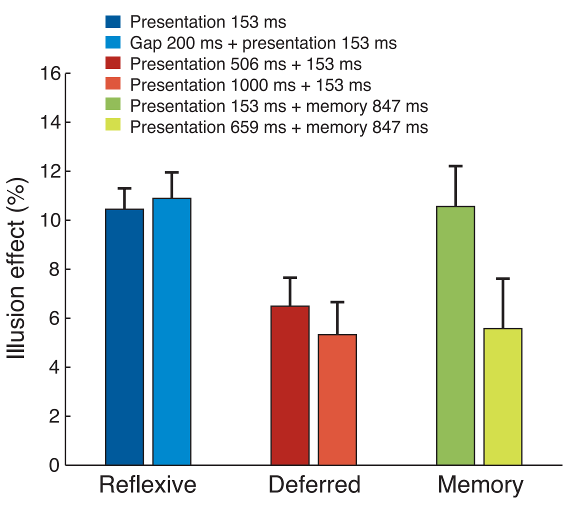

Figure 2. Illusion effects averaged across subjects for reflexive, deferred, and memory-guided saccades of Experiment 1A. Error bars represent *SEM*.

In this experiment, three temporal factors were modulated to examine their influence on the illusion effect. First, saccade latency was modulated by introducing a gap before the appearance of the stimulus in one of the reflexive saccade blocks. As can be seen when comparing the two blue bars in Figure 2, the illusion effect did not differ between normal reflexive saccades and reflexive-gap saccades ($p = 0.496$). However, saccade latency was also only slightly (22 ms) shorter for reflexive-gap saccades than for normal reflexive saccades (see Table 1, $p < 0.05$). To further examine the suggested relationship between latency and the magnitude of the illusion effect (de Grave & Bruno, 2010; van Zoest & Hunt, 2011), we categorized the saccades of both reflexive conditions into three bins based on the 33⅓ and 66⅔ percentile in latency (per stimulus). This yielded an illusion effect of 11.7 ± 1.2% (latency 161 ± 5 ms) for the fastest bin, 10.5 ± 1.2% (latency 187 ± 8 ms) for the middle bin, and 8.5 ± 0.7% (latency 236 ± 18 ms) for the slowest bin (measures in mean ± *SEM*). Thus, the effects were larger for saccades with shorter latencies, $F(2, 16) = 4.69$, $p = 0.025$.

Secondly, we modulated the response delay (i.e., the time between the onset of the MLI and the go signal) by using deferred and memory-guided saccades. The results in Figure 2 do not show a decreasing illusion effect for increasing response delays. For example, the illusion effect for the memory-guided saccades with 153 ms presentation time (1000 ms response delay) did not differ significantly from the effect on reflexive saccades (0 ms response delay). Further, while response delay was equal for deferred saccades after 1000 ms MLI presentation and memory-guided saccades after 153 ms MLI presentation, the illusion effects differed (see Figure 2).

The differences between illusion effects in different conditions seem to be caused by the modulation of presentation time. Figure 2 shows that the effects were relatively large for conditions with 153 ms presentation time, but smaller for longer presentation times. Specifically, the illusion effects were significantly larger in the two reflexive conditions than in the two deferred saccade conditions (all $p < 0.01$). There was no significant difference in illusion effect between reflexive saccades and memory-guided saccades with 153 ms presentation time ($p > 0.05$), but memory-guided saccades with 659 ms presentation were less affected by the illusion than memory-guided saccades with 153 ms presentation time ($p > 0.05$). Thus, the illusion effect decreased as subjects gathered more information about the position of the target. Taken together, the results of

Saccade type	Experiment	Presentation time (ms)	Response delay (ms)	Latency (ms)
Reflexive	1B	12	0	229 ± 10
	1B	24	0	218 ± 11
	1B	47	0	218 ± 13
	1B	94	0	193 ± 12
	1B	153	0	180 ± 9
	1B	200	0	183 ± 8
	1A	153	0	198 ± 12
	1A - gap	153	0	176 ± 6
Deferred	1C	153	0	260 ± 21
	1C	306	153	206 ± 16
	1C	459	306	191 ± 13
	1A	659	506	251 ± 18
	1A	1153	1000	213 ± 12
Memory	1A	153	1000	205 ± 15
	1A	659	1506	199 ± 14

Table 1. Presentation time, response delay, and saccade latency (mean ± *SEM*) per condition.

Experiment 1A suggest that presentation time is the most important factor in determining the size of the illusion effect.

Experiment 1B and 1C

To study the influence of presentation time in more detail, we performed two additional experiments: a reflexive saccade experiment with presentation times between 12 and 200 ms (Experiment 1B), and a deferred saccade experiment with presentation times of 153, 306, and 459 ms (Experiment 1C). Table 1 provides an overview of the presentation times and response delays that were used in the different experiments, with the corresponding saccade latencies.

The illusion effects for the reflexive saccades of Experiment 1B are depicted by the blue filled circles in Figure 3. The ANOVA indicated no effect of presentation time on the illusion effect, $F(5, 40) = 0.69$, $p = 0.631$. The results of the deferred saccades of Experiment 1C are depicted by the three leftmost red squares in Figure 3. Here, the illusion effect was significantly influenced by presentation time, $F(2, 16) = 3.92$, $p = 0.041$, with larger illusion effects in the condition with 153 ms presentation time than in the condition with 459 ms presentation time ($p < 0.05$). The results of both additional experiments are discussed in relation to the results of Experiment 1A in the next section.

Overall results of Experiment 1

Figure 3 plots the results of all saccadic conditions of Experiment 1 as a function of presentation time. The data demonstrate a sudden decrease in illusion effect between 200 and 306 ms presentation time. We therefore fitted a step function to the data. The best fit (($R^2 = 0.93$)) was obviously obtained for a step that separates the effects for up to 200 ms presentation times (mean 10.9%) from the effects for presentation times of 306 ms and longer (mean 6.0%). We also fitted a simple linear function with presentation time as predictor, which yielded an R^2 of 0.69. The fit of the linear function was compared to the fit of the step function by calculating the Akaike information criterion (AIC) as: $AIC = N \ln(SSE/N) + 2p$, where N is the number of data points, SSE is the sum of squared errors, and p the number of fitted parameters (two for the linear function, three for the step function). The difference in AIC ($\Delta AIC = AIC_{linear} - AIC_{step}$) was 19.0, meaning that the step function explained the data much better

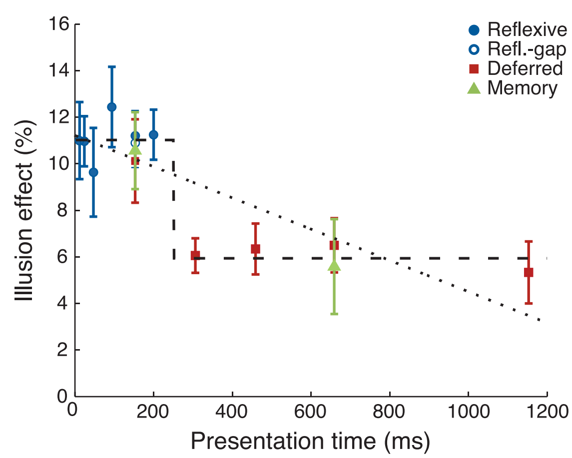

Figure 3. Mean percentage illusion effect on saccades as a function of MLI presentation time (Experiment 1A, 1B, and 1C). For reflexive saccades with a presentation time of 153 ms, the mean illusion effect of Experiment 1A and 1B is depicted. Error bars represent *SEM*; the dotted and dashed lines indicate the best fitting linear and step functions.

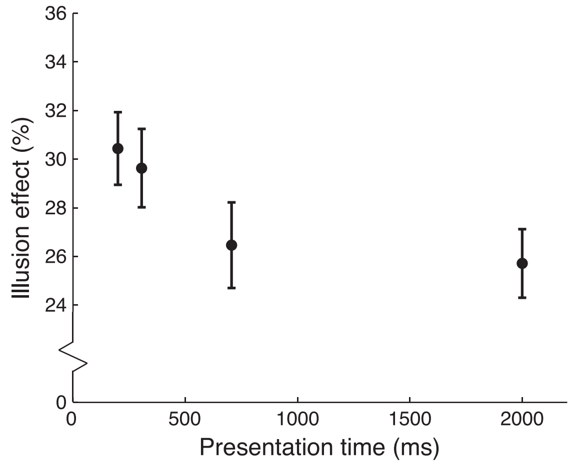

Figure 4. Mean percentage illusion effect on perceptual judgments as a function of MLI presentation time.

than the linear function. As a rule of thumb, ΔAIC > 10 indicates that there is essentially no support for the linear fit (Burnham & Anderson, 2004).

Experiment 2: Perceptual judgments

We investigated whether the dependency of the MLI effect on presentation time is specific to a saccade task, by performing a perceptual judgment task with various presentation times of the MLI. Figure 4 shows that although the overall effects on perceptual judgments were larger than those on saccades, the effect of the illusion on length judgments of the MLI was also influenced by its presentation time, $F(3, 54) = 13.94$, $p < 0.001$. Specifically, the illusion effects for the 200 and 306 ms presentation times differed significantly from the effects for the 706 and 2000 ms presentation times (all $p < 0.001$). Thus, if we would fit these results with a step function as we did for the saccadic results, the step would be slightly later in time for the perceptual judgments (between 306 and 706 ms presentation time) than for saccades.

Discussion

The present series of experiments investigated the influence of three temporal factors (latency, response delay, and presentation time) on the MLI effect using reflexive, deferred, and memory-guided saccades. We compared the results to the results of a perceptual judgment task. We aimed to test two hypotheses about visual processing for perception and action. The two visual systems hypothesis (Goodale & Milner, 1992; Milner & Goodale, 2006, 2008) states that memory-guided saccades and perceptual judgments are based on a ventral representation and are therefore highly susceptible to the illusion, whereas reflexive and deferred saccades are based on dorsal processing and are therefore largely immune to the illusion. As a contrasting hypothesis, it has been argued that there is a common visual representation that is used for both perception and action (e.g., Franz, 2001) which may become more accurate over time (van Zoest & Hunt, 2011). According to the latter hypothesis, the effect of the illusion will decrease as presentation time increases, independent of saccade type.

We found the largest illusion effects on reflexive saccades, which is in contrast with the two visual systems prediction. Interestingly, we found an equally large illusion effect on memory-guided saccades after a shortly (153 ms) presented MLI. Presentation time turned out to be the most important factor in determining the size of the MLI effect. Overall, presentation times up to 200 ms resulted in relatively large illusion effects on saccades, while presentation times of 300 ms and longer resulted in relatively small effects (Figure 3). Remarkably, the illusion effects on perceptual judgments showed a similar time course (Figure 4), although the decrease in illusion effect occurred for slightly longer durations. Thus, for both perceptual judgments and saccades, the effect of the illusion decreased with longer presentation times, but not in a linear fashion. Our results are in accordance with the hypothesis that our visual representation becomes more accurate over time.

In contrast with the results of our study, de Grave and Bruno (2010) did not find a significant difference in illusion effect on saccades for short (80 ms; effect 20.7 $\pm$ 1.7%) and long (300 ms, effect 18.5 $\pm$ 1.4%) presentation times. For the interpretation of this result, it is important to notice that the average latency in their experiment was 183 $\pm$ 4 ms for the trials with 300 ms presentation time, which effectively reduces presentation time to below 200 ms. For this effective presentation time, our step function in Figure 3 predicts the same illusion effect as for 80 ms presentation time. So the lack of effect of presentation time reported by de Grave and Bruno is in line with our findings.

Although presentation time turned out to be the most important factor, the influence of latency and response delay were also examined in our experiment. For reflexive saccades, latency reflects the processing time of the illusion, whereas for deferred and memory-guided saccades, processing time is mainly determined by the response delay. Previous studies have shown an influence of latency, with larger effects of the Müller-Lyer and Judd illusion (i.e., the directional version of the MLI) on reflexive saccades with shorter latencies (de Grave & Bruno, 2010; van Zoest & Hunt, 2011). Although we found a similar effect of latency on the illusion effects on reflexive saccades (with and without gap) in runs with constant presentation time, latency or response delay could not explain the effects for the deferred and memory-guided saccades.

It has been suggested that the MLI affects reflexive saccades less than voluntary saccades (DiGirolamo et al., 2008; McCarley & Grant, 2008; McCarley et al., 2003; but see Knox & Bruno, 2007). Our results do not fit with this idea: Reflexive and memory-guided saccades were not affected differently by the illusion when presentation time was equal. In studies that did find smaller effects on reflexive saccades (DiGirolamo et al., 2008; McCarley & Grant, 2008; McCarley et al., 2003), subjects performed deferred saccades in response to the appearance of a target dot at the vertex of the MLI ("reflexive") or in response to an auditory go signal, without a target dot ("voluntary"). Although McCarley and Grant (2008) took the larger illusion effects on voluntary than on reflexive saccades (15%–19% and 6%–7%, respectively) as evidence for the two visual systems hypothesis, there are two counterarguments. First, it can be argued that their reflexive condition was not truly reflexive, as subjects were provided with a preview of the illusion instead of responding to its appearance. Second, the presence of a target dot in the reflexive condition (that was absent in the voluntary condition) may have provided the subjects with more information about the veridical target position, resulting in smaller illusion effects. Since presentation time was equal in the two conditions, it needs to be tested whether the difference in illusion effect was caused by the absence or presence of a dot or whether other factors were (also) playing a role.

Knox and Bruno (2007) reported larger effects on reflexive than on voluntary saccades. This difference in effect could in fact be the result of different presentation times. An illusion effect of 22 ± 8% was reported for reflexive-gap saccades, where the MLI was presented for 200 ms, and an effect of 11 ± 11% for memory-guided saccades ("voluntary"), where the MLI was presented for 1 s. In accordance to our results, it seems that the longer presentation time of the MLI for memory-guided saccades reduced the illusion effect.

Although in the present experiment the illusion effects on saccades (Figure 3) and perceptual judgments (Figure 4) showed a similar time course, there are two substantial differences. First, the sudden decrease in illusion effects took place at a slightly longer presentation time for perceptual judgments than for saccades. Second, the overall illusion effects were larger on perception than on saccades. Due to methodological differences between the tasks, the illusion effects cannot be compared directly. Since it is not possible to match saccadic and perceptual tasks without making several assumptions that are hard to justify, we concentrated on comparing the time courses of the effects. Larger illusion effects on saccades than on perceptual judgments appeared in several other studies on the MLI (McCarley & Grant, 2008; van Zoest & Hunt, 2011). These differences between the saccadic and perceptual results argue against the direct use of the same representation for both tasks. A possible explanation is that visual information for perception and action is processed via the same route, but that the response does not result from the direct use of the same representation (Smeets, Brenner, de Grave, & Cuijpers, 2002). On the basis of our results, we cannot exclude the possibility that information for perception and action is processed independently. However, neuroimaging studies suggest that both ventral and dorsal areas are involved in the perception of the MLI, with reciprocal connections between the two streams (Plewan, Weidner, Eickhoff, & Fink, 2012; Weidner, Boers, Mathiak, Dammers, & Fink, 2010). Based on these findings and on our finding that all saccade types were affected by the illusion and its presentation time in the same way, we can conclude that the distinction made by the two visual systems hypothesis is very unlikely.

What is the mechanism behind the sudden decrease in illusion effect when presentation time increases? Apparently, at first sight of the illusion, contextual information contributes more strongly to the representation of the target, whereas later in time the representation becomes more veridical. The fact that we found large effects of context with short presentation times clearly conflicts with the current view that context independent (egocentric) representations are created on a moment-to-moment basis and are transient, whereas representations that take contextual information into account (i.e., allocentric representations) build up over time and serve spatial memory (Burgess, 2006; Goodale et al., 2004; Tatler & Land, 2011).

We might explain our results in terms of feedforward and recurrent processing of visual information (Lamme & Roelfsema, 2000). The onset of the stimulus would activate the successive hierarchical levels of the visual cortex through feedforward connections, reaching higher levels within the ventral and dorsal streams within approximately 100 ms (Lamme & Roelfsema, 2000). Here, high-level cortical neurons build an initial representation of the gist of the scene. The feedforward sweep of information is followed by recurrent processing, where information from high-level areas is fed back to primary visual areas. The first feedforward-recurrent loop of processing might not have reached higher-level areas within 200 ms, resulting in large effects of the illusion. In order to explain our data with this theory, we would have to assume two things. The first assumption would be that the representation cannot become more veridical when the stimulus is no longer present, despite the fact that there may still be time for processing, for example when performing memory-guided saccades. This assumption implies that when there is no visual input reaching low-level areas, there is no effect of feedback from higher-level areas. Second, the visual representation of the target does not improve any further after a certain presentation time. In the end, the context cannot completely be ignored, meaning that the representation does not become truly veridical. Future research is needed to investigate where and how contextual information is integrated in our spatial representation.

Conclusions

In conclusion, presentation time of the MLI is an important factor in determining the size of the illusion effect on saccade amplitude and perceptual judgments. With longer presentation of the illusion, our spatial representation becomes more accurate, resulting in a sudden decrease of the illusion effect. The finding that the effect of the illusion is independent of saccade type provides further evidence against the two visual systems hypothesis. Our results may be explained by means of a feedforward and recurrent model of visual information processing, in which after the initial feedforward processing, information from higher cortical areas is fed back to primary visual areas as long as these areas receive visual input. This study supports the view that our visual representation is dynamic and becomes more accurate when we look at an object for a longer time.

Keywords: vision, gaze, display duration, dorsal stream, ventral stream

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References

Aglioti, S., DeSouza, J. F., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology, 5*(6), 679–685. [PubMed] [Article]

Binsted, G., & Elliott, D. (1999). The Muller-Lyer illusion as a perturbation to the saccadic system. *Human Movement Science, 18*(1), 103–117. doi: 10.1016/S0167-9457(98)00038-4. [Article]

Brenner, E., & Smeets, J. B. J. (1996). Size illusion influences how we lift but not how we grasp an object. *Experimental Brain Research, 111*(3), 473–476. [PubMed]

Bridgeman, B., Peery, S., & Anand, S. (1997). Interaction of cognitive and sensorimotor maps of visual space. *Perception & Psychophysics, 59*(3), 456–469. [PubMed]

Bruno, N., Knox, P. C., & de Grave, D. D. J. (2010). A metanalysis of the effect of the Muller-Lyer illusion on saccadic eye movements: No general support for a dissociation of perception and oculomotor action. *Vision Research, 50*(24), 2671–2682. doi:10.1016/j.visres.2010.09.016. [PubMed] [Article]

Burgess, N. (2006). Spatial memory: How egocentric and allocentric combine. *Trends in Cognitive Sciences, 10*(12), 551–557. doi:10.1016/j.tics.2006.10.005. [PubMed] [Article]

Burnham, K. P., & Anderson, D. R. (2004). Multimodel inference—Understanding AIC and BIC in model selection. *Sociological Methods & Research, 33*(2), 261–304. doi: 10.1177/0049124104268644. [Article]

de Grave, D. D. J., & Bruno, N. (2010). The effect of the Muller-Lyer illusion on saccades is modulated by spatial predictability and saccadic latency. *Experimental Brain Research, 203*(4), 671–679. doi: 10.1007/s00221-010-2275-6. [PubMed]

de Grave, D. D. J., Smeets, J. B. J., & Brenner, E. (2006). Why are saccades influenced by the Brentano illusion? *Experimental Brain Research, 175*(1), 177–182. doi:10.1007/s00221-006-0536-1. [PubMed] [Article]

DiGirolamo, G. J., McCarley, J. S., Kramer, A. F., & Griffin, H. J. (2008). Voluntary and reflexive eye movements to illusory lengths. *Visual Cognition, 16*(1), 68–89. doi:10.1080/13506280701339160. [Article]

Elliott, D., & Lee, T. D. (1995). The role of target information on manual-aiming bias. *Psychological Research, 58*(1), 2–9.

Fischer, B., & Ramsperger, E. (1984). Human express saccades: Extremely short reaction times of goal directed eye movements. *Experimental Brain Research, 57*(1), 191–195. [PubMed]

Franz, V. H. (2001). Action does not resist visual illusions. *Trends in Cognitive Sciences, 5*(11), 457–459. [PubMed] [Article]

Franz, V. H., Gegenfurtner, K. R., Bulthoff, H. H., & Fahle, M. (2000). Grasping visual illusions: No evidence for a dissociation between perception and action. *Psychological Science, 11*(1), 20–25. [PubMed] [Article]

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences, 15*(1), 20–25. [PubMed] [Article]

Goodale, M. A., Westwood, D. A., & Milner, A. D. (2004). Two distinct modes of control for object-directed action. *Progress in Brain Research, 144,* 131–144. [PubMed]

Knox, P. C., & Bruno, N. (2007). When does action resist visual illusion? The effect of Muller-Lyer stimuli on reflexive and voluntary saccades. *Experimental Brain Research, 181*(2), 277–287. doi:10.1007/s00221-007-0927-y. [PubMed] [Article]

Lamme, V. A., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences, 23*(11), 571–579. [PubMed] [Article]

McCarley, J. S., & Grant, C. (2008). State-trace analysis of the effects of a visual illusion on saccade amplitudes and perceptual judgments. *Psychonomic Bulletin & Review, 15*(5), 1008–1014. doi:10.3758/PBR.15.5.1008. [PubMed] [Article]

McCarley, J. S., Kramer, A. F., & DiGirolamo, G. J. (2003). Differential effects of the Muller-Lyer illusion on reflexive and voluntary saccades. *Journal of Vision, 3*(11):9, 751–760, http://www.journalofvision.org/content/3/11/9, doi: 10:1167/3.11.9. [PubMed] [Article]

Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action* (2nd ed.). New York: Oxford University Press.

Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia, 46*(3), 774–785. doi:10.1016/j.neuropsychologia.2007.10.005. [PubMed] [Article]

Munoz, D. P. (2002). Commentary: Saccadic eye movements: overview of neural circuitry. *Progress in Brain Research, 140,* 89–96. doi:10.1016/S0079-6123(02)40044-1. [PubMed]

Plewan, T., Weidner, R., Eickhoff, S. B., & Fink, G. R. (2012). Ventral and dorsal stream interactions during the perception of the Muller-Lyer illusion: Evidence derived from fMRI and dynamic causal modeling. *Journal of Cognitive Neuroscience, 24*(10), 2015–2029, doi:10.1162/jocn_a_00258. [PubMed] [Article]

Smeets, J. B. J., & Brenner, E. (1995). Perception and action are based on the same visual information: Distinction between position and velocity. *Journal of Experimental Psychology: Human Perception and Performance, 21*(1), 19–31. [PubMed] [Article]

Smeets, J. B. J., Brenner, E., de Grave, D. D. J., & Cuijpers, R. H. (2002). Illusions in action: Consequences of inconsistent processing of spatial attributes. *Experimental Brain Research, 147*(2), 135–144. doi:10.1007/s00221-002-1185-7. [PubMed] [Article]

Tatler, B. W., & Land, M. F. (2011). Vision and the representation of the surroundings in spatial memory. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 366*(1564), 596–610. doi:10.1098/rstb.2010.0188. [PubMed]

van Zoest, W., & Hunt, A. R. (2011). Saccadic eye movements and perceptual judgments reveal a shared visual representation that is increasingly accurate over time. *Vision Research, 51*(1), 111–119. doi:10.1016/j.visres.2010.10.013. [PubMed] [Article]

Weidner, R., Boers, F., Mathiak, K., Dammers, J., & Fink, G. R. (2010). The temporal dynamics of the Muller-Lyer illusion. *Cerebral Cortex, 20*(7), 1586–1595. doi:10.1093/cercor/bhp217. [PubMed] [Article]

Westwood, D. A., & Goodale, M. A. (2003). Perceptual illusion and the real-time control of action. *Spatial Vision, 16*(3-4), 243–254. [PubMed]

Westwood, D. A., Heath, M., & Roy, E. A. (2000). The effect of a pictorial illusion on closed-loop and open-loop prehension. *Experimental Brain Research, 134*(4), 456–463. [PubMed] [Article]

Wong, E., & Mack, A. (1981). Saccadic programming and perceived location. *Acta Psychologica, 48*(1-3), 123–131. [PubMed] [Article]