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The Müller-Lyer illusion affects visuomotor updating in the dorsal visual stream

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ABSTRACT

To guide our actions, the brain has developed mechanisms to code target locations in egocentric coordinates (i.e., with respect to the observer), and to update these when the observer moves. The latter mechanism, called visuomotor updating, is implemented in the dorsal visual stream of the brain. In contrast, the ventral visual stream is assumed to transform target locations into an allocentric reference frame that is highly sensitive to visual contextual illusions. Here, we tested the effect of the Müller-Lyer illusion on visuomotor updating in a double-step saccade task. Using the same paradigm in a 3T fMRI scanner, we investigated the effect of the illusion on the neural correlate of the updating process. Participants briefly viewed the Brentano version of the Müller-Lyer illusion with a target at its middle vertex, while fixating at one of the two endpoints of the illusion. Shortly after the disappearance of the stimulus, the eyes' fixation point moved to a position outside the illusion. After a delay, participants made a saccade to the remembered position of the target. The landing position of this saccade was systematically displaced in a manner congruent with the perceptual illusion, showing that visuomotor updating is affected by the illusion. fMRI results showed that the BOLD response in the occipito-parietal cortex (area V7) and the intraparietal sulcus related to planning of the saccade to the updated target was also modulated by the configuration of the illusion. This suggests that the dorsal visual stream represents perceived rather than physical locations of remembered saccade targets.

1. Introduction

To guide our actions in the environment, our brain needs to specify relevant locations relative to our body, that is, in an egocentric reference frame. The continuous movement of our eyes and body complicates egocentric coding, but the brain has developed mechanisms to update target locations when we move, a process called visuomotor updating (for reviews see Klier and Angelaki, 2008; Medendorp, 2011). The coding and updating of (remembered) target locations is implemented in the dorsal visual stream, which is a series of anatomically connected areas from the primary visual cortex to the posterior parietal cortex (Colby and Goldberg, 1999; Goodale and Milner, 1992; Medendorp et al., 2003; Mishkin et al., 1983). The ventral visual stream, which links the primary visual cortex to the inferior temporal cortex, transforms spatial arrangements of objects into an allocentric representation that is viewer-invariant and thus remains constant during self-motion (Goodale and Milner, 1992; Honda et al., 1998; Milner and Goodale, 2008; Mishkin et al., 1983).

The extent to which these two visual streams function independently has been hotly debated (for reviews see e.g., Schenk et al., 2011; Westwood and Goodale, 2011). Behavioural studies involving visual contextual illusions have been used to address this issue. Because allocentric representations take context into account, perception and memory-guided actions, which are both mediated by the ventral stream, can be assumed to be highly sensitive to visual contextual illusions, such as the Ebbinghaus or the Müller-Lyer illusion (Goodale and Milner, 1992; Milner and Goodale, 2008). For the visual control of goal-directed actions, mediated by the dorsal stream, locations need to be specified relative to the observer and irrespective of context. If visual context is processed exclusively in the ventral stream, then visuomotor control and updating, which are dorsal stream functions, should

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be immune to contextual illusions.

While several studies support the hypothesis that illusions do not affect the visual control of action, but only affect perception and memory-guided actions (e.g., Aglioti et al., 1995; Bridgeman et al., 1997; Westwood et al., 2000), other studies have found evidence against this hypothesis (e.g., Brenner and Smeets, 1996; Franz et al., 2009; Taghizadeh and Gail, 2014). For example, the Müller-Lyer illusion not only changes the perceived length of a line by its inward or outward pointing arrowheads, but can also change the amplitude of pointing movements and saccadic eye movements along its shaft (e.g., Binsted and Elliott, 1999; Post and Welch, 1996)[1]. The presence of an illusion effect in the visual control of action suggests that either both visual streams play a role in visuomotor control or that both streams, thus also the dorsal stream, are sensitive to visual context. In this study, we used the Müller-Lyer illusion to examine how contextual cues affect visuomotor updating and how they affect the neural correlate of the updating process in the dorsal visual stream.

The first aim is to examine the role of contextual cues in visuomotor updating. We designed a double-step saccade paradigm that required updating of a target within the context of the Brentano version of the Müller-Lyer illusion. The task is based on the observation that the Brentano illusion induces errors in the amplitude of single saccades along the illusion, but not in saccades that start from a side position (De Grave et al., 2006). The decisive outcome of our paradigm are the errors that occur when participants briefly view the illusion with a target at its middle vertex, but only saccade to this target after an intervening saccade to a side position. If the target that is updated after the intervening saccade is unaffected by the illusion, we would expect the saccade to this target to be correct as if it were a single saccade from a side position. In contrast, if the updated target were affected by the illusion, the endpoint of the second saccade would show an error as if the saccade were directed along the shaft of the illusion.

The second aim of this study is to investigate the effect of contextual cues on the neural representation of the target in the dorsal visual stream, using the same task in an fMRI scanner. To this end, we exploited the finding that in memory-guided saccade tasks, areas in the dorsal stream show activation contralateral to the visual target in a gaze-centred reference frame (e.g., Schluppeck et al., 2006; Sereno et al., 2001). Medendorp et al. (2003) further showed that the activation swaps across hemispheres if the remembered target position reverses visual hemifield relative to gaze. We hypothesised that if the dorsal stream represents the correct physical position of the target, the neural activation in the dorsal stream should be independent of the illusion. In contrast, if the target representation is affected by the context of the illusion, we expect that in each hemisphere, the remembered target is more strongly represented when its position is biased into the contralateral visual field than when its position is biased into the ipsilateral visual field.

2. Materials and methods

2.1. Participants

2.1.1. Behavioural experiment

Eleven volunteers took part in the behavioural version of the double-step saccade experiment at the VU University Amsterdam. All participants had normal or corrected-to-normal vision. Seven participants successfully performed the experiment (aged 23–31 years, four men). Four participants were excluded from the analysis because they performed less than 50% of the trials correctly. This was due to difficulty keeping stable fixation, or to incorrect execution of the second saccade (see Section 2.5 for exclusion criteria). Written informed consent was provided. The study was part of a research programme that was approved by the local ethics committee (Faculty of Human Movement Sciences, VU University Amsterdam, The Netherlands).

2.1.2. fMRI experiment

Twenty-seven participants completed the same double-step saccade experiment in a 3T fMRI scanner at the Radboud University Nijmegen after performing a training session outside the scanner. All participants had normal or corrected-to-normal vision and no known neurological deficits. Eye movements were recorded during scanning. Five participants were excluded from the analysis because of excessive head movement (one participant; >3 mm within a run), sleepiness (two participants; eyes open in only 73 and 80% of time), difficulty keeping fixation (one participant; $<60\%$ correct trials), or insensitivity to the illusion (one participant). As a result, 22 participants were included in the analysis (aged 18–31 years, nine men). Two of them had also taken part in the behavioural version of the experiment. Participants gave their written informed consent in accordance with the local ethics committee (CMO Committee on Research Involving Human Participants, region Arnhem-Nijmegen, The Netherlands). Participants were offered course credit or financial compensation for their participation.

2.2. Setup

In the behavioural experiment and the fMRI training session, participants were seated in a dimly lit room, with their head stabilized by a chin rest positioned ~ 52 cm from a computer screen (36×27 cm^2, 1024×768 pixels, 85 Hz). At this distance, 1.0 cm on the screen corresponds to approximately 1.1° of visual angle. Visual stimuli were controlled using the Psychophysics toolbox (Brainard, 1997) for Matlab (Mathworks Ltd., USA). 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 accuracy within 0.5°.

In the fMRI experiment, participants lay supine in the scanner, with their head stabilized inside a head coil using foam padding. The legs, and for some participants also the neck and/or elbows, were supported by cushions to make them feel more comfortable and to reduce movement. Stimuli were projected onto a screen that was viewed via a mirror above the participant's head. Eye movements of the left eye were recorded at 1000 Hz via a second mirror above the participant's head, using a long range Eyelink 1000 eye tracker (SR Research Ltd., Canada) standing on an arch over the participant's lower legs. The eye was illuminated by an infra-red light mounted on a flexible branch next to the head.

MRI images were acquired using a Siemens Trio 3T scanner (Siemens Tim TRIO, Germany) with a 32-channel phased array head coil. A T2*-weighted multi-echo sequence of four echoes (echo times [TE] 9, 19.3, 29.6 and 39.8 ms, repetition time [TR] 2320 ms, flip angle [FA] 90°) was used. The sequence encompassed 38 slices, covering the whole brain (in-plane voxel size 3.3×3.3 mm^2, slice thickness 3.0 mm with 10% gap, field of view [FOV] 211×211 mm^2). We acquired 150 volumes per run. The first run started with 30 extra volumes in which no task was performed to estimate the T2* value per voxel for combining the multiple echoes. High-resolution anatomical images were acquired using a T1-weighted MP-RAGE GRAPPA sequence of 192 volumes (TE 3.0 ms, TR 2300 ms, FA 8°, $1.0 \times 1.0 \times 1.0$ mm^3 voxels, FOV 256×256 mm^2).

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[1] Although this illusion can also influence the hand opening of grasping movements (e.g., Daprati and Gentilucci, 1997), it has been argued that hand opening is not an accurate measure of how size is processed for grasping (e.g., Biegstraaten et al., 2007; Franz et al., 2009; Haffenden et al., 2001).

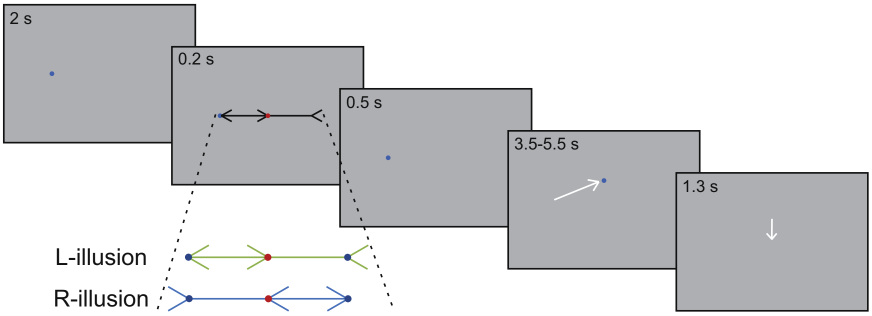

Fig. 1. Illustration of the double-step saccade task. Participants were instructed to fixate the blue dot on the left or right of the screen, and remember the position of the red target dot within the Brentano illusion while keeping fixation. The displacement of the fixation dot triggered a visually guided saccade to above or below the target (white arrow in fourth frame). After a delay of a few seconds, the fixation dot disappeared and participants made a second saccade towards the remembered position of the target (white arrow in last frame). Note that the target was always on the same vertical line as the second fixation position. The timing illustrated here corresponds to the fMRI experiment; the timing in the behavioural experiment was slightly different (see Section 2.4). Inset: The two configurations of the Brentano illusion. In the top configuration, depicted in green, the left part of the horizontal shaft will be perceived shorter (L-illusion) while in the bottom configuration, depicted in blue, the right part will be perceived shorter (R-illusion). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.3. Stimuli

The stimuli and timing slightly differed between the two experiments, because small adaptations were made after the behavioural experiment to optimise the task for the fMRI experiment. Below, we describe the stimuli for the behavioural experiment and mention the aspects that differed in the fMRI experiment. The stimuli consisted of a blue fixation dot and a black horizontal Brentano illusion with a red (fMRI: white) target dot at its middle vertex (see Fig. 1). Both dots had a diameter of 0.4° of visual angle. The Brentano illusion had a shaft length of two times 9.9° (fMRI: two times 9.0°), in ~0.1° thick black lines. The inward or outward pointing fins were 3.0° (fMRI: 2.7°) each, and were connected to the ends of the two shafts with an angle of 30° or 150°. The initial fixation position was 9.9° (fMRI: 9.0°) to the left or right of the screen centre. The Brentano illusion was presented to the right or left of the fixation dot so that the middle vertex with the target was always presented at the screen centre. The second fixation position was 4.4° (fMRI: 4.5°) above or below the middle vertex of the Brentano illusion.

There were thus eight different stimulus configurations: the first fixation position could be at the left or right of the screen, the second fixation position could be above or below the target, and the configuration of the illusion would make the left or the right part of the horizontal shaft be perceived shorter (*L-illusion* and *R-illusion*, see Fig. 1). These eight stimulus configurations were presented in random order in the behavioural experiment, and in pseudo-random order in the fMRI experiment, such that one repetition of all eight configurations was presented before the next repetition started and two identical configurations could never appear in sequence. In both experiments, the stimuli were presented on a noisy background (i.e., each pixel had a grey value from a Gaussian distribution with mean 0.5 and standard deviation 0.05, with zero being black and one being white). A structured background was chosen to improve the accuracy of the memory-guided saccades (Gnadt et al., 1991). The background changed after each presentation of the illusion and at the start of each new trial in order to disrupt iconic visual memory (Curtis et al., 2004).

2.4. Procedure

2.4.1. Behavioural experiment

Fig. 1 illustrates the task. Each trial started with a fixation dot that was presented to the left or right of the screen centre for 1 s. Then, the Brentano illusion with the fixation dot at its left or right vertex and the target dot at its middle vertex was presented for 0.2 s. Participants were instructed to keep fixation and to remember the position of the target. After the illusion had disappeared and the background had changed, participants fixated for another 0.5 s. Next, the fixation dot moved to a position straight above or below the position of the previously presented target. After a delay period of 2, 3, 4, or 5 s, the fixation dot disappeared. Participants were instructed to follow the fixation dot when it moved to its new position, and to make a second saccade to the remembered position of the target when the fixation dot disappeared. After 1.8 s, a new trial started with a new background and a new fixation dot. Thus, total trial duration was 5.5 to 8.5 s.

After 16 practise trials, participants performed two runs of 10 repetitions of each stimulus configuration ($10 \times 8 = 80$ trials per run), with a short break in between the runs. Twenty percent (32 trials) randomly presented catch trials were added in which the second fixation dot had a horizontal offset of 1.7° with respect to the target. This was done to prevent participants from noticing that the second fixation and the target were always positioned straight above each other. A beep tone sounded if the participant made a saccade towards the Brentano illusion before the fixation dot moved to indicate that the participant had made an error. These trials were repeated in random order at the end of the run.

2.4.2. fMRI experiment

We used a fast event-related design, as shown in Fig. 1. Each trial started with a fixation dot that was presented to the left or right of the screen centre for 2 s. Then, the Brentano illusion with the target dot at its middle vertex was presented for 0.2 s, while the fixation dot remained visible. After the illusion had disappeared, participants fixated for another 0.5 s. Next, the fixation dot moved to a position above or below the position of the previously presented target. After a random time period of 3.5–5.5 s (uniform distribution), the fixation dot disappeared. Participants were instructed to follow the fixation dot when it moved to its new position, and make a second saccade to the remembered position of the target when the fixation dot disappeared. After 1.3 s, a new trial started. Thus, total trial duration was 7.5–9.5 s.

Participants performed a training session outside the scanner in the week before the fMRI session. During this session, two runs of five repetitions of each stimulus configuration were performed ($5 \times 8 = 40$ trials per run). The task was identical to the task performed in the fMRI scanner, except that 25% (20 trials) catch trials were added in which the second fixation dot had a horizontal offset of 0.9° with respect to the target. In addition, an error tone sounded if the participant made a saccade towards the Brentano illusion before the fixation dot moved.

In the fMRI scanner, participants performed at least five runs of five repetitions of each stimulus configuration ($5 \times 8 = 40$ trials per run) without feedback. During breaks in between runs, image acquisition was halted and the experimenter spoke with the participant. An anatomical image was acquired after most or all functional runs. The participant determined the duration of breaks and the timing of the anatomical scan. During debriefing after the experiment, none of the participants reported having noticed that the target and the second fixation were always vertically aligned.

2.5. Data-analysis

2.5.1. Behavioural experiment

Horizontal and vertical eye velocities were calculated from the eye positions given by the eye tracker and then upsampled to 1000 Hz by linear interpolation. Saccades were defined using a threshold of 30°/s for the resultant velocity (i.e., the square root of the sum of squares of the horizontal and vertical velocity), looking backward and forward in time from a minimum peak velocity of 100°/s. Saccade onset was defined as the last sample before eye velocity crossed the 30°/s threshold, and offset was defined as the first sample of a period of 10 ms below the threshold. Saccades with an amplitude of 2° or more were analysed. Eye positions of each trial were defined relative to the mean eye position during the first 20 ms of the presentation of the Brentano illusion (i.e., the end of the first fixation interval). Trials were discarded if a blink occurred during the presentation of the illusion, if the first saccade started before the displacement of the fixation dot, or if the eye position during the delay following the first saccade did not stay within 3° of the fixation dot. Trials were also discarded if the horizontal endpoint of the second saccade was not within 5° (50% of shaft length) of the target, if the vertical endpoint was not within 3° of the target, or if the saccade duration was longer than 100 ms.

To investigate the effect of the Brentano illusion on visuomotor updating, we examined the second saccade of each trial. The amplitude of the second saccade was defined as the difference between the eye positions at saccade onset and offset. Note that at the onset of this saccade the eye was always directed at the visual fixation dot that remained visible until the end of the delay. An effect of the illusion on the second saccade would be expressed by a non-zero horizontal amplitude, despite the physical target being on the same vertical line as the second fixation position. We tested this using one-sample *t*-tests. In addition, we tested for differences in absolute horizontal and vertical amplitude between conditions, by performing a repeated measures ANOVA with the within-subjects factors ‘vertical direction’ (down or up) and ‘illusion configuration’ (L-illusion and R-illusion). Note that the first fixation position (left or right) was not considered since this is only relevant for the first saccade.

2.5.2. fMRI experiment

2.5.2.1. Eye movement data. Eye movements were recorded in all participants except one, due to a technical problem. For the remaining 21 participants, horizontal and vertical eye velocities were calculated from the eye positions given by the eye tracker. Saccades were detected if their resultant velocity (i.e., the square root of the sum of squares of the horizontal and vertical velocity) was higher than 50°/s for minimal 10 consecutive ms, and their amplitude was larger than 2°. Saccade onset and offset were defined as the last sample of a 10 ms interval where eye velocity was below the threshold. In order to keep as many trials as possible in the fMRI analysis and because the gaze data were relatively noisy, the exclusion criteria were slightly more tolerant than those of the behavioural experiment. Trials were included based on the delay and the second saccade. If the participant made one or more saccades larger than 2° during the delay, the delay was included in the error regressor of the general linear model (see *General Linear Model and Regions of Interest*) and this trial was discarded from the behavioural analysis. Trials were also discarded from the behavioural analysis if the vertical amplitude of the second saccade was smaller than 1.5° or if its angle with respect to the vertical was larger than 45°. Finally, the same statistical analyses were performed as in the behavioural experiment.

2.5.2.2. fMRI data preprocessing. MRI data preprocessing and statistical analyses were carried out using the SPM8 Toolbox (Statistical Parametric Mapping; http://www.fil.ion.ucl.ac.uk/spm/software/spm8/) and Matlab (Mathworks Ltd., USA). First, the functional images were spatially realigned to the first echo of the first volume. Next, the multi-echo data were combined using the PAID algorithm (Poser et al., 2006). Slices were temporally aligned to the centre (19th) slice to accommodate for slice-timing differences. The anatomical image was coregistered to the mean functional image. The anatomical and functional images were normalised to MNI space (Montreal Neurological Institute) by unified segmentation. Spatial smoothing was applied using a Gaussian kernel with a full-width half-maximum of 6 mm.

2.5.2.3. General linear model and regions of interest. BOLD data were analysed by means of a general linear model (GLM). For each participant we defined eight regressors of interest, each convolved with a double-gamma hemodynamic response function (Friston et al., 1998). Two impulse regressors captured the visual presentation of the illusion to the left and right of the first fixation position, one impulse regressor captured the visual and movement-related activation of the displacement of the fixation dot and execution of the first saccade, and one impulse regressor captured the movement-related activation of the second saccade. Four square-wave regressors were included for the planning of the second saccade to either configuration of the illusion and from above or below the target. These square waves spanned the delay phase of each trial from 0.5 s after the displacement of the fixation dot (i.e., approximately the end of the first saccade) until the disappearance of the fixation dot (i.e., the cue to make the second saccade).

Fourteen regressors of non-interest were added to the model. One impulse regressor captured the task-unrelated activation at the start of each run. Using the eye movement data obtained during scanning, an error regressor was created for delays in which the participant broke fixation. Finally, the six movement parameters for head translation and rotation and their first derivatives were included in the model.

Using the regressor that captured the execution of the second saccade, we defined bilateral saccade-related regions of interest (ROI) in the occipito-parietal, posterior parietal and frontal cortex (see Section 3 for details). To investigate the neural correlate of saccade planning to the updated target, we extracted for each ROI the mean β weights across voxels, for each of the four regressors on the delay phase. These β weights reflect the amplitude of the BOLD response. The contrast of interest was computed for each unilateral ROI as the sum of the two regressors capturing saccade planning to an updated target presented within the contra-illusion (i.e., the L-illusion for the right hemisphere and the R-illusion for the left hemisphere) minus the sum of the two regressors capturing saccade planning to an updated target within the ipsi-illusion (i.e., the R-illusion for the right hemisphere and the L-illusion for the left hemisphere). Next, to assess whether the BOLD response during the delay was lateralized as a result of the illusion, we computed a contralateral bias C that scales the contrast to the sum of the BOLD response (e.g., Schluppeck et al., 2006; Van Pelt et al., 2010) as

$$C = \frac{\beta_{\mathrm{contra-illusion}} - \beta_{\mathrm{ipsi-illusion}}}{|\beta_{\mathrm{contra-illusion}}| + |\beta_{\mathrm{ipsi-illusion}}|}$$

with $\beta_{\mathrm{contra\text{-}illusion}}$ the β weight during saccade planning toward the contra-illusion, and with $\beta_{\mathrm{ipsi\text{-}illusion}}$ the β weight during saccade planning toward the ipsi-illusion. The contralateral bias can range between −1 and 1, with negative values indicating a higher BOLD amplitude for ipsilateral targets, 0 indicating no difference between ipsilateral and contralateral targets, and positive values indicating a higher BOLD amplitude for contralateral targets.

To examine our prediction that the BOLD response has a higher amplitude when the position of the updated target is biased to the contralateral visual field as a result of the illusion, we tested whether the contralateral biases, averaged across hemispheres, were different from zero. This was done using one-sample Wilcoxon signed rank tests. We used a nonparametric test because the biases were not normally distributed. We did not correct for multiple comparisons because of the hypothesis-driven nature of this analysis. We also tested the relationship between the size of the contralateral bias and the size of the saccadic illusion effect, using Spearman's correlation coefficient.

3. Results

3.1. Behavioural experiment

On average, 67% (range: 53–84%) of the double-step saccade trials were considered correct and included in the analysis. Trials were removed when we failed to detect a saccade (4%), when the first saccade started before the displacement of the fixation dot (7%), when eye position did not stay within 3° of the fixation dot during the delay following the first saccade (13%), when the vertical endpoint of the second saccade was not within 3° of the target (4%), and/or because one of the remaining criteria (see Methods) was not fulfilled (5%). Fig. 2A depicts the trajectories of correct saccades of an example participant. To determine whether the updated target is affected by the context of the Brentano illusion, we examined the characteristics of the second saccade that was directed to the remembered position of this target. The physical position of the target was always straight above or below the second fixation position, thus entailing a purely vertical saccade if the updated target were not affected by the illusion. However, our results show a clear illusion effect, expressed as a non-zero horizontal saccade amplitude in each condition (downward to L-illusion −1.7 ± 0.3°, $t(6)=6.6$, $p=0.001$; upward to L-illusion −1.4 ± 0.3°, $t(6)=4.2$, $p=0.006$; downward to R-illusion 0.8 ± 0.2°, $t(6)=4.0$, $p=0.007$; upward to R-illusion 1.0 ± 0.2°, $t(6)=4.6$, $p=0.004$).

Concerning differences between conditions, the ANOVA revealed that the absolute horizontal amplitude of the second saccade was slightly larger for the L-illusion than for the R-illusion ($F(1,6)=6.173$, $p=0.048$), while there was no effect of vertical direction (down or up; $F(1,6)=0.021$, $p=0.890$). Furthermore, the absolute vertical amplitude of the second saccade was not affected by illusion configuration ($F(1,6)=0.171$, $p=0.693$) or vertical direction ($F(1,6)=0.001$, $p=0.975$; grand mean 4.6 ± 0.2). Fig. 2B shows the average horizontal amplitude of the second saccade for the L-illusion and the R-illusion, averaged over the vertical direction of the second saccade. Expressed as a percentage of a single shaft length of the illusion, the mean effect approximates 15% for the L-illusion and 9% for the R-illusion.

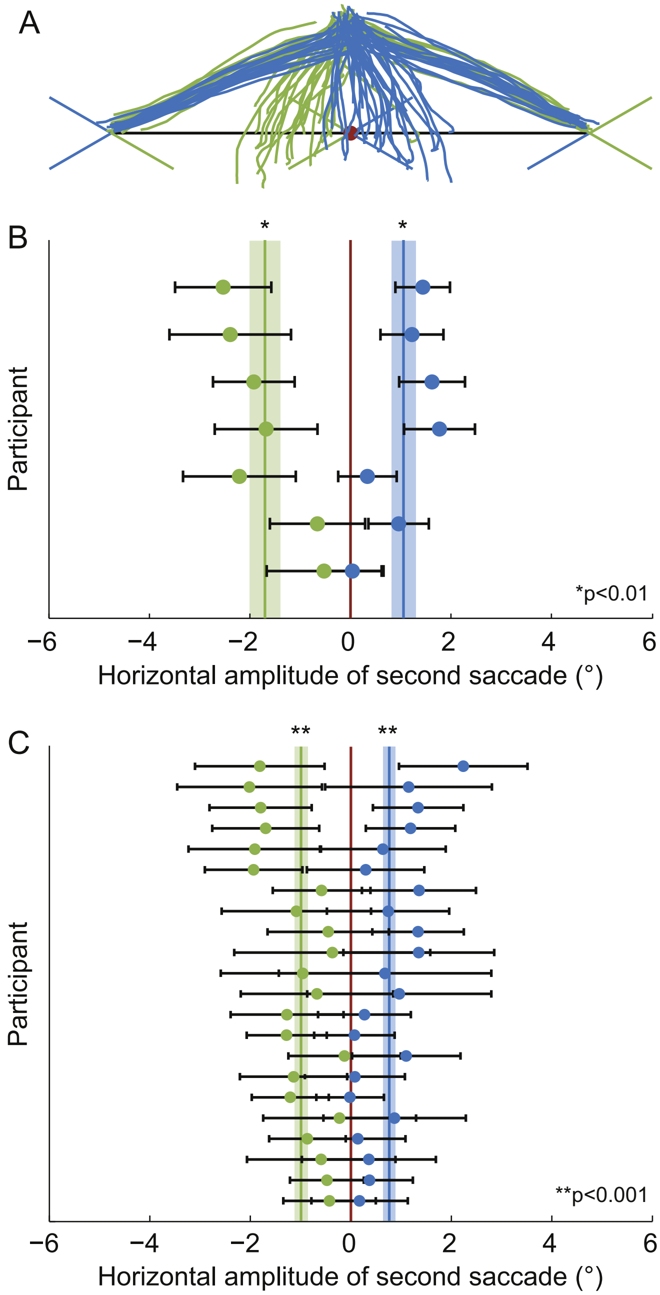

Fig. 2. Behavioural data of both experiments. **A.** First and second saccade trajectories of an example participant, for the L-illusion (green) and R-illusion (blue). Note that the illusion was not visible when the saccades were executed. **B** and **C.** The mean horizontal amplitude of the second saccade (in degrees of visual angle [°]), separately for the L-illusion (green dots) and the R-illusion (blue dots), for each participant in the behavioural experiment (B) and the fMRI experiment (C). The coloured lines with shaded areas indicate the mean ± 1 standard error across participants. Asterisks indicate that the mean is significantly different from zero. Participants are ordered according to the size of the illusion effect. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. fMRI experiment

In total, 115 functional runs were acquired (5–7 runs per participant). Runs that contained less than 50% correct trials were excluded from the behavioural and GLM analysis. The analyses were performed on the remaining 104 runs (3–6 runs per participant),

3.2.1. *Eye movement data*

On average, 83% of the double-step saccade trials (range: 67–99% per participant) were considered correct and included in the behavioural analysis. Trials were removed when one or more saccades were made during the delay (9%), when we failed to detect the second saccade (7%), when the vertical amplitude of the second saccade was smaller than 1.5° (2%), and/or when the angle of the second saccade with respect to the vertical was larger than 45° (4%).

Eye movement behaviour during fMRI scanning was consistent with that in the behavioural experiment. The illusion brought about a non-zero horizontal amplitude of the second saccade in each condition (downward to L-illusion $-1.0 \pm 0.2°$, $t(20)=6.9$, $p<0.001$; upward to L-illusion $-1.1 \pm 0.2°$, $t(20)=7.6$, $p<0.001$; downward to R-illusion $0.8 \pm 0.1°$, $t(20)=6.0$, $p<0.001$; upward to R-illusion $0.7 \pm 0.1°$, $t(20)=5.1$, $p=0.004$). Although the horizontal amplitudes were again slightly larger for the L-illusion than for the R-illusion, this difference was not significant ($F(1,20)=1.692$, $p=0.129$), neither was the effect of vertical direction ($F(1,20)=2.556$, $p=0.126$). The absolute vertical amplitude of the second saccade was slightly larger for downward than for upward saccades (downward $4.3 \pm 0.1°$, upward $3.9 \pm 0.2°$, $F(1,20)=6.695$, $p=0.018$) but was not influenced by the illusion configuration ($F(1,20)=0.009$, $p=0.924$). Fig. 2C shows the horizontal amplitude of the second saccade per participant, averaged over the vertical direction. Expressed as a percentage of a single shaft length of the illusion, the mean effect approximates 12% for the L-illusion and 9% for the R-illusion, which is comparable to the illusion effect in the behavioural experiment

3.2.2. *Saccade- and illusion-related activation*

In the analysis of the fMRI data, we first identified regions that were involved in the execution of the second saccade, using a random-effects group GLM analysis across all 22 participants. As can be seen in Fig. 3AB, saccade-related activation was found in bilateral occipital cortex and across the frontoparietal saccade network consistent with previous studies (for a review see Silver and Kastner, 2009). In the occipital cortex clusters of significantly activated voxels were found slightly posterior to the parieto-occipital sulcus, corresponding to V7 (also named IPS0; Leoné et al., 2014; Schluppeck et al., 2005; Swisher et al., 2007). In the posterior parietal cortex, activation was found along the IPS (Berman et al., 1999; Leoné et al., 2014; Swisher et al., 2007). In the frontal cortex, we found activation around the junction of the precentral sulcus and the superior frontal sulcus, corresponding to the human (superior) frontal eye fields (FEF; Berman et al., 1999; Heide et al., 2001; Kastner et al., 2007; Leoné et al., 2014; Neggers et al., 2012; Van Pelt et al., 2010). In addition, activation was found anterior to the inferior precentral sulcus in the ventral premotor cortex (Heide et al., 2001), a region that has also been named lateral or inferior FEF (Neggers et al., 2012). More superior, significant voxels were found near the interhemispheric fissure, within a region that can be classified as the human supplementary eye fields (Luna et al., 1998; Neggers et al., 2012; Van Pelt et al., 2010). The MNI coordinates and corresponding *t*-values of the peaks of these clusters within the frontoparietal saccade network are shown in Table 1. The peaks reported by the studies that are cited above are within 10 mm of the peaks that were found in the present study.

To determine whether these saccade-related areas are sensitive to the illusion, we first defined bilateral regions of interest (ROIs) corresponding to the clusters of V7, IPS and (superior) FEF described above, including all voxels that were significant in the whole-brain analysis at $p<0.01$ (family-wise error corrected). SEF was not included because this area does not show a clear contralateral response (Kastner et al., 2007; Van Pelt et al., 2010). Of interest is the BOLD response during the delay preceding the second saccade, reflecting the planning of the second saccade to the updated target that was presented within the illusion. As a result of the illusion, the representation of the updated target could be biased to the left or the right of the vertical meridian. Given the contralateral topography of the saccade-related areas, this should, within each hemisphere, give rise to a difference in BOLD amplitude for the two configurations of the illusion. In contrast, if the representation of the target is insensitive to the illusion, we should ideally find an equal BOLD response in the left and right hemisphere for the L-illusion and the R-illusion.

Table 1
Peak MNI coordinates of clusters in the frontoparietal saccade network, used as regions of interest. The table reports clusters of significantly activated voxels during execution of the second saccade ($p<0.01$ family wise error-corrected, $t(1,21)>7.1$).

Functional label	Brodmann Area	Hemisphere	*x*	*y*	*z*	Number of voxels	*t*-value
V7	BA19	Left	−28	−76	26	56	13.2
		Right	28	−72	26	46	10.2
IPS	BA7	Left	−25	−53	52	76	10.3
		Right	18	−63	49	38	9.3
			24	−46	49	14	8.4
sFEF	BA6	Left	−19	−10	52	16	8.2[a]
		Right	34	−6	52	11	7.7
iFEF/PMv	BA6	Left	−55	3	26	87	10.7
		Right	61	7	16	44	9.6
SEF	BA6	Left	−2	−3	59	13	7.8
		Right	11	3	52	7	9.0
			14	−3	65	3	7.7
			11	3	65	3	7.7

IPS=intraparietal sulcus, FEF=frontal eye fields, PMv=ventral premotor cortex, SEF=supplementary eye fields

[a] This elongated cluster contained a second peak at −32, −10, 49 with a slightly lower *t*-value of 8.1.

We first computed the contrast between the BOLD amplitude during saccade planning to a remembered target on the illusion that would cause a bias into the contralateral visual field minus the BOLD amplitude during saccade planning to a remembered target on the illusion that would cause a bias into the ipsilateral field (i.e., $\beta_{\text{contra-illusion}} - \beta_{\text{ipsi-illusion}}$). Fig. 3C shows the mean β weights for this contrast in each of the ROIs. As hypothesised, left and right V7 and IPS showed a larger BOLD amplitude for saccade planning to an updated target within the contra-illusion than to an updated target within the ipsi-illusion. In comparison, whereas right FEF showed a higher BOLD amplitude for saccade planning to the contra-illusion than to the ipsi-illusion, this effect is opposite in left FEF.

Next, we computed the contralateral bias by scaling this difference in β weights to the sum of the absolute β weights. As can be seen in Fig. 3D, V7, IPS and FEF all show a contralateral bias (V7 $W_s=212$, $z=2.8$, $p=0.006$; IPS $W_s=196$, $z=2.3$, $p=0.024$; FEF $W_s=194$, $z=2.2$, $p=0.028$), meaning that the BOLD amplitude is larger during saccade planning toward the contra-illusion than toward the ipsi-illusion. Note that in FEF this effect is mainly driven by a large contralateral bias in the right hemisphere. When we related the behavioural results to the neural results, we did not find significant correlations between the size of the illusion effect and the contralateral bias in V7 and FEF (V7 $r_s=0.112$, $p=0.630$; FEF $r_s=-0.178$, $p=0.440$). In IPS, however, but found a significant negative correlation in IPS ($r_s=-0.443$, $p=0.044$), which is

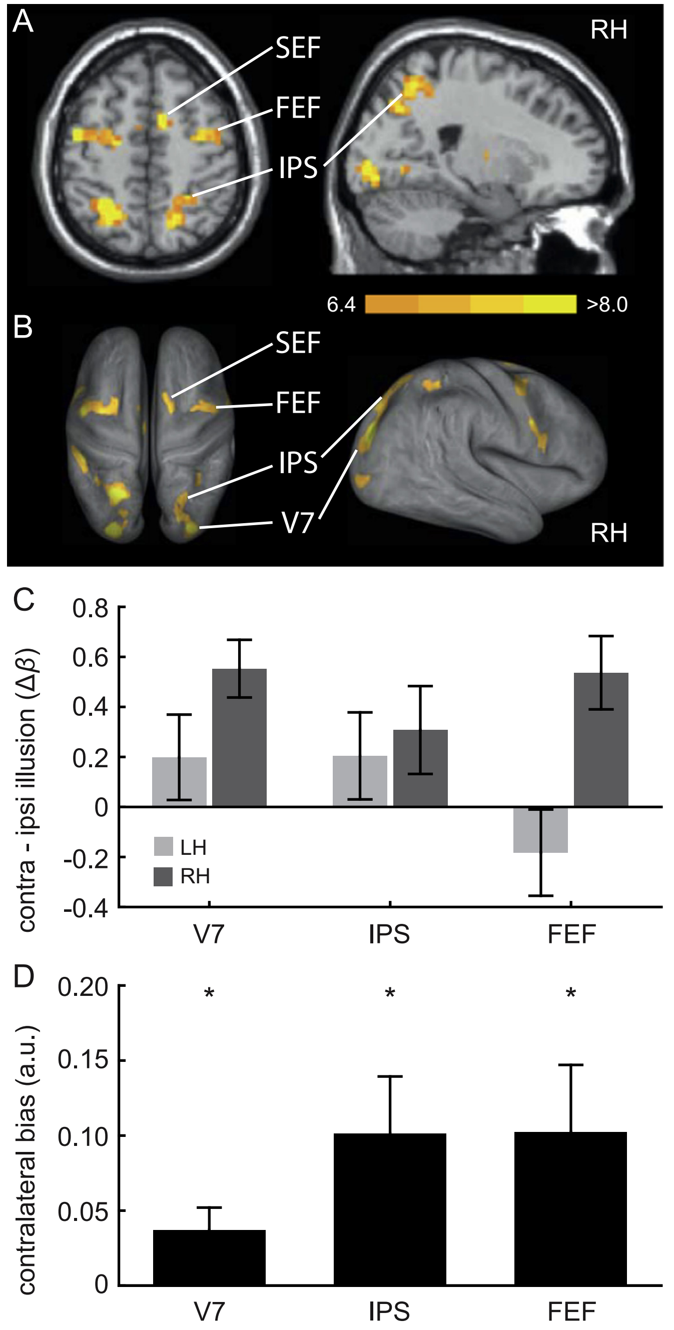

Fig. 3. BOLD data. A. Statistical map of the BOLD response during the execution of the second saccade, averaged across all 22 participants ($p < 0.05$ family wise error-corrected, $t(1,21) > 6.4$, orange to yellow colour coding indicates the t-value). Data are presented on an axial and sagittal section of the brain, in neurological convention. B. The same map as in A, but now overlaid on an inflated brain. C. β weights for the contrast of saccade planning to an updated target presented within the contra-illusion minus saccade planning to an updated target within the ipsi-illusion, averaged within the regions of interest. D. Contralateral bias in β weights. Asterisks indicate that the mean is significantly different from zero ($p < 0.05$, uncorrected). In C and D, the error bars indicate the standard error across participants. IPS=intraparietal sulcus, FEF=frontal eye fields, SEF=supplementary eye fields.

opposite to our prediction.

Taken together, these results show that the BOLD response in V7, IPS and FEF during saccade planning becomes partly lateralized as a result of the context of the illusion in which the target was presented. Our data do not show a relationship between the size of the illusion effect and the strength of the lateralization.

4. Discussion

We investigated the influence of visual context, provided by the Brentano version of the Müller-Lyer illusion, on visuomotor updating for saccades. Participants performed a double-step saccade task in which the second saccade was directed towards a remembered target on the illusion. The results show that the updated target is affected by the Brentano illusion; the second saccade landed to the left or right of the target position, depending on the configuration of the illusion. Using fMRI, we investigated whether these illusion effects can be linked to the updating of an 'erroneous' neural target representation in the dorsal visual stream. Indeed, although the physical position of the target was always straight up or down from the preceding fixation position, we found that the BOLD response in occipital area V7 and in the intraparietal sulcus (IPS) during saccade planning was affected by the configuration of the illusion. Specifically, in left V7 and IPS we found a higher BOLD amplitude when planning a saccade to a target that is remembered to the right of its position (i.e., the contra-illusion) than when planning a saccade to a target that is remembered to the left of its position (i.e., the ipsi-illusion). Similarly, right V7 and IPS showed a higher BOLD amplitude for saccade planning to the contra-illusion than to the ipsi-illusion. Thus, the illusion caused a significant contralateral bias in V7 and IPS. We also found a contralateral bias in BOLD amplitude in the frontal eye fields (FEF). However, this was mainly driven by a strong contralateral bias in the right hemisphere. We did not find a relationship between the size of the illusion effect and the contralateral bias.

In a double-step saccade task, accurate performance is achieved by updating the gaze-centered vector specifying the position of the second target (that is, relative to the starting position of the first movement) after the intervening movement. We investigated the effect of presenting an illusion of length along the vector that specifies the target position. Behavioural experiments have found that while the Müller-Lyer illusion strongly affects the perceived length of the horizontal shaft, the perceived position of the end of the shaft is hardly affected (Gillam and Chambers, 1985; Mack et al., 1985; but see Morgan et al., 1990). Moreover, it has been shown that saccades perpendicular to the orientation of the Brentano illusion are not affected (De Grave et al., 2006), suggesting that the position of the target *can* be accurately encoded relative to a fixation position outside the illusion. However, in the current experiment we did find an effect of the illusion on the endpoint of the second saccade, even though it was generated from a position perpendicular to the illusion. This implies that the length of the initial non-updated visual vector that specifies the target on the illusion is affected by the illusion, and as such causes an error after updating. One could argue that this result is relatively straightforward because the task required updating of remembered targets, which are suggested to be highly sensitive to visual illusions (Milner and Goodale, 2008). However, in a previous study we did not find differences in illusion effects between visually-guided and memory-guided saccades (De Brouwer et al., 2014), suggesting that De Grave et al.'s results would also hold in memory conditions.

Using fMRI, we showed that the neural representation of the updated target in saccade-related areas V7, IPS and FEF is modulated by the configuration of the illusion. The finding of a contralateral bias in these areas during memory-guided saccade planning is consistent with studies that used physically lateralized saccade targets (e.g., Kastner et al., 2007; Schluppeck et al., 2006; Sereno et al., 2001; Van Pelt et al., 2010). To our knowledge, this is the first study to show that representations for saccade targets are affected by visual context. We note that the contralateral biases are relatively weak. A possible reason is that the effect of the illusion resulted in an average saccade angle of only 13° with respect to the vertical meridian, compared to angles of 30° or larger that were used in previous memory-guided saccade studies performed in the fMRI scanner. The weakness of the effects may also explain why we did not find a correlation between the size of the illusion effect and the contralateral bias.

An interesting question is where the illusion has originated. Previous fMRI studies have shown that both the superior parietal cortex in the dorsal visual stream (Plewan et al., 2012; Walter and Dassonville, 2008; Weidner and Fink, 2007) and the lateral occipital cortex in the ventral visual stream (LOC; Plewan et al., 2012; Weidner and Fink, 2007) are involved in perceptual tasks involving contextual illusions, with bidirectional connections between the two areas (Plewan et al., 2012). Furthermore, an MEG showed that the activations in the ventral visual stream precede the activations in parietal cortex, suggesting that the ventral stream forms a representation of the illusion (Weidner et al., 2010). A memory-guided grasping experiment without illusions, performed in an fMRI scanner, showed that LOC was active during the presentation of the stimulus, but also at the time of action. This suggests that the ventral stream is re-activated to provide relevant information about object properties to guide the dorsal stream in performing the action (Singhal et al., 2013). Given these findings, the effects that we see in the IPS may be the result of direct interactions with LOC. We could not assess this hypothesis, because we did not perform a separate localizer task or a condition without the illusion to contrast to our task in order to identify LOC. Alternatively, the presence of illusion-dependant modulations of the BOLD response in occipito-parietal area V7 may suggest that illusory feedback proceeds to higher dorsal visual stream areas via early visual cortex.

Indeed, effects of contextual illusions have been demonstrated in early visual cortex. Using a size illusion of two physically identical spheres (Murray et al., 2006) or rings (Fang et al., 2008) in a three-dimensional scene of a hallway (i.e., a 3D version of the Ponzo illusion), it was shown that the retinotopic representation of the object changes in accordance with its perceived angular size. The spatial distribution of V1 activation was more eccentric for the perceptually larger than for the perceptually smaller object. Further, inter-individual variability in the strength of the Ebbinghaus illusion and the three-dimensional version of the Ponzo illusion have been shown to correlate with the surface area of central V1 defined by retinotopic mapping (Schwarzkopf and Rees, 2013; Schwarzkopf et al., 2010). Finally, the perceived size of an afterimage or test stimulus, following an adaptor stimulus, has been shown to modify the BOLD response in V1. A larger perceived size corresponded to a stronger response in more eccentric regions (Sperandio et al., 2012), or a larger activated surface area (Pooresmaeili et al., 2013). The studies above suggest that V1 activation is modulated by feedback from higher cortical areas, possibly in the ventral visual stream.

The FEF are known to maintain the motor goal of the saccade (Curtis et al., 2004). Because the second saccade was systematically biased into either the left or right visual field as a result of the illusion, we expected to find a contralateral bias in this area. While this expectation was matched in the right FEF, the results of the left FEF did not match our expectation. A possible explanation for this result is that the retinotopic maps in FEF show a lesser preference for contralateral saccades than the maps in the IPS (Kagan et al., 2010; Neggers et al., 2012). Because the effect of the illusion on saccades was small, participants had an average horizontal error of 0.9° for a vertical amplitude of 4.1°, it is possible that we could detect an effect of the illusion better in the posterior parietal cortex than in the frontal cortex.

In the dorsal stream regions that we selected, V7 and IPS, several factors could have contributed to the BOLD response during the delay preceding the second saccade: memory of the updated visual target, memory of the motor goal for the planned saccade, or spatial attention to the remembered location. V7 is generally considered a visual area, showing topography for visual stimuli and visual spatial attention, as well as for memory-guided saccades (Schluppeck et al., 2005; Silver et al., 2005; Tootell et al., 1998). The IPS, or more generally the PPC, has been implicated in visual spatial attention and sensorimotor transformations. Anti-reach and anti-saccade tasks have been performed to distinguish between sensory target representations and movement plans. During the delay phase preceding a pro- or anti-saccade, the PPC shows a sustained response to both the visual target and the saccade goal, with a stronger response to the visual stimulus during the first part of the delay, and a stronger response to the saccade goal during the second part of the delay (Medendorp et al., 2005; Saber et al., 2015; Van Der Werf et al., 2008). In contrast, participants who were adapted to left–right reversing prisms in a delayed reaching task showed directional selectivity in the PPC that was fixed to the visual coordinates of the remembered goal throughout the delay (Fernandez-ruiz et al., 2007). With the current data, we cannot distinguish between the factors that could have contributed to the BOLD response in V7 and IPS.

5. Conclusions

We used a double-step saccade task involving the Brentano illusion task to show that visual context (1) systematically affects the landing position of saccades in a visuomotor updating task and (2) modulates the BOLD response in the occipito-parietal and posterior parietal cortex related to saccade planning. These findings indicate that the dorsal visual stream takes context into account, and thereby represents perceived rather than physical locations of remembered saccade targets.

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References

Aglioti, S., DeSouza, J.F., Goodale, M.A., 1995. Size-contrast illusions deceive the eye but not the hand. Curr. Biol. 5, 679–685.

Berman, R.A., Colby, C.L., Genovese, C.R., Voyvodic, J.T., Luna, B., Thulborn, K.R., Sweeney, J.A., 1999. Cortical networks subserving pursuit and saccadic eye movements in humans: an fMRI study. Hum. Brain Mapp. 8, 209–225.

Biegstraaten, M., De Grave, D.D.J., Brenner, E., Smeets, J.B.J., 2007. Grasping the Müller-Lyer illusion: not a change in perceived length. Exp. Brain Res. 176, 497–503. http://dx.doi.org/10.1007/s00221-006-0744-8.

Binsted, G., Elliott, D., 1999. Ocular perturbations and retinal/extraretinal information: the coordination of saccadic and manual movements. Exp. Brain Res. 127, 193–206. http://dx.doi.org/10.1007/s002210050789.

Brainard, D.H., 1997. The psychophysics toolbox. Spat. Vis. 10, 433–436. http://dx.doi.org/10.1163/156856897 × 00357.

Brenner, E., Smeets, J.B., 1996. Size illusion influences how we lift but not how we grasp an object. Exp. Brain Res. 111, 473–476. http://dx.doi.org/10.1007/BF00228737.

Bridgeman, B., Peery, S., Anand, S., 1997. Interaction of cognitive and sensorimotor maps of visual space percept. Psychophysics 59, 456–469.

Colby, C.L., Goldberg, M.E., 1999. Space and attention in parietal cortex. Annu. Rev.

Neurosci. 22, 319–349. http://dx.doi.org/10.1146/annurev.neuro.22.1.319.

Curtis, C.E., Rao, V.Y., D'Esposito, M., 2004. Maintenance of spatial and motor codes during oculomotor delayed response tasks. J. Neurosci. 24, 3944–3952. http://dx.doi.org/10.1523/JNEUROSCI.5640-03.2004.

Daprati, E., Gentilucci, M., 1997. Grasping an illusion. Neuropsychologia 35, 1577–1582.

De Brouwer, A.J., Brenner, E., Medendorp, W.P., Smeets, J.B.J., 2014. Time course of the effect of the Muller-Lyer illusion on saccades and perceptual judgments. J. Vis. 14, 1–11. http://dx.doi.org/10.1167/14.1.4.

De Grave, D.D.J., Smeets, J.B.J., Brenner, E., 2006. Why are saccades influenced by the Brentano illusion? Exp. Brain Res. 175, 177–182. http://dx.doi.org/10.1007/s00221-006-0536-1.

Fang, F., Boyaci, H., Kersten, D., Murray, S.O., 2008. Attention-dependent representation of a size illusion in human V1. Curr. Biol. 18, 1707–1712. http://dx.doi.org/10.1016/j.cub.2008.09.025.

Fernandez-ruiz, J., Goltz, H.C., DeSouza, J.F.X., Vilis, T., Crawford, J.D., Joseph, F.X., 2007. Human parietal "reach region" primarily encodes intrinsic visual direction, not extrinsic movement direction, in a visual motor dissociation task. Cereb. Cortex 17, 2283–2292. http://dx.doi.org/10.1093/cercor/bhl137.

Franz, V.H., Hesse, C., Kollath, S., 2009. Visual illusions, delayed grasping, and memory: no shift from dorsal to ventral control. Neuropsychologia 47, 1518–1531. http://dx.doi.org/10.1016/j.neuropsychologia.2008.08.029.

Friston, K.J., Fletcher, P., Josephs, O., Holmes, A., Rugg, M.D., Turner, R., 1998. Event-related fMRI: characterizing differential responses. Neuroimage 7, 30–40. http://dx.doi.org/10.1006/nimg.1997.0306.

Gillam, B., Chambers, D., 1985. Size and position are incongruous: measurements on the Muller-Lyer figure. Percept. Psychophysics 37, 549–556.

Gnadt, J.W., Bracewell, R.M., Andersen, R.A., 1991. Sensorimotor transformation during eye movements to remembered visual targets. Vision Res. 31, 693–715.

Goodale, M.A., Milner, A.D., 1992. Separate visual pathways for perception and action. Trends Neurosci. 15, 20–25.

Haffenden, A.M., Schiff, K.C., Goodale, M.A., 2001. The dissociation between perception and action in the Ebbinghaus illusion: nonillusory effects of pictorial cues on grasp. Curr. Biol. 11, 177–181. http://dx.doi.org/10.1016/S0960-9822(01)00023-9.

Heide, W., Binkofski, F., Seitz, R.J., Posse, S., Nitschke, M.F., Freund, H.-J., Kömpf, D., 2001. Activation of frontoparietal cortices during memorized triple-step sequences of saccadic eye movements: an fMRI study. Eur. J. Neurosci. 13, 1177–1189.

Honda, M., Wise, S.P., Weeks, R.A., Deiber, M.P., Hallett, M., 1998. Cortical areas with enhanced activation during object-centred spatial information processing. A PET study. Brain 121, 2145–2158. http://dx.doi.org/10.1093/brain/121.11.2145.

Kagan, I., Iyer, A., Lindner, A., Andersen, R.A., 2010. Space representation for eye movements is more contralateral in monkeys than in humans. Proc. Natl. Acad. Sci. 107, 7933–7938. http://dx.doi.org/10.1073/pnas.1002825107.

Kastner, S., DeSimone, K., Konen, C.S., Szczepanski, S.M., Weiner, K.S., Schneider, K. A., 2007. Topographic maps in human frontal cortex revealed in memory-guided saccade and spatial working-memory tasks. J. Neurophysiol. 97, 3494–3507. http://dx.doi.org/10.1152/jn.00010.2007.

Klier, E.M., Angelaki, D.E., 2008. Spatial updating and the maintenance of visual constancy. Neuroscience 156, 801–818. http://dx.doi.org/10.1016/j.neuroscience.2008.07.079.

Leoné, F.T.M., Toni, I., Medendorp, W.P., 2014. Two-dimensional spatial tuning for saccades in human parietofrontal cortex. Neuroimage 87, 476–489. http://dx.doi.org/10.1016/j.neuroimage.2013.09.067.

Luna, B., Thulborn, K.R., Strojwas, M.H., Mccurtain, B.J., Berman, R.A., Genovese, R., Sweeney, J.A., 1998. Dorsal cortical regions subserving visually guided saccades in humans: an fMRI study. Cereb. Cortex 8, 40–47.

Mack, A., Heuer, F., Villardi, K., Chambers, D., 1985. The dissociation of position and extent in Muller-Lyer figures. Percept. Psychophys. 37, 335–344.

Medendorp, W.P., 2011. Spatial constancy mechanisms in motor control. Philos. Trans. R. Soc. Lond. B Biol. Sci. 366, 476–491. http://dx.doi.org/10.1098/rstb.2010.0089.

Medendorp, W.P., Goltz, H.C., Vilis, T., 2005. Remapping the remembered target location for anti-saccades in human posterior parietal cortex. J. Neurophysiol. 94, 734–740. http://dx.doi.org/10.1152/jn.01331.2004.

Medendorp, W.P., Goltz, H.C., Vilis, T., Crawford, J.D., 2003. Gaze-centered updating of visual space in human parietal cortex. J. Neurosci. 23, 6209–6214.

Milner, A.D., Goodale, M.A., 2008. Two visual systems re-viewed. Neuropsychologia 46, 774–785. http://dx.doi.org/10.1016/j.neuropsychologia.2007.10.005.

Mishkin, M., Ungerleider, L.G., Macko, K.A., 1983. Object vision and spatial vision: two cortical pathways. Trends Neurosci. 6, 414–417.

Morgan, M.J., Hole, G.J., Glennerster, A., 1990. Biases and sensitivities in geometrical illusions. Vis. Res. 30, 1793–1810. http://dx.doi.org/10.1016/0042-6989(90)90160-M.

Murray, S.O., Boyaci, H., Kersten, D., 2006. The representation of perceived angular size in human primary visual cortex. Nat. Neurosci. 9, 429–434. http://dx.doi.org/10.1038/nn1641.

Neggers, S.F.W., van Diepen, R.M., Zandbelt, B.B., Vink, M., Mandl, R.C.W., Gutteling, T.P., 2012. A functional and structural investigation of the human fronto-basal volitional saccade network. PLoS One 7. http://dx.doi.org/10.1371/journal.pone.0029517.

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. J. Cogn. Neurosci. 24, 2015–2029. http://dx.doi.org/10.1162/jocn_a_00258.

Pooresmaeili, A., Arrighi, R., Biagi, L., Morrone, M.C., 2013. Blood oxygen level-dependent activation of the primary visual cortex predicts size adaptation illusion. J. Neurosci. 33, 15999–16008. http://dx.doi.org/10.1523/JNEUROSCI.1770-13.2013.

Poser, B.A., Versluis, M.J., Hoogduin, J.M., Norris, D.G., 2006. BOLD contrast sensitivity enhancement and artifact reduction with multiecho EPI: parallel-acquired inhomogeneity-desensitized fMRI. Magn. Reson. Med. 55, 1227–1235. http://dx.doi.org/10.1002/mrm.20900.

Post, R.B., Welch, R.B., 1996. Is there dissociation of perceptual and motor responses to figural illusions? Perception 25, 569–581. http://dx.doi.org/10.1068/p250569.

Saber, G.T., Pestilli, F., Curtis, C.E., 2015. Saccade planning evokes topographically specific activity in the dorsal and ventral streams. J. Neurosci. 35, 245–252. http://dx.doi.org/10.1523/JNEUROSCI.1687-14.2015.

Schenk, T., Franz, V., Bruno, N., 2011. Vision-for-perception and vision-for-action: which model is compatible with the available psychophysical and neuropsychological data? Vis. Res. 51, 812–818. http://dx.doi.org/10.1016/j.visres.2011.02.003.

Schluppeck, D., Curtis, C.E., Glimcher, P., Heeger, D.J., 2006. Sustained activity in topographic areas of human posterior parietal cortex during memory-guided saccades. J. Neurosci. 26, 5098–5108. http://dx.doi.org/10.1523/JNEUROSCI.5330-05.2006.

Schluppeck, D., Glimcher, P., Heeger, D.J., 2005. Topographic organization for delayed saccades in human posterior parietal cortex. J. Neurophysiol. 94, 1372–1384. http://dx.doi.org/10.1152/jn.01290.2004.

Schwarzkopf, D.S., Rees, G., 2013. Subjective size perception depends on central visual cortical magnification in human V1. PLoS One 8, e60550. http://dx.doi.org/10.1371/journal.pone.0060550.

Schwarzkopf, D.S., Song, C., Rees, G., 2010. The surface area of human V1 predicts the subjective experience of object size. Nat. Neurosci. 14, 28–30. http://dx.doi.org/10.1038/nn.2706.

Sereno, M.I., Pitzalis, S., Martinez, A., 2001. Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. Science 294, 1350–1354. http://dx.doi.org/10.1126/science.1063695.

Silver, M.A., Kastner, S., 2009. Topographic maps in human frontal and parietal cortex. Trends Cogn. Sci. 13, 488–495. http://dx.doi.org/10.1016/j.tics.2009.08.005.

Silver, M.A., Ress, D., Heeger, D.J., 2005. Topographic maps of visual spatial attention in human parietal cortex. J. Neurophysiol. 94, 1358–1371. http://dx.doi.org/10.1152/jn.01316.2004.

Singhal, A., Monaco, S., Kaufman, L.D., Culham, J.C., 2013. Human fMRI reveals that delayed action re-recruits visual perception. PLoS One 8, e73629. http://dx.doi.org/10.1371/journal.pone.0073629.

Sperandio, I., Chouinard, P.A., Goodale, M.A., 2012. Retinotopic activity in V1 reflects the perceived and not the retinal size of an afterimage. Nat. Neurosci. 15, 540–542. http://dx.doi.org/10.1038/nn.3069.

Swisher, J.D., Halko, M.A., Merabet, L.B., McMains, S.A., Somers, D.C., 2007. Visual topography of human intraparietal sulcus. J. Neurosci. 27, 5326–5337. http://dx.doi.org/10.1523/JNEUROSCI.0991-07.2007.

Taghizadeh, B., Gail, A., 2014. Spatial task context makes short-latency reaches prone to induced Roelofs illusion. Front. Hum. Neurosci. 8, 673. http://dx.doi.org/10.3389/fnhum.2014.00673.

Tootell, R.B., Hadjikhani, N., Hall, E.K., Marrett, S., Vanduffel, W., Vaughan, J.T., Dale, a M., Marett, S., Vanduffel, W., Vaughan, J.T., Dale, A.M., 1998. The retinotopy of visual spatial attention. Neuron 21, 1409–1422. http://dx.doi.org/10.1016/S0896-6273(00)80659-5.

Van Der Werf, J., Jensen, O., Fries, P., Medendorp, W.P., 2008. Gamma-band activity in human posterior parietal cortex encodes the motor goal during delayed prosaccades and antisaccades. J. Neurosci. 28, 8397–8405. http://dx.doi.org/10.1523/JNEUROSCI.0630-08.2008.

Van Pelt, S., Toni, I., Diedrichsen, J., Medendorp, W.P., 2010. Repetition suppression dissociates spatial frames of reference in human saccade generation. J. Neurophysiol. 104, 1239–1248. http://dx.doi.org/10.1152/jn.00393.2010.

Walter, E., Dassonville, P., 2008. Visuospatial contextual processing in the parietal cortex: an fMRI investigation of the induced Roelofs effect. Neuroimage 42, 1686–1697. http://dx.doi.org/10.1016/j.neuroimage.2008.06.016.

Weidner, R., Boers, F., Mathiak, K., Dammers, J., Fink, G.R., 2010. The temporal dynamics of the Muller-Lyer illusion. Cereb. Cortex 20, 1586–1595. http://dx.doi.org/10.1093/cercor/bhp217.

Weidner, R., Fink, G.R., 2007. The neural mechanisms underlying the Muller-Lyer illusion and its interaction with visuospatial judgments. Cereb. Cortex 17, 878–884. http://dx.doi.org/10.1093/cercor/bhk042.

Westwood, D.A., Goodale, M.A., 2011. Converging evidence for diverging pathways: neuropsychology and psychophysics tell the same story. Vis. Res. 51, 804–811. http://dx.doi.org/10.1016/j.visres.2010.10.014.

Westwood, D.A., Heath, M., Roy, E.A., 2000. The effect of a pictorial illusion on closed-loop and open-loop prehension. Exp. Brain Res. 134, 456–463.