



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.

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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 cm², 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 mm², slice thickness 3.0 mm with 10% gap, field of view [FOV] 211 × 211 mm²). 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 × 1.0 × 1.0 mm³ voxels, FOV 256 × 256 mm²).

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).

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