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Special issue: Review

Dynamic representations of visual space for perception and action



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ABSTRACT

The division of labor in visual processing between two anatomically relatively separate cortical pathways, a ventral and a dorsal stream, has been hotly debated in the last decades. One influential model is the What & How pathway model, suggesting that the separation is along ventral perception versus dorsal action, although the degree of functional separation between the two streams is controversial. An implication of this model is that perception and memory-guided movements are highly sensitive to visual contextual illusions, whereas visually-guided movements are largely immune to them. Here, we summarize our recent behavioral and imaging data obtained in single and double saccade paradigms that test this proposal, with a focus on the role of time in visuomotor processing and updating. We describe results showing that presentation time of the illusion affects both saccade amplitude and perceptual judgments in a similar way. We also discuss behavioral findings showing that visuomotor updating is affected by illusory context. Complementary neuroimaging data suggest a neural correlate of these findings in dorsal stream areas. Taken together, these results are suggestive of a dynamic, common visual representation that drives both perception and action, or – at least – that there is no absolute functional specialization of the two visual processing streams.

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1. Introduction

Visual processing in the human brain is generally described as being organized along two largely segregated streams, a dorsal pathway and a ventral pathway, both originating in the primary visual cortex. The dorsal stream projects to the posterior parietal cortex and the ventral pathway projects to the

inferotemporal cortex. It has been suggested that these two pathways are not just anatomically distinct, but also code functionally distinct properties of objects. Based on anatomical and functional evidence in the macaque monkey, Ungerleider and Mishkin (1982) posed that the ventral stream is crucial for ‘object vision’, that is, the identification (‘what’) of objects, whereas the dorsal stream is crucial for ‘spatial vision’, that is, the location (‘where’) of objects.

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Goodale, Milner and their co-workers tested this model by examining the behaviour of patients with lesions in these streams. They found that patients with damage in the ventral stream have poor perception of objects, but have no problem in grasping them (Goodale et al., 1994; but see, 1991; Hesse, Ball, & Schenk, 2012; Himmelbach, Boehme, & Karnath, 2012). Likewise, Rossit, Szymanek, Butler, and Harvey (2010) showed greatly reduced accuracy and increased latencies for memory-guided saccades but not for reflexive saccades in a patient with ventral stream damage. The opposite was found in optic ataxia patients with damage in the dorsal visual stream, who show difficulty in acting upon objects, even though they perceive them accurately (Jakobson, Archibald, Carey, & Goodale, 1991; Goodale et al., 1994; but see; Pisella et al., 2000).

Based on such observations, Goodale and Milner proposed the What & How pathway model, which distinguishes between the processing of visual information for perception ('what' vision for perception') and action ('how' vision for action'). According to this model, the task of the ventral stream is to transform visual input into perceptual representations for the purpose of conscious perception. The ventral stream processes object characteristics such as shape, size and color and their embeddedness in a visual context. This information can be stored in long-term memory, and allows the ventral stream to contribute to action planning based on remembered information. In contrast, the dorsal stream is involved in the real-time guidance of action, coding object information based on current visual inputs in a metrically accurate manner relative to the observer. The dorsal stream can specify actions that are carried out immediately, allowing to act upon unpredictable events.

This model of visual processing has been very influential, sparking many studies and experiments over the last 25 years (see for instance the other papers in this issue). Not only has the functional independence of the two streams been questioned (Schenk & McIntosh, 2010), the number of pathways is also under study (Pisella, Binkofski, Lasek, Toni, & Rossetti, 2006; Rizzolatti & Matelli, 2003). Others have related the distinction between connection types, such as feedback and feedforward interactions, to the functional dichotomies in visual processing (Lamme & Roelfsema, 2000). In the following we will review some of our recent behavioral and imaging work on visuomotor processing and updating in the context of the What & How pathway model and its alternative accounts.

2. Tricking vision

An interesting implication of the What & How pathway model is that our perception is highly sensitive to visual contextual illusions, but that our actions are largely immune to these illusions. The rationale is as follows. For perception, it is essential that the ventral visual stream encodes the size, orientation, and location of objects relative to other objects, that is, in an allocentric frame of reference (Goodale & Milner, 1992; Milner & Goodale, 2008). Because the ventral stream interprets the visual input at a global, pictorial level, its contribution to perception and memory-guided actions will be highly sensitive to visual contextual illusions. In contrast,

acting upon an object requires the dorsal visual stream to compute the actual size of the object, and its position and motion with respect to the observer, that is, in an egocentric frame of reference. Because the dorsal stream interprets visual information relative to the observer, the actions it specifies are assumed to be largely immune to contextual illusions.

Thus, Milner and Goodale predicted that perceptual judgments and goal-directed actions would be differentially affected by visual contextual illusions. In support, they showed that the size of the center disk in the Ebbinghaus illusion biases perceptual size judgments when viewing this disk but not the grip aperture when grasping this disk (Aglioti, DeSouza, & Goodale, 1995; Haffenden, Schiff, & Goodale, 2001). This interpretation, however, has been questioned (see Smeets & Brenner, 2006 for review). One criticism is that the perceptual and the motor task were not appropriately matched (Franz, Gegenfurtner, Bülthoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999). More specifically, in the original studies, two discs with different context circles were shown simultaneously. In the perception task, subjects had to compare the two central discs, while in the grasping task they acted on only one of them, which could have led to an asymmetry in the result. The asymmetry disappeared when perceptual and grasping tasks both operate on a single Ebbinghaus figure. However, this counter-argument does not seem to hold for other illusions (Stöttinger, Soder, Pfusterschmied, Wagner, & Perner, 2010). Another counter-argument is that grip aperture is not an appropriate measure of how size is processed for action (Smeets & Brenner, 2006), which is strengthened by the finding that other motor aspects of grasping, such as lift and grip force, perhaps based on object properties coded ventrally (Gallivan, Cant, Goodale, & Flanagan, 2014), are affected by illusions of size (Brenner & Smeets, 1996; Jackson & Shaw, 2000).

Because reaching and grasping are under voluntary control, and their trajectories susceptible to visual feedback, researchers have resorted to saccades to study the effects of illusions on visuomotor processing.

3. Look at the dot

Saccades are generally regarded as ballistic movements whose trajectory, once started, cannot be influenced by incoming sensory information. This makes these movements very well suited to study the effects of visual contextual illusions on visuomotor processing.

Over the years, a large set of data has been collected about the effects of visual illusions on saccades (Bruno, Knox, & de Grave, 2010; Fracasso, Targher, Zampini, & Melcher, 2013; Knox, 2006; Melmoth, Grant, Solomon, & Morgan, 2015). For example, Knox (2006) showed a reduction in saccade amplitude when saccades were executed to the end of an occluded line, consistent with the known perceptual compression of the line (i.e., Kanizsa's compression illusion). Melmoth et al. (2015) reported a bias in saccades to a target embedded in the Poggendorff illusion. However, the majority of the work with saccades has been performed with the Müller-Lyer illusion, an illusion that makes a horizontal line appear shorter or longer by the context of its inward or outward

pointing arrowheads. Already in 1967, Yarbus described how natural saccadic eye movements are affected by this illusion, resulting in shorter saccade amplitudes for the perceptually shorter illusion, and longer amplitudes for the perceptually longer illusion (Yarbus, 1967). Later, these observations were confirmed in controlled experiments (Bernardis, Knox, & Bruno, 2005; Binsted & Elliott, 1999; De Grave, Smeets, & Brenner, 2006). A review on the effect of the Müller–Lyer illusion on saccades showed that the effect of this illusion ranges from virtually zero to about 30% of saccade amplitude, depending on experimental conditions, such as predictability of the spatial characteristics of the illusion, the presence of postsaccadic visual feedback, saccade latency and other factors (Bruno et al., 2010).

According to the What & How hypothesis, an important distinction between the processing in the ventral and dorsal stream lays in the role of time: the processing in the (illusion-resistant) dorsal stream is real-time, whereas the processing in the (illusion-prone) ventral stream is slow. In line with this distinction, several authors (e.g., McCarley, Kramer, & DiGirolamo, 2003) reported that reflexive saccades are less prone to effects of the Müller–Lyer illusion than voluntary saccades. As reflexive saccades have generally shorter latencies, it might be that differences in temporal aspects of the tasks are the underlying cause of the wide range of illusion effects that have been reported.

In an attempt to find consistencies in illusion effects, we recently examined the role of time in the processing of the Müller–Lyer illusion for saccades and perception (de Brouwer, Brenner, & Smeets, 2016; de Brouwer, Brenner, Medendorp, & Smeets, 2014). We performed a set of experiments in which participants made a single leftward or rightward saccade from a fixation point at one vertex of the Müller–Lyer illusion to a target at its other vertex, while we recorded eye position. We used both a ‘compressing’ and an ‘expanding’ ML illusion and compared the amplitude of saccades along the horizontal shaft in these two configurations. We used various shaft lengths to deter stereotyped responses based on memory of the stimuli, and verified that the saccade amplitude scaled with shaft length. Furthermore, subjects received no feedback about their performance, so they did not know whether their saccades were performed correctly or not, and as the stimulus was never present at saccade offset, they could not correct for amplitude errors due to the illusion.

We examined four temporal factors in the processing of visuomotor information for saccades: 1) reaction time of the saccade, i.e., saccade latency 2) presentation time of the illusion; 3) time between the appearance of the illusion and the cue to make an eye movement, i.e., response delay; and 4) time between the disappearance of the illusion and the cue to make an eye movement, i.e., memory delay. Fig. 1A illustrates the relationship between these factors.

To examine the effect of saccadic latency, participants were instructed to move their eyes to the target as quickly as possible in response to the onset of the stimulus (i.e., memory delay and response delay both equal to zero). The stimulus was shown for either 12, 24, 47, 94, 153 or 200 msec. Saccade latency was further modulated by introducing a temporal gap before the appearance of the stimulus. We called this the reflexive saccade condition.

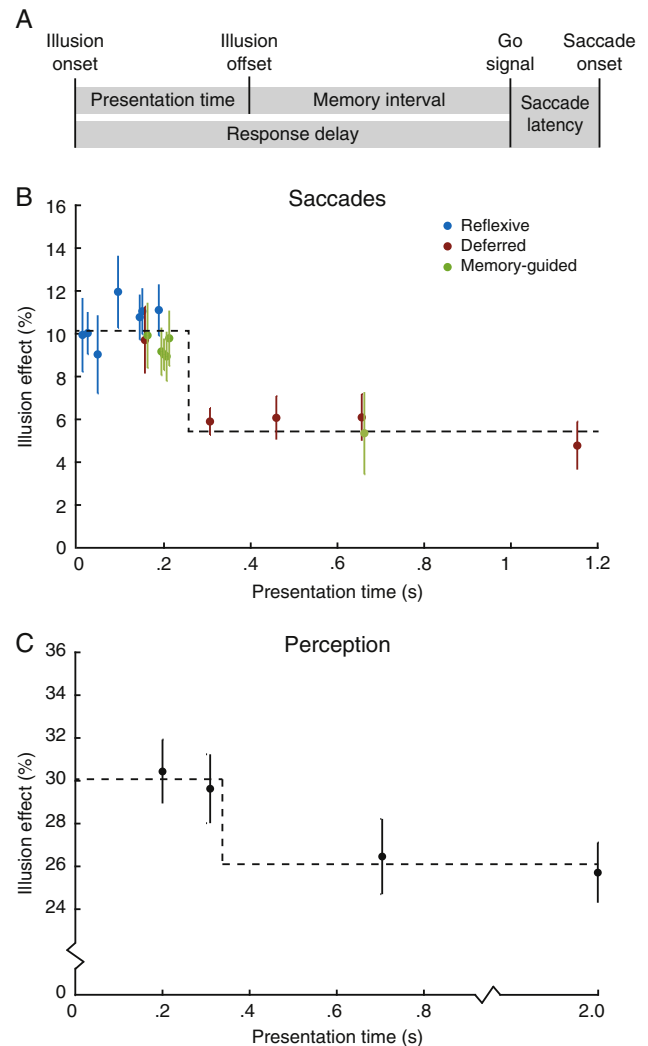


Fig. 1 – Effect of time on perceiving and acting in an illusory context. A. Relationship between presentation time of the illusion, response delay, memory delay and saccade latency in saccade tasks. For reflexive saccades, memory delay and response delay are both equal to zero. For deferred saccades, a response delay is introduced while keeping memory delay zero. For memory-guided saccade, there is a non-zero memory delay. B. Illusion effects for reflexive, deferred and memory-guided saccades as a function of the presentation time of the illusion. C. As B, but for perceptual judgments.

We examined the effect of presentation time in the deferred saccade condition, in which subjects viewed the stimulus for a certain amount of time (153, 306, 459, 659 or 1153 msec) before they made the saccade.

Finally, in the memory-guided saccade condition, subjects viewed the stimulus for 153, 200 or 659 msec, and subsequently kept fixation for up to 1800 msec (the memory delay), after which they made the saccade.

We computed the illusion effect as follows. We first determined the median saccade amplitude for each participant and condition. We then calculated the illusion effect as the difference between the median amplitude of saccades

along the compressing and expanding configuration, divided by the length of the shaft of illusion. The result is the influence of the illusion as a percentage of shaft length, which were averaged across shaft lengths and leftward and rightward saccade directions.

For comparison, subjects also performed a perception task, in which the illusion with three different shaft lengths was presented for 200, 306, 706 or 2000 msec and participants had to estimate the length with a precision of .5 cm. The illusion effect was determined as follows. We first calculated the average estimated length for each stimulus configuration. For each participant, we fitted the estimated lengths as a linear function of the true shaft lengths, reflecting the subject's perceptual gain. Illusion effects were then calculated by taking the difference in estimated length for the compressing and expanding Müller–Lyer illusion and correcting this by the perceptual gain to account for differences between subjects. Illusion effects were averaged across shaft lengths.

Fig. 1B and C shows the results of both the saccade and perception experiments, demonstrating that presentation time is the only variable that seriously affects the illusion effect. Saccade latency only had a very small effect; memory delay did not influence the illusion effect. Illusion effects were largest for reflexive saccades and memory-guided saccades with a brief presentation time, even when the memory interval went up to 1.8 sec. In fact, irrespective of the saccade type, the data show a clear drop in size of the effect if subjects viewed the stimulus for longer than 200 msec, as captured by the fitted step function (dotted line). Interestingly, the perception task showed a similar time course although this task showed larger effects of the illusion (up to three times larger), as reported before (McCarley & Grant, 2008; van Zoest & Hunt, 2011). This perceptual time course corroborates a recent report of Bertulis, Surkys, Bulatov, and Bielevičius (2014), who also found the Müller–Lyer illusion to be strongest at early stages of visual processing and to gradually decrease with the elongation of presentation time.

The saccade results could be viewed in disagreement with the work by McCarley and colleagues, who suggested that reflexive saccades are affected less by the illusion than voluntary saccades (DiGirolamo, McCarley, Kramer, & Griffin, 2008; McCarley & Grant, 2008; McCarley et al., 2003). However, strictly speaking, their reflexive saccade condition was not truly reflexive; their participants had previewed the illusion for 506 msec before they looked at the dot presented on its vertex. In this respect, their reflexive condition mimics our deferred saccade condition, for which we found lower illusion effects (about 6%) than for truly reflexive saccades. Based on Figure 3 in McCarley et al. (2003), we estimated their illusion effect at 7%, which is close to the value in our study (see Fig. 1).

For completeness, we also revisited our data to check whether the illusion effect we report for the reflexive saccade condition, is a measure of an effect that in fact builds up across trials. This was not the case; the illusion effect did not differ across four consecutive bins of trials in the experiment [ANOVA, $F(3,24) = 1.7, p = .20$].

Because reflexive and memory-guided saccades behave so similarly in our experiment, even when both are tested in separate blocks of trials, they are difficult to reconcile with the What & How pathway model. This model states that memory-

guided saccades and perceptual judgments are based on a ventral representation and should therefore be highly susceptible to the illusion, while reflexive and deferred saccades are based on dorsal processing and are therefore largely immune to the illusion. Also the finding that the illusion is stronger and more robust perceptually than in saccades cannot be used to argue for the What & How pathway model (Franz, Fahle, Bulthoff, & Gegenfurtner, 2001). But the observation that the saccade and perception task have overlapping time courses, supports the alternative view that there is a shared dynamic visual representation (Yildirim & Cornelissen, 2015; van Zoest & Hunt, 2011), even though the two tasks may not necessarily need to tap into this representation at the same level.

If a common visual representation, originating in primary visual cortex (V1) drives both perception and action, one could ask why blindsight patients with lesions in V1 can still make accurate saccades to stimuli presented in the blind field (Danckert & Rossetti, 2005; Goodale & Milner, 2004). One explanation is that, despite a V1 lesion, visual information can still reach the saccade areas in parietal and frontal cortex through other connections (Lyon, Nassi, & Callaway, 2010; Salin & Bullier, 1995). Furthermore, if the V1-bypassing projections also have chromatic and shape sensitivity, this explanation can also explain why blindsight patients can correctly guess the shapes and colors of items without consciously perceiving them (Weiskrantz, Cowey, & Hodinott-Hill, 2002). This suggests that the lesion does not block the complete access of perception to these attributes, which would be consistent with the idea that perception and action make use of the same information. Because this information is inherently redundant, it is possible that two different tasks (even within the same domain) can make use of aspects of this information.

One could argue that the susceptibility to the illusion reflects the way the visual system processes scenes in a functional separation of spatial frequencies (DeValois & DeValois, 1990). Low spatial frequency filters, as implemented by the fast magnocellular/dorsal pathway, process coarse visual information and high pass filters, implemented by the slow parvocellular/ventral pathway, provide fine detail (Kauffmann, Ramanoël, & Peyrin, 2014). Within this notion, the longer the illusion is viewed the better the real metrics can be computed and the smaller the illusion effect. However, this reasoning would not explain why the illusion effect differs for saccades directed along the illusion compared to when starting from a position perpendicular to the illusion (De Grave et al., 2006).

If the 'what' and 'how' rely on a dynamic visual representation, why do the illusion effects decrease after 200 msec? A possible answer could be found in the notion that cortical streams for vision are hierarchically organized. Successive levels of the visual cortex are reached through feedforward connections within 100 msec, where elements are grouped to extract the gist of scene, including the illusory context (Clarke & Tyler, 2015; Lamme & Roelfsema, 2000; Schmolesky et al., 1998). This feedforward sweep is followed by a recurrent projection, such that information of high-level areas is fed back to the early regions, allowing modulations of activity in these regions based on actual grouping, which could then

reduce illusory effects but only if the scene is still visible. As a result, the first feedforward-recurrent loop of processing may take 200 msec, resulting in the large effects of the illusion with short presentation times, as we found.

If this theory is accepted, the results in Fig. 1 have two further implications. First, the memory-guided saccade and perception results suggest that visual representations cannot become more veridical when the stimulus is no longer present, even though there may still be time for processing. Second, the deferred saccade and the perception results suggest that the spatial representation of the target does not improve any further after a presentation time of about 200 msec.

The results could be reconciled with the What & How pathway model by assuming that the dorsal spatial processing (i.e., in the parietal cortex) in itself is insensitive to the illusory context, but that the ventral spatial representation would influence the motor output at some stage (e.g., via the frontal cortex; Schall, Morel, King, & Bullier, 1995). An alternative explanation – inconsistent with the What & How pathway model – is that the dorsal stream itself is sensitive to illusory context. To test between these possibilities, in the next section we will describe a task that requires dorsal processing and allows for studying the activity in the pathways by fMRI (de Brouwer, Smeets, Gutteling, Toni, & Medendorp, 2015).

4. Track the dot

The allocentric representation of spatial arrangements of objects in the ventral visual stream can be considered viewer-invariant and thus remains constant during self-motion. The egocentric representation of a target in the dorsal visual stream that is used to guide actions like saccades, however, needs updating when the observer moves. This process, called visuomotor updating, is known to also reside in the dorsal stream (for reviews see Klier & Angelaki, 2008; Medendorp, 2011). According to the What & How pathway model, the dorsal stream is immune to contextual illusions, so the visuomotor updating processes should be immune as well. We recently tested this proposal, for which we used a double-step saccade task.

In the double-step task, subjects make sequential saccades to two targets that are flashed in quick succession and have disappeared before the start of the first saccade (Hallett & Lightstone, 1976). Thus, to guide the second saccade, its spatial dimensions must be computed based on the initial retinal coordinates of the target and the metrics of the intervening first saccade. We used this task such that it required visuomotor updating within the context of the Brentano version of the Müller–Lyer illusion. The Brentano illusion is the ‘double’ version of the Müller–Lyer illusion, consisting of two connected horizontal lines of which one appears shorter than the other, depending in the configuration of the arrowheads.

For single saccades, the Brentano illusion is known to cause a systematic amplitude error (i.e., a deviation from the ideal saccadic displacement) if the saccade is directed along the illusion, but not a direction error if it starts from a position perpendicular to the orientation of the illusion (De Grave et al.,

2006). Thus the position of the target can be accurately encoded relative to a fixation position outside the illusion. We reasoned that this error provides the opportunity to test the effect of the illusion in a visuomotor updating task. If participants briefly view the illusion with a target at its middle vertex, but only saccade to this target after an intervening saccade to a target perpendicular to the illusion, then there are two possible outcomes. First, if visuomotor updating is immune to the illusion, the endpoint of the second saccade will be correct, as if it were a single saccade from the perpendicular position. In contrast, if visuomotor updating is affected by the illusion, the endpoint of the second saccade would show an error as if the saccade were directed along the illusion.

Our results clearly demonstrated an effect of the illusion on the visuomotor updating process (Fig. 2), although illusion effects were stronger in some subjects than others. When subjects viewed the target embedded within the illusion, and made a saccade to it after they deviated their eyes to a position perpendicular to the illusion, they made the same saccade errors as if they had moved their eyes to this target without the intervening saccade (Fig. 2A). In other words, it looks like they were making the second saccade based on an updated, but illusory target vector.

One could argue that in this task, in which the two targets are presented sequentially, subjects could only rely on a visuomotor updating strategy to perform the second saccade. For instance, if the two targets were presented simultaneously instead, the brain could also code the dimensions of the second saccade based on the allocentric information about the location of the second saccade target relative to the first, which should result in an accurate second saccade. But this is not what happened (de Brouwer, Medendorp, & Smeets, 2016). The illusion caused systematic errors in the endpoint of the second saccade, irrespective of whether the targets were presented sequentially or simultaneously. The illusion effect on double-step saccades was similar to the effect on single saccades along the illusion, suggesting that our participants used an egocentric visuomotor updating strategy. Of note, we did find a reduced variability in saccade endpoints when allocentric information was consistently available, but not when its presence varied from trial to trial. Thus, although there was a small benefit of allocentric information, we conclude that egocentric visuomotor updating dominates in a double-step saccade task within an illusory context. This process, however, operates on illusory target positions.

This experimental result in itself is not more in conflict with the What & How pathway model than the result that single saccades are affected by the illusion. However, unlike the single-saccade task, this visuomotor updating task allows us to investigate the question whether these behavioral results indeed reflect the neural representation of the illusory target in the dorsal visual stream. We tested this by using a visuomotor updating task in an fMRI scanner.

5. A bold question

The double-step paradigm allows for an even more direct test of the What & How pathway model. For this, we rely on a

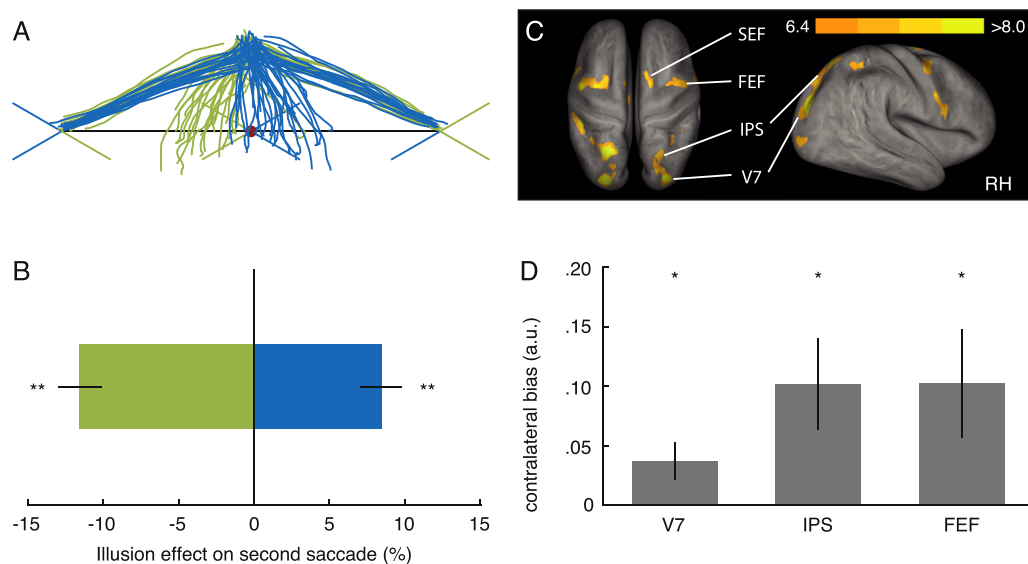


Fig. 2 – Spatial updating within an illusory context. A. First and second saccade trajectories (in green or blue) of a single subject, starting from either the left or right side of the illusion with the configuration (arrowheads) in the corresponding color. The illusion was not visible when the saccades were executed. **B.** Horizontal bias of the second saccade, averaged across participants, depends on the illusion configuration. For both illusion configurations, the bias is significantly different from zero. $**p < .001$. **C.** BOLD response during the execution of the second saccade, presented on an inflated brain. Data is the average of 22 participants. SEF = supplementary eye fields, FEF = frontal eye fields, IPS = intraparietal sulcus, V7 = visual area 7. **D.** Lateralization of the BOLD response prior to the second saccade due to the illusory context. Error bars indicate standard errors across participants. $*p < .05$.

fundamental organizing principle in the cerebral cortex: topography. Over the last ten years, imaging studies have shown various topographic areas along the dorsal visual stream involved in spatial coding and saccade planning, including extrastriate, parietal and frontal regions (Curtis & D'Esposito, 2003; Jerde & Curtis, 2013; Schluppeck, 2006; Sereno, Pitzalis, & Martinez, 2001; Silver & Kastner, 2009). These regions show a higher BOLD signal when a saccade is planned toward a target in the contralateral visual field than to a location in the ipsilateral field.

Using fMRI, Medendorp, Goltz, Vilis, and Crawford (2003) have previously exploited the contralateral topography to test the ramifications of visuomotor updating processes in the brain. They showed, using a double saccade paradigm, that when the first saccade reversed the horizontal direction of the remembered target of the second saccade, there is a reorganization of BOLD activity across the two cortical lobules, with the highest signal in the hemisphere contralateral to the hemifield that covers the remapped location of the target. This shows that the brain dynamically updates the target of saccade in an eye-centered reference frame.

We reasoned that this approach could also be applied to test visuomotor updating mechanisms in the context of the Brentano illusion. Following the behavioral results, we hypothesized that if the target representation in the dorsal visual stream is affected by the context of the illusion, we expect that for a target that is remembered to the left of its actual position, it is more strongly represented in the right dorsal stream when updated after the first saccade. Vice versa, for a target that is remembered to the right of its actual position, we expect a stronger representation in left dorsal stream when

updated after the first saccade. In contrast, if visuomotor updating operates with the physical position of the target, the neural activation in the dorsal stream would not be related to the illusion.

We used a rapid event-related design to address this question, following the behavioral paradigm described above. Because the time interval prior to the second saccade was varied, we were able to separate the processing in this interval from the motor-related activity of the preceding first saccade or the forthcoming second saccade. Moreover, we pseudorandomly interleaved the two illusion configurations and subtracted the associated BOLD responses so that positive results would only be obtained if the update of the target representation of the second saccade is affected by the illusion.

Our results show a clear effect of the illusion on the spatial selectivity of the BOLD signal in extrastriate area V7, the intraparietal sulcus and the frontal eye fields (Fig. 2C and D). We did not find an across-subject correlation between the size of the illusion effect and the tuning of the BOLD signal, which may be related to the small size of the effects. These findings indicate that areas in the dorsal visual stream are sensitive to visual context: they represent perceived rather than physical target locations (de Brouwer et al., 2015).

These results thus speak to the question of whether the modulation of neural activity we found occurred as a result of interactions with the ventral visual stream, or whether the dorsal stream itself is sensitive to visual context. One could argue that if the illusion effects have a sole ventral basis, they can only penetrate into the planning of single saccades through direct ventral modulations of the dorsal oculomotor

maps. Based on the illusion effects reported for single saccades, such a ventral–dorsal interaction will cause amplitude biases for saccades along the illusion but not for saccades directed orthogonal to the illusion. Therefore, if the visuomotor updating mechanism operates with correct target locations, a direct ventral inflection would not affect the updated representation after the first saccade. Because we found a spatial bias in the BOLD signal prior to the second saccade, i.e., in relation to the updated target, we suggest that the target representation in the dorsal stream itself is affected by the illusion.

No other studies have exploited a saccadic updating paradigm to distinguish between ventral and dorsal processing, making it difficult to place these results in a broader imaging context. A series of studies by Weidner, Fink, and colleagues have investigated the neural processes behind the perception of the Müller–Lyer illusion using MEG and fMRI (Plewan, Weidner, Eickhoff, & Fink, 2012; Weidner & Fink, 2007; Weidner, Boers, Mathiak, Dammers, & Fink, 2010). They showed that the bilateral lateral occipital cortex, part of the ventral visual stream, and the right superior parietal cortex, part of the dorsal stream, are both involved in processing the illusion, with bidirectional connections between the two areas (Plewan et al., 2012). Saber, Pestilli, and Curtis (2015) showed recently that saccade planning evokes topographically specific activity in the dorsal and ventral streams. Other studies have shown that the ventral as well as the dorsal stream contain object representations, even when action planning is not involved (Konen & Kastner, 2008; Roth & Zohary, 2015). All these observations are in general support of the present results.

6. Summary and conclusion

In 1992, Goodale and Milner proposed a functional distinction between the ventral and dorsal visual stream. They originally argued that the processing of visual information for perception ('what') and memory-guided action takes place in the ventral visual stream, whereas the processing of visual information for visually-guided action ('how') takes place in the dorsal visual stream. An interesting implication of this What & How pathway model is that perception and memory-guided movement are highly sensitive to visual contextual illusions, whereas visually-guided movements are largely immune to these illusions.

The findings of the experiments reviewed do not support a strong version of this original model. We report a robust effect of the Müller–Lyer or Brentano illusion on saccades, indicating that saccades are not immune to visual illusions.

We further report that illusions affect visually-guided and memory-guided saccades similarly, suggesting that a common representation drives these movements. The time-dependent modulation of the illusion effects can be explained by a hierarchical model of visual processing, in which contributions of feedforward and recurrent processing determine what one perceives and how one acts.

We further describe that visuomotor updating – a function of the dorsal visual stream – is affected by the illusion. The BOLD response in areas in the dorsal visual stream is

modulated by the configuration of the illusion. This demonstrates that not only the ventral stream, but also the dorsal stream, is sensitive to visual context. This adds to the idea, supported by previous literature (Schenk & McIntosh, 2010), that there is no absolute functional distinction between the two streams, but rather that they manifest a strong interconnected network, sharing various processing characteristics (de Haan & Cowey, 2011).

Whether the observations that we report should be interpreted as a falsification of the What & How pathway model, or rather suggest a refinement of the model is a semantic discussion. Our result cannot be taken to imply that no other functional distinctions between the two streams exist, for example, between egocentric versus allocentric coding. At the very least, as argued by other researchers (e.g., Schenk & McIntosh, 2010; Schenk, Franz, & Bruno, 2011), our results suggest that functional specializations of the dorsal and ventral visual stream are relative rather than absolute.

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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, 679–685.
- Bernardis, P., Knox, P., & Bruno, N. (2005). How does action resist visual illusion? Uncorrected oculomotor information does not account for accurate pointing in peripersonal space. *Experimental Brain Research*, 162(2), 133–144. <http://dx.doi.org/10.1007/s00221-004-2121-9>.
- Bertulis, A., Surkys, T., Bulatov, A., & Bielevičius, A. (2014). Temporal dynamics of the Opperl-Kundt illusion compared to the Müller-Lyer illusion. *Acta Neurobiologiae Experimentalis*, 74(4), 443–455.
- Binsted, G., & Elliott, D. (1999). The Müller-Lyer illusion as a perturbation to the saccadic system. *Human Movement Science*, 18(1), 103–117. [http://dx.doi.org/10.1016/S0167-9457\(98\)00038-4](http://dx.doi.org/10.1016/S0167-9457(98)00038-4).
- Brenner, E., & Smeets, J. B. J. (1996). Size illusion influences how we lift but not how we grasp an object. *Experimental Brain Research*, 111(June), 473–476. <http://dx.doi.org/10.1007/BF00228737>.
- de Brouwer, A. J., Brenner, E., Medendorp, W. P., & Smeets, J. B. J. (2014). Time course of the effect of the Müller-Lyer illusion on saccades and perceptual judgments. *Journal of Vision*, 14(1), 1–11. <http://dx.doi.org/10.1167/14.1.4>.
- de Brouwer, A. J., Brenner, E., & Smeets, J. B. J. (2016). Keeping a target in memory does not increase the effect of the Müller-Lyer illusion on saccades. *Experimental Brain Research*, 234(4), 977–983. <http://dx.doi.org/10.1007/s00221-015-4520-5>.
- de Brouwer, A. J., Medendorp, W. P., & Smeets, J. B. (2016 Nov 1). Contributions of gaze-centered and object-centered coding in a double-step saccade task. *Journal of Vision*, 16(14), 12. <http://dx.doi.org/10.1167/16.14.12>.

- de Brouwer, A. J., Smeets, J. B. J., Gutteling, T. P., Toni, I., & Medendorp, W. P. (2015). The Müller-Lyer illusion affects visuomotor updating in the dorsal visual stream. *Neuropsychologia*, 77, 119–127. <http://dx.doi.org/10.1016/j.neuropsychologia.2015.08.012>.
- Bruno, N., Knox, P. C., & de Grave, D. D. J. (2010). A meta-analysis of the effect of the Müller-Lyer illusion on saccadic eye movements: No general support for a dissociation of perception and oculomotor action. *Vision Research*, 50(24), 2671–2682. <http://dx.doi.org/10.1016/j.visres.2010.09.016>.
- Clarke, A., & Tyler, L. K. (2015). Understanding what we see: How we derive meaning from vision. *Trends in Cognitive Sciences*, 19(11), 677–687. <http://dx.doi.org/10.1016/j.tics.2015.08.008>.
- Curtis, C. E., & D'Esposito, M. (2003). Success and failure suppressing reflexive behavior. *Journal of Cognitive Neuroscience*, 15(3), 409–418. <http://dx.doi.org/10.1162/089892903321593126>.
- Danckert, J., & Rossetti, Y. (2005). Blindsight in action: What can the different sub-types of blindsight tell us about the control of visually guided actions? *Neuroscience and Biobehavioral Reviews*, 29(7), 1035–1046. <http://dx.doi.org/10.1016/j.neubiorev.2005.02.001>.
- De Grave, D. D. J., Smeets, J. B. J., & Brenner, E. (2006). Why are saccades influenced by the Brentano illusion? *Experimental Brain Research*, 175, 177–182. <http://dx.doi.org/10.1007/s00221-006-0536-1>.
- De Valois, R. L., & De Valois, K. K. (1990). *Spatial vision*. In *Oxford psychology series 14*. New York: Oxford University Press.
- 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. <http://dx.doi.org/10.1080/13506280701339160>.
- Fracasso, A., Targher, S., Zampini, M., & Melcher, D. (2013). Fooling the eyes: The influence of a sound-induced visual motion illusion on eye movements. *PLoS One*, 8(4), e62131. <http://dx.doi.org/10.1371/journal.pone.0062131>.
- Franz, V. H., Fahle, M., Bülthoff, H. H., & Gegenfurtner, K. R. (2001). Effects of visual illusions on grasping. *Journal of Experimental Psychology: Human Perception and Performance*, 27(5), 1124–1144. <http://dx.doi.org/10.1037/0096-1523.27.5.1124>.
- Franz, V. H., Gegenfurtner, K. R., Bülthoff, H. H., & Fahle, M. (2000). Grasping visual illusions: No evidence for a dissociation between perception and action. *Psychological Science*, 11(1), 20–25.
- Gallivan, J. P., Cant, J. S., Goodale, M. A., & Flanagan, J. R. (2014). Representation of object weight in human ventral visual cortex. *Current Biology*, 24(16), 1866–1873. <http://dx.doi.org/10.1016/j.cub.2014.06.046>.
- Goodale, M. A., Meenan, J. P., Bülthoff, H. H., Nicolle, D. A., Murphy, K. J., & Racicot, C. I. (1994). Separate neural pathways for the visual analysis of object shape in perception and prehension. *Current Biology*, 4(7), 604–610. [http://dx.doi.org/10.1016/S0960-9822\(00\)00132-9](http://dx.doi.org/10.1016/S0960-9822(00)00132-9).
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–25. [http://dx.doi.org/10.1016/0166-2236\(92\)90344-8](http://dx.doi.org/10.1016/0166-2236(92)90344-8).
- Goodale, M. A., & Milner, A. D. (2004). *Sight unseen: An exploration of conscious and unconscious vision*. Oxford University Press.
- Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, 349, 154–156.
- de Haan, E. H. F., & Cowey, A. (2011). On the usefulness of “what” and “where” pathways in vision. *Trends in Cognitive Sciences*, 15(10), 460–466. <http://dx.doi.org/10.1016/j.tics.2011.08.005>.
- 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. *Current Biology*, 11(3), 177–181. [http://dx.doi.org/10.1016/S0960-9822\(01\)00023-9](http://dx.doi.org/10.1016/S0960-9822(01)00023-9).
- Hallett, P. E., & Lightstone, A. D. (1976). Saccadic eye movements towards stimuli triggered by prior saccades. *Vision Research*, 16(1), 107–114.
- Hesse, C., Ball, K., & Schenk, T. (2012). Visuomotor performance based on peripheral vision is impaired in the visual form agnostic patient DF. *Neuropsychologia*, 50(1), 90–97. <http://dx.doi.org/10.1016/j.neuropsychologia.2011.11.002>.
- Himmelbach, M., Boehme, R., & Karnath, H. O. (2012). 20 years later: A second look on DF's motor behaviour. *Neuropsychologia*, 50(1), 139–144. <http://dx.doi.org/10.1016/j.neuropsychologia.2011.11.011>.
- Jackson, S. R., & Shaw, A. (2000). The Ponzo illusion affects grip-force but not grip-aperture scaling during prehension movements. *Journal of Experimental Psychology: Human Perception and Performance*, 26(1), 418–423. <http://dx.doi.org/10.1037//0096-1523.26.1.418>.
- Jakobson, L. S., Archibald, Y. M., Carey, D. P., & Goodale, M. A. (1991). A kinematic analysis of reaching and grasping movements in a patient recovering from optic ataxia. *Neuropsychologia*, 29(8), 803–809.
- Jerde, T. A., & Curtis, C. E. (2013). Maps of space in human frontoparietal cortex. *Journal of Physiology, Paris*, 107(6), 510–516. <http://dx.doi.org/10.1016/j.jphysparis.2013.04.002>.
- Kauffmann, L., Ramanoël, S., & Peyrin, C. (2014). The neural bases of spatial frequency processing during scene perception. *Frontiers in Integrative Neuroscience*, 8, 37. <http://dx.doi.org/10.3389/fnint.2014.00037>.
- 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>.
- Knox, P. C. (2006). The effect of Kanizsa's compression illusion on reflexive saccades. *Experimental Brain Research*, 175(4), 764–768. <http://dx.doi.org/10.1007/s00221-006-0741-y>.
- Konen, C. S., & Kastner, S. (2008). Representation of eye movements and stimulus motion in topographically organized areas of human posterior parietal cortex. *Journal of Neuroscience*, 28(33), 8361–8375. <http://dx.doi.org/10.1523/JNEUROSCI.1930-08.2008>.
- 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.
- Lyon, D. C., Nassi, J. J., & Callaway, E. M. (2010). A disynaptic relay from superior colliculus to dorsal stream visual cortex in macaque monkey. *Neuron*, 65(2), 270–279. <http://dx.doi.org/10.1016/j.neuron.2010.01.003>.
- 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. <http://dx.doi.org/10.3758/PBR.15.5.1008>.
- McCarley, J. S., Kramer, A. F., & DiGirolamo, G. J. (2003). Differential effects of the Müller-Lyer illusion on reflexive and voluntary saccades. *Journal of Vision*, 3(11), 751–760. <http://dx.doi.org/10.1167/3.11.9>.
- Medendorp, W. P. (2011). Spatial constancy mechanisms in motor control. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 366(1564), 476–491. <http://dx.doi.org/10.1098/rstb.2010.0089>.
- Medendorp, W. P., Goltz, H. C., Vilis, T., & Crawford, J. D. (2003). Gaze-centered updating of visual space in human parietal cortex. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 23(15), 6209–6214. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/12867504>.
- Melmoth, D., Grant, S., Solomon, J. A., & Morgan, M. J. (2015). Rapid eye movements to a virtual target are biased by illusory context in the Poggendorff figure. *Experimental Brain Research*, 233(7), 1993–2000. <http://dx.doi.org/10.1007/s00221-015-4263-3>.

- Milner, A. D., & Goodale, M. A. (2008). Two visual systems re-viewed. *Neuropsychologia*, 46(3), 774–785. <http://dx.doi.org/10.1016/j.neuropsychologia.2007.10.005>.
- Pavani, F., Boscagli, I., Benvenuti, F., Rabuffetti, M., & Farnè, A. (1999). Are perception and action affected differently by the Titchener circles illusion? *Experimental Brain Research*, 127(1), 95–101. <http://dx.doi.org/10.1007/s002210050777>.
- Pisella, L., Binkofski, F., Lasek, K., Toni, I., & Rossetti, Y. (2006). No double-dissociation between optic ataxia and visual agnosia: Multiple sub-streams for multiple visuo-manual integrations. *Neuropsychologia*, 44(13), 2734–2748. <http://dx.doi.org/10.1016/j.neuropsychologia.2006.03.027>.
- Pisella, L., Gréa, H., Tilikete, C., Vighetto, A., Desmurget, M., Rode, G., et al. (2000). An “automatic pilot” for the hand in human posterior parietal cortex: Toward reinterpreting optic ataxia. *Nature Neuroscience*, 3(7), 729–736. <http://dx.doi.org/10.1038/76694>.
- Plewan, T., Weidner, R., Eickhoff, S. B., & Fink, G. R. (2012). Ventral and dorsal stream interactions during the perception of the Müller-Lyer illusion: Evidence derived from fMRI and dynamic causal modeling. *Journal of Cognitive Neuroscience*, 24(10), 2015–2029. http://dx.doi.org/10.1162/jocn_a_00258.
- Rizzolatti, G., & Matelli, M. (2003). Two different streams form the dorsal visual system: Anatomy and functions. *Experimental Brain Research*, 153(2), 146–157. <http://dx.doi.org/10.1007/s00221-003-1588-0>.
- Rossit, S., Szymanek, L., Butler, S. H., & Harvey, M. (2010 Jan). Memory-guided saccade processing in visual form agnosia (patient DF). *Experimental Brain Research*, 200(1), 109–116. <http://dx.doi.org/10.1007/s00221-009-2074-0>.
- Roth, Z. N., & Zohary, E. (2015). Position and identity information available in fMRI patterns of activity in human visual cortex. *The Journal of Neuroscience*, 35(33), 11559–11571. <http://dx.doi.org/10.1523/JNEUROSCI.0752-15.2015>.
- Saber, G. T., Pestilli, F., & Curtis, C. E. (2015). Saccade planning evokes topographically specific activity in the dorsal and ventral streams. *The Journal of Neuroscience*, 35, 245–252.
- Salin, P. A., & Bullier, J. (1995). Corticocortical connections in the visual system: Structure and function. *Physiological Reviews*, 75(1), 107–154. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/7831395>.
- Schall, J. D., Morel, A., King, D. J., & Bullier, J. (1995). Topography of visual cortex connections with frontal eye field in macaque: Convergence and segregation of processing streams. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 15(6), 4464–4487. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/7540675>.
- 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? *Vision Research*, 51(8), 812–818. <http://dx.doi.org/10.1016/j.visres.2011.02.003>.
- Schenk, T., & McIntosh, R. D. (2010). Do we have independent visual streams for perception and action? *Cognitive Neuroscience*, 1(1), 52–78. <http://dx.doi.org/10.1080/17588920903388950>.
- Schluppeck, D. (2006). Sustained activity in topographic areas of human posterior parietal cortex during memory-guided saccades. *Journal of Neuroscience*, 26(19), 5098–5108. <http://dx.doi.org/10.1523/JNEUROSCI.5330-05.2006>.
- Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., Schall, J. D., et al. (1998). Signal timing across the macaque visual system. *Journal of Neurophysiology*, 79(6), 3272–3278. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9636126>.
- Sereno, M., Pitzalis, S., & Martinez, A. (2001). Mapping of contralateral space in retinotopic coordinates by a parietal cortical area in humans. *Science*, 294(November), 1350–1354. Retrieved from <http://www.sciencemag.org/content/294/5545/1350.short>.
- Silver, M. A., & Kastner, S. (2009). Topographic maps in human frontal and parietal cortex. *Trends in Cognitive Sciences*, 13(11), 488–495. <http://dx.doi.org/10.1016/j.tics.2009.08.005>.
- Smeets, J. B. J., & Brenner, E. (2006). 10 years of illusions. *Journal of Experimental Psychology: Human Perception and Performance*, 32(6), 1501–1504. <http://dx.doi.org/10.1037/0096-1523.32.6.1501>.
- Stöttinger, E., Soder, K., Pfusterschmied, J., Wagner, H., & Perner, J. (2010). Division of labour within the visual system: Fact or fiction? Which kind of evidence is appropriate to clarify this debate? *Experimental Brain Research*, 202(1), 79–88. <http://dx.doi.org/10.1007/s00221-009-2114-9>.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). The Massachusetts Institute of Technology. <http://dx.doi.org/10.1093/cercor/bhg093>.
- Weidner, R., Boers, F., Mathiak, K., Dammers, J., & Fink, G. R. (2010). The temporal dynamics of the Müller-Lyer illusion. *Cerebral Cortex*, 20(7), 1586–1595. <http://dx.doi.org/10.1093/cercor/bhp217>.
- Weidner, R., & Fink, G. R. (2007). The neural mechanisms underlying the Müller-Lyer illusion and its interaction with visuospatial judgments. *Cerebral Cortex*, 17(4), 878–884. <http://dx.doi.org/10.1093/cercor/bhk042>.
- Weiskrantz, L., Cowey, A., & Hodinott-Hill, I. (2002). Prime-sight in a blindsight subject. *Nature Neuroscience*, 5(2), 101–102. <http://dx.doi.org/10.1038/nn793>.
- Yarbus, A. L. (1967). *Eye movements during perception of complex objects*. In *Eye movements and vision* (pp. 171–211). New York: Plenum Press.
- Yildirim, F., & Cornelissen, F. W. (2015). Saccades follow perception when judging location. *i-Perception*, 6(6). <http://dx.doi.org/10.1177/2041669515619513>, 2041669515619513.
- 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. <http://dx.doi.org/10.1016/j.visres.2010.10.013>.