

The neural mechanisms underlying the Müller-Lyer illusion and its interaction with visuospatial judgments

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Abstract

Arrows terminating a line can distort the perceived line-length. This so called Müller-Lyer illusion can be used in healthy human subjects to mimic the performance of neglect patients in visuospatial judgments (e.g., in the landmark task). In this study we investigated the neural mechanisms underlying the Müller-Lyer illusion, the landmark task and their interaction. This was achieved by parametrically manipulating the magnitude of the Müller-Lyer illusion both in a landmark and a luminance (control) task. As expected (e.g., Fink et al. 2000), the landmark task activated right posterior parietal cortex and right temporo-occipital cortex. In contrast, the neural processes associated with the strength of the Müller-Lyer illusion were located bilaterally in lateral occipital cortex as well as right superior parietal cortex. The data converge with but also extend neuropsychological data which indicate maintained line-length illusion in neglect patients. In addition, our results support the size-constancy scaling hypothesis (Gregory, 1968) as a putative mechanism underlying line-length illusions. Furthermore, activation that was driven by both the task as well as the strength of the Müller-Lyer illusion was observed in right intraparietal sulcus (IPS) thus arguing in favour of an interaction of illusory information with the top-down processes underlying visuospatial judgements in right parietal cortex.

Introduction

Visuospatial neglect is often associated with impaired visuospatial judgements as expressed by, e.g., an inability to correctly bisect a horizontal line, i.e., impaired performance of the line bisection task (see, e.g., Marshall & Halligan, 1989). That this impairment is perceptual rather than motor intentional or premotor can be demonstrated using the Landmark task, a perceptual variant of the line-bisection task (Milner et al., 1993; Bisiach et al., 1998). In this task, patients fail to correctly judge whether a pre-bisected line has been accurately bisected or not.

Interestingly, visuospatial judgements involved in the landmark task can also be distorted in healthy subjects. For example, performance in the landmark or the line bisection task can be manipulated when the stimuli used are combined with a variant of the Müller-Lyer illusion (Müller-Lyer, 1889). In the Müller-Lyer illusion the length of a line is overestimated when its ends are terminated with arrows pointing inward ($><$) and is underestimated when its ends are terminated with arrows pointing outward ($<>$). Combining the Müller-Lyer illusion stimuli with landmark stimuli results in the Brentano version of the Müller-Lyer illusion. This type of the illusion uses three arrows that are arranged in such a way that one half of the line is apparently expanded while the other half appears to be compressed (Fig. 1). This illusion can then result in an incorrect judgement of a pre-bisected line: The position of an arrow that appears to correctly bisect a horizontal line in the middle is actually shifted.

Despite the similarity of the illusion-induced impairment of a visuospatial judgement and the performance of neglect patients, the two phenomena are often considered to have different origins (Vallar et al., 2000): The illusory effects induced by the Müller-Lyer figures can be preserved in patients with visuospatial neglect (Ro & Rafal, 1996) and these effects persist irrespective of the illusion inducing arrows being presented within or outside the neglected visual hemifield (Vallar et al., 2000, Olk et al. 2001; Mattingley et al. 1995). Accordingly, Vallar et al. (2000) and Daini et al. (2001) suggested that the neural structures involved in generating the Müller-Lyer illusion may reside in areas different from those which when lesioned may cause neglect, e.g., extrastriate cortex.

Evidence for an involvement of early visual processes in the generation of the Müller-Lyer illusion has recently been reported by Busch & Müller (2004; see also Rensink & Enns, 1995). In a behavioural study they demonstrated that information generated by the illusion is capable to generate pop-out in visual search tasks. This finding implicates a pre-attentive representation of illusory information as has been suggested for other visual illusions, e.g., the Kanizsa illusion (Ffytche & Zeki, 1996; Ritzl et al., 2003) or the Ebbinghaus illusion (Busch & Müller, 2004). Nevertheless, the magnitude of the illusion can be influenced by top-down control. Tsal (1984) demonstrated that an observer can deliberately change the magnitude of the Müller-Lyer line length illusion by selectively orienting spatial attention to the illusion-inducing wings.

The current study was designed to answer two questions. First, we intended to replicate the results of earlier studies investigating the neural correlates of the landmark task (Fink et al. 2000; 2002; 2003; Weiss et al., 2003). Second and more importantly, we were interested in the neural basis of the Müller-Lyer illusion and its interaction with top-down processes. We accordingly investigated the neural effects induced by the Müller-Lyer illusion and whether these differed depending on the task relevance of the line length. Using fMRI we employed a variant of the landmark task based upon the Brentano version of the Müller-Lyer illusion (explained in Fig. 1). Subjects were asked to judge whether or not a horizontal line was correctly pre-bisected. For control, subjects had to decide whether the upper and the lower fin of the middle of the three arrows were of the same or of a different luminance. In both conditions the magnitude of the induced length illusion was varied systematically by changing the angle between the two fins of the illusion inducing arrows.

Figure 1 about here

Based on previous work we expected the landmark task to activate a right lateralized network of brain areas involving superior and inferior parietal cortex (Fink et al., 2000; 2001; 2002; 2003;

Weiss et al., 2003). The Müller-Lyer illusion was hypothesized to involve extrastriate visual areas as predicted by Vallar et al. (2000) and as demonstrated for other visual illusions (Ffytche & Zeki, 1996; Ritzl et al., 2003).

Materials and Methods

Participants

Fifteen subjects (6 female) participated in a single fMRI session. All observers were right-handed, as assessed by the Edinburgh Handedness Inventory (Oldfield, 1971). Participants' ages ranged from 19 to 29 years with a mean age of 25. All subjects gave informed consent prior to the experiment in accordance with the Helsinki declaration.

Stimuli

Stimuli were displayed by an LCD projector on a back-projection screen mounted in the bore of the magnet in front of the subject's head. The screen was seen via a mirror system which was mounted on top of the head coil.

At one of four possible locations on the screen a pre-bisected horizontal line (with a length of 9.7° visual angle) was presented. This line was bisected by an arrow. Two more arrows were presented at the line's ends (Figure 1). Across trials the arrow bisecting the horizontal and the two arrows at the line's ends were independently varied in three aspects: i) regarding the angles between the arrows' fins, ii) the position at which the horizontal line was bisected, and iii) the luminance of the bisection arrows' fins.

Figure 2 about here

Angles

The strength of the Müller-Lyer line-length illusion was parametrically varied, by modifying the

angle between the fins of the illusion inducing arrows (Fig. 2). Parametric variation was assigned randomly on a trial by trial basis. The fins of the bisection arrow and the arrows at the two ends of the horizontal line were counterrotated, i.e. an angle α between the fins of the inner arrow resulted in an angle $\beta = (360^\circ - \alpha)$ between the fins of the outer arrows (Fig. 2). With this procedure α -values smaller than 180° were supposed to increase the perceived length of the left half and to decrease the perceived length of the right half of the horizontal line, whereas α -values greater than 180° were supposed to lead to converse effects. No illusion was expected to be evoked by $\alpha = 180^\circ$.

In order to specify the magnitude of the illusion induced, each subject performed a psychophysical pre-test in the MR-scanner. Subjects were presented with the stimuli described above, with the bisecting arrow either shifted to the left or to the right end of the line. The stimuli were presented at one of four different locations (i.e., upper/left, upper/right, lower/left, or lower/right, relative to the centre of the screen). On each trial, the position was assigned randomly with the constraint that no position was repeated on consecutive trials. The subjects' task was to decide whether the bisection arrow was shifted to the left or to the right from their perceived line-centre and to indicate this via button press (left button presses were to be used when the bisection arrow was shifted to the left and right button presses when the bisection arrow was shifted to the right). On the basis of the adaptive modified binary search (MOBS) algorithm described by Tyrrell & Owens (1988) the position of the bisecting arrow was varied until the difference between a right and a left choice decision was smaller than 0.1° visual angle. This position was regarded as the participants straight-ahead and was taken as indicative of the apparent line-center. The distance between this position and the real line-center reflected the illusion magnitude. This procedure was carried out for all 7 angle configurations in order to estimate the illusion strength induced by each angle configuration. Figure 2 (right column) shows the deviations of the apparent line-centers from the real line-center separate for all angle configurations averaged across subjects.

Position of bisection

The bisecting arrow was located at one of seven possible positions, each position was equally likely and varied randomly from trial to trial. The positions were derived by the psychophysical pre-test described above. Therefore each position matched the subject's apparent line-center for one of the different angle configurations. Hence, for each angle configuration an apparently correct bisected line was observed in one seventh of all cases.

Luminance of fins

On each trial one of the two fins of the inner arrow was randomly selected and its luminance was assigned to one of seven possible luminance values. One of these luminance values matched the luminance of the remaining fin. Therefore in one seventh of all trials the luminance of the upper and lower fin of the middle arrow were of equal luminance. The luminance values were graded and linearly scaled on the basis of the illusion magnitudes estimated for the length illusion.

The just noticeable difference (JND) was separately determined for luminance differences and line displacement. The mean magnitude of the length illusion induced by an increase of $\alpha=45^\circ$ was estimated. This value was then divided by the accordant line-displacement JND. The illusion could then be expressed in JND units. This factor was used to determine the values of the luminance parameters such that the difference between the different luminance values matched the difference in apparent line length in terms of JNDs.

Task & Design

Trials were presented blockwise embedded in blocks consisting of 7 trials. Trial duration was 2 s followed by an intertrial-interval (ITI) of either 0.5 or 1.5 s. Prior to each block, a task instruction was presented for three seconds, informing the subject whether to perform the landmark task (instruction: "length") or the control task (instruction: "luminance") or whether a baseline block (instruction: "break") was presented. 24 blocks of each sort were presented in a randomized order.

In the landmark task, subjects were asked to judge whether the line was correctly pre-bisected

and to indicate this via button press. Apparently correct pre-bisected lines required a middle finger button press, apparently incorrect pre-bisected lines required a button press via the index finger.

In the control task, subjects were asked to judge luminance-differences between the upper and the lower part of the bisection-arrow. When there was no luminance difference this was to be indicated via a middle finger button press, differences in luminance were to be indicated via an index-finger button press.

fMRI Measurement

Functional images were acquired on a 1.5 Tesla SONATA MRI system (Siemens, Erlangen, Germany) using a T2*-weighted echo planar (EPI) sequence (TR = 3.02 s, TE=66 ms). 593 volumes were acquired each consisting of thirty axial slices, allowing for whole brain coverage. Slice thickness was 4 mm and interslice distance 0.4 mm, with a 20 cm FOV and a 64 x 64 image matrix, and a 3.1 x 3.1 x 4 mm³ voxel size. Images were spatially realigned to the fifth volume (see below) to correct for interscan movement, synchronized to the middle slice to correct for differences in slice acquisition time, and normalized to a standard EPI template volume (MNI template provided by SPM, see below). The data were then smoothed with a Gaussian kernel of 8 mm full-width half-maximum.

Data Analysis

SPM

Data were analyzed with Statistical Parametric Mapping software SPM2, Wellcome Department of Imaging Neuroscience, London (Friston et al. 1995). The first four images were excluded from the analysis, because they cover the time period the MR signal needs to reach a steady state.

Two onset regressors were defined, one for the landmark-task and one for the control condition. For each onset regressor, two additional regressors including parametric modulations were included, the first of which represented the magnitude of the induced illusion irrespective of its

direction, i.e. each onset was modulated with the absolute value of the line-center shift induced by the angle configuration in the respective trial. The second regressor included the referring luminance difference between the upper and lower fins of the inner arrow.

The haemodynamic response to each different event type was modelled using a canonical synthetic haemodynamic response function (HRF). The six head movement parameters were included as confounds.

In order to identify the main effect of the experimental task, a first level linear contrast was calculated, comparing events in the landmark task with the luminance task and (vice versa). This contrast was taken to the second level and a random effects analysis was performed employing a corrected threshold of $P < 0.01$ at the cluster level ($P < 0.001$ cutoff at the voxel level).

Likewise the effect of the parametric modulation of the illusion size was first calculated on a first level and then taken to the second level where a random effects analysis was performed using a corrected threshold of $P < 0.01$ at the cluster level ($P < 0.001$ cutoff at the voxel level). The identical procedure was carried out for the parametric modulation of luminance.

In order to assess the effect of the task on the length-illusion (and vice versa), the regressors reflecting the parametric modulation induced by the magnitude of the length illusion in the two different tasks were contrasted on a first level and then taken to the second level with a threshold of $P < 0.01$ at the cluster level ($P < 0.001$ cutoff at the voxel level).

Results

Behavioural results

The estimated illusion magnitudes were averaged for all subjects separately for each angle configuration. As predicted, α -angle values smaller than 180° shifted the subjective line-center to the left, as indicated by negative values in Figure 2 (right column). The subjective line-center shift to the left was strongest for 45° , medium for 90° and weakest for 135° . An α -angle of 180° induced a small shift to the right as indicated by positive values on the y-axis. α -angles greater than 180°

gradually increased shifts to the right side.

A one-way repeated measures analysis of variance (ANOVA) of illusion-magnitude with the factor inducing angle (levels: 45°, 90°, 135°, 180°, 225°, 270°, 315°) revealed a significant main effect ($F(1,14) = 158.97$, $MS_e = 138.379$, $p < 0.0001$).

Functional imaging

Landmark task

Activations associated with the landmark task were assessed comparing the trials in which subjects performed the landmark- or the control-task, respectively. Significant differential activations were observed in two brain areas: As expected (Fink et al., 2000; 2001; Weiss et al., 2000; 2003) a large cluster of activation was found in right superior parietal cortex spreading out to the anterior part of the intraparietal sulcus. A second activation was found in the right inferior temporal cortex at the transition to the right middle occipital gyrus (Figure 3, Table 1a). The reverse contrast did not reveal any significant differential activation at our predefined statistical criteria. Lowering the threshold to $P < 0.001$, uncorrected, differential activations were observed in the right inferior parietal cortex (46 -70 46) and the right occipital cortex (34 -90 -10).

Figure 3 + Table 1 about here

Illusion strength

Areas which correlated with the strength of the Müller-Lyer line length illusion were explored by looking at the regressor representing the parametric modulation of the illusion strength. Positive values represent activations associated with the magnitude of the illusion, i.e. those areas that show a signal increase with an increasing illusion-magnitude.

Significant activations were found bilaterally in the lateral occipital cortex with their local maxima lying in the inferior occipital gyrus. A further activation was observed at the superior end

of the right superior parietal lobule (see Figure 4 & Table 1b).

Figure 4 about here

Task and parametric modulation

In order to investigate the interaction of the task with the neural effects of the length illusion, the separate parametric regressors for both tasks reflecting the induced illusion were contrasted (Modulation regressor of the landmark task > Modulation regressor of the luminance task). This analysis revealed one single significant cluster of activation which was located in the right intraparietal sulcus. The opposite contrast revealed no significant activations (see Figure 5, Table 1c).

Figure 5 about here

Discussion

Task

As expected, stronger activations in the landmark compared to the control task were found in the right superior parietal cortex spreading out to the intraparietal sulcus and to the inferior parietal cortex, further activation was observed in the right temporo-occipital cortex. One could argue that differential eye movements across conditions could have contributed to the differential activations observed. However, if the landmark task, in combination with Müller-Lyer figures, induced a differential pattern of saccades (compared to the luminance task, in combination with Müller-Lyer figures), then the contrast Landmark > Luminance (Control) should be affected. The effects observed in this contrast, however, replicate the findings reported in previous studies investigating the landmark and the line bisection task using more typical stimuli (Fink et al. 2000; 2002; 2003; Weiss et al., 2003). It therefore seems unlikely that these neural effects are specifically related to

differential effects induced by the Müller-Lyer illusion. Furthermore, the cluster of activation observed in the current (and previous studies) does not support the view that the activations might be related to the preparation and/or execution of saccades. If this was the case, one would have expected bilateral activations of the intraparietal sulcus rather than right lateralized activation of the posterior parietal cortex. Right superior parietal activation observed in this study was previously reported by Fink et al. (2003) (maximum peak: 4 mm more medial), Fink et al. (2002) (maximum peak: 4 mm more medial; 2 mm inferior) or Fink et al. (2000) (maximum peak: 2 mm medial, 2 mm more posterior, 8 mm inferior). Activation in posterior temporal cortex at the transition to occipital cortex activation has been reported by Fink et al. (2000) (8 mm more lateral, 2 mm more posterior, 2 mm more superior). Our data confirm these findings and thereby strengthen the view, that these areas subserve visuospatial judgements. These findings are also consistent with neuropsychological data implying visual processing areas (Ferber & Karnath, 2001) and right parietal cortex (Milner et al., 1993; Bisiach et al., 1998) in the landmark task.

Illusion strength

As indicated by the behavioural data, varying the angle between the two fins of the illusion inducing wings resulted in a variation of the illusion strength. Increasing the angle of a fin from the vertical changed the induced illusion as reflected in the misjudgement of a correct line-bisection. Angles smaller than 180° led to a displacement of the position considered to represent a correct bisection of the line towards the left. This perfectly fits the predictions based on previous studies of the effect of the Müller-Lyer illusion. Negative angle values (outgoing wings on the left part of the line in combination with ingoing wings at the right part of the line) result in an overestimation of the length of the left part of the line and an underestimation of the length of the right part of the horizontal line. In order to match the apparent length of both lines, the bisection line has to be shifted to the left. Likewise, angles greater than 180° result in a displacement of the apparent line-center to the right. In our study, the strongest deviations from the real line-center, irrespective of the

direction, were observed with wing angles of $\alpha = 45^\circ$ and $\alpha = 315^\circ$. The strength of the perceived illusion (irrespective of its direction) was entered into the analysis of the functional imaging data as a regressor for the parametric modulation. Illusion size modulated the haemodynamic response bilaterally in lateral occipital cortex and in right superior parietal cortex such that these areas responded differently with increasing magnitude of the size-illusion induced by the Müller-Lyer illusion.

Lateral occipital cortex

The activation observed in lateral occipital cortex bilaterally is in good accordance with the findings of Vallar et al. (2000). Their data indicate that the length-illusion may be spared in patients with left visuospatial neglect resulting from parietal or temporo-parietal damage. They suggested that the anatomical basis of the Müller-Lyer illusion is located in occipital extrastriate cortex close to regions that are dedicated to the processing of illusory contours (Ffytche & Zeki, 1996). Daini et al. (2002) provided converging evidence for this assumption by showing that in patients with hemianopia, the lack of experiencing the illusion correlated with the degree of damage in occipital regions. Their conclusion, that the neural processes underlying the Müller-Lyer illusion are likely to occur in occipital cortex, is strongly supported by our data and is further specified by the finding that it is the lateral occipital cortex (LOC) which is critically involved in generating the Müller-Lyer illusion.

The LOC is known to subserve object recognition and the processing of object related information (Malach et al., 1995). However, what makes the LOC a likely candidate for the generation of the Müller-Lyer illusion is that it is involved in grouping processes as well as in the size-independent representation of objects. Altmann et al. (2003; see also Kourtzi & Huberle, 2005) demonstrated that the LOC participates in grouping-processes like the integration of local elements to global forms. Interestingly, grouping has been demonstrated to play an important role in the Müller-Lyer illusion (Moore & Egeth, 1997). Rensink & Enns (1995) reported that visual search for

a Müller-Lyer figure is based on complete and integrated configurations rather than on component segments. Furthermore, the LOC contains size invariant representations of object shapes that are independent of the defining low-level visual cues (Grill-Spector et al., 1999; Grill-Spector et al., 2001). Together with information about the distance of an object, which is estimated by the visual system as early as in V1 or V2 (Dobbins et al., 1998), such representations are necessary preconditions for size constancy, i.e. the ability to perceive the true size of an object irrespective of the observer's distance (see, e.g., von Helmholtz, 1910). Size constancy has been suggested to be one of the major mechanism underlying the Müller-Lyer illusion: Gregory (1968) demonstrated that size illusions induced by the Müller-Lyer figures are linked to alterations of the perceived depth. According to Gregory, the wings attached to the shaft of the Müller-Lyer illusion function as depth features which generate a spatial bias of the perceived object position towards or away from the observer. Accordingly, size constancy scaling may alter the perceived object size.

Posterior parietal cortex

In addition to the LOC, the right superior parietal cortex (SPC) contributes to the processing of the Müller-Lyer line-length illusion. Like the LOC, when lesioned in its own right, the SPC is not typically associated with visuospatial neglect. In turn, patients suffering from visuospatial neglect typically don't show length illusions deficits (Daini et al., 2002, Olk et al. 2001; Vallar et al., 2000; Mattingley et al., 1995). As mentioned above, this finding holds only as long as neglect patients do not additionally suffer from visual field deficits (Daini et al., 2002). Daini et al. (2002) suggested that the generation of the Müller-Lyer illusion thus involves occipital areas as well as areas dedicated to visuospatial processing. While a dysfunction of one of these areas can be compensated, a dysfunction of both areas results in a lack of experiencing the illusion.

Although right SPC is not typically related to visuospatial neglect it is known to be involved in a variety of tasks requiring visuospatial processing like attentional orienting, (Corbetta et al. 1993, Wojciulik & Kanwisher, 1999, Thiel et al, 2005, Giessing et al., 2004), mental rotation (Alivisatos

& Petrides, 1997; Kosslyn et al., 1998, Bestmann et al., 2002), or the preparation of pointing movements and saccades (Connolly et al., 2000; Astafiev et al. 2003). An involvement of this area in the generation of a visuospatial illusion, as demonstrated in the current study, can therefore be easily linked to visuospatial processes. For example, Andersen (1997) suggested that the posterior parietal cortex is involved in the transformation of retinotopic information into higher-order spatial reference frames. Merriam, Genovese & Colby (2003) demonstrated that posterior parietal cortex is involved in updating spatial representations. This is an important precondition to form spatially constant neural representations of the environment. Such representations are altered by the Müller-Lyer illusion. Following the size-constancy account by Gregory (1968), and given the aforementioned role of LOC, we suggest that the SPC involvement observed in our study may reflect integration processes of the stimuli affected by the Müller-Lyer illusion.

Images including depth cues are ambiguous, as they apparently provide 3D-depth information but are in fact flat. According to Gregory (1968), ambiguity is also critical for the Müller-Lyer illusion. Resolving ambiguous information is another function of posterior parietal cortex. Kleinschmidt et al. (1998) reported parietal activation in subjects watching bistable ambiguous figures like the Rubin-vase. Posterior parietal activation was observed whenever the subject's perception switched between the two percepts. Similar activations have also been observed in experiments dedicated to binocular rivalry (see e.g. Lumer et al. 1998). Funk & Pettigrew (2003) reported an involvement of parietal cortex related to the phenomenon of motion induced blindness, where moving stimuli prevent the perception of stationary dots. Thus activation in posterior parietal cortex is observed whenever perceptual ambiguities are resolved and a perceptual content is modified.

In summary, the superior parietal cortex and the lateral occipital cortex have been demonstrated to play an important role in aspects of visual processing that are essential for the generation of size-constancy and the coding of neural representations of the surrounding, as well as resolving ambiguous percepts. These processing capacities represent neural implementations of requirements

postulated by Gregory (1968) in his size-constancy theory of the Müller-Lyer illusion. We therefore suggest that the Müller-Lyer illusion is induced by an interaction of lateral occipital and superior parietal cortex. Lateral occipital cortex is supposedly involved in grouping of the line segments to an integrated Müller-Lyer figure, as well as in forming a size-invariant representation of it. 2D-depth cues and size-constancy scaling may then modify size perception. The posterior parietal cortex seems to integrate these types of information into a common spatial frame of reference and may thereby modify the percept.

Task dependent modulation

The magnitude of the Müller-Lyer illusion was differentially coded in the right IPS depending on whether subjects performed the landmark- or the luminance-task. Therefore, the Müller-Lyer illusion and top-down processes interact. As the Müller-Lyer illusion is coded pre-attentively (Rensink & Enns, 1995; Busch & Müller, 2004), the activation in the right IPS is likely to reflect an interaction of bottom-up and top-down processes. Whether this interaction reflects the integration of both streams of information or alternatively represents its effect on subsequent neural processes such as the execution of saccades is unclear. McCarley, Kramer & DiGirolamo, (2003) reported effects of the Müller-Lyer illusion on voluntary and reflexive saccades. We would then however expect activations within a network of brain areas associated with the generation of eye-movements (see e.g. Mort et al., 2003; Luna et al., 1998), which have not been observed in our study, even when the statistical criterion was lowered to $p < 0.001$ uncorrected. We therefore suggest that right IPS is involved in integrating bottom-up and top-down information.

Theoretically, the integration of both streams of information could occur on several levels of processing. First, early representations of illusory information could be altered depending on the nature of the task performed by the subjects. Accordingly, the neural representation of illusory information, which is located in LOC and SPC, should be different in the landmark compared to the luminance condition. The data do not support such an account.

Second, unchanged representations of illusory information could be handled differentially by higher level cognitive processes. If so, modulation of neural signals were expected to occur at locations associated with these processes. Actually, the interaction was observed in right IPS, which is involved in the endogenous control of visuospatial attention (see Corbetta & Shulman, 2002 for an overview) and visuospatial judgements per se (see, e.g., Fink et al., 2000). The activation was further located adjacent to the parietal activation associated with visuospatial processing in the current experiment (main contrast for task: landmark task > luminance task). We therefore suggest, that early representations of the magnitude of the illusion remain unchanged and that illusory information is differentially used by higher level cognitive processes.

Conclusions

Perceiving the Müller-Lyer line-length illusion activates neural structures involved in object perception as well as structures involved in performing visuospatial judgements. In line with the predictions based on previous neuropsychological studies (Vallar et al., 2000; Daini et al. 2002) these areas are not typically associated with visuospatial neglect. These findings are also in accordance with a model proposed by Gregory (1968) which suggests size constancy scaling as an effective mechanism for the line-length illusion. Further, illusion induced illusory line-length information and cognitive set interact in the right IPS, which suggest that the strength of the illusion selectively alters higher cognitive processes involved in visuospatial judgments.

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Table 1

Structure	Z-Score	MNI
<i>a) Landmark > Control</i>		
Superior parietal cortex	4.85	R (42 -34 44)
Inferior temporal sulcus/ Middle occipital gyrus	4.25	R (56 -58 -10)
<i>b) Illusion strength</i>		
Inferior occipital gyrus	5.10	R (36 -78 -6)
Superior parietal cortex	5.03	R (14 -66 68)
Inferior occipital gyrus	4.78	L (-46 -74 -6)
<i>c) Interaction: Illusion strength x task</i>		
Intraparietal sulcus	4.46	R (44 -52 56)

Table legends

Table 1: List of activations related to a) the landmark compared to the control task, b) the illusion strength, and c) the interaction between illusion strength and task. Coordinates were defined within MNI-space.

Figure legends:

Figure 1: Brentano version of the Müller-Lyer illusion. Subjects had to decide whether the arrow in the center correctly bisects the horizontal line (a) or not (b).

Figure 2: Left column: Example stimuli showing the seven different angle configurations.

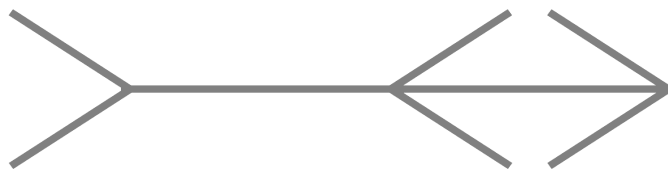
Increasing the angle α between the two fins of the arrow in the center, decreased the angle β between the fins of the arrows to the right and to the left. Right column: Bars indicate the shift of the apparent line-center from the real line-center in $^{\circ}$ visual angle, averaged for all subjects separately for different angle configurations (shown in the left column).

Figure 3: Glass-brain images and surface rendering of functional contrasts testing for stronger activations in the landmark compared to the control task.

Figure 4: Glass-brain images and surface rendering of functional contrasts testing for activation associated with the magnitude of the Müller-Lyer illusion.

Figure 5: Glass-brain images and surface rendering of functional contrasts testing for activation associated with the difference of the parametric modulation in the landmark compared to the control task.

a



b

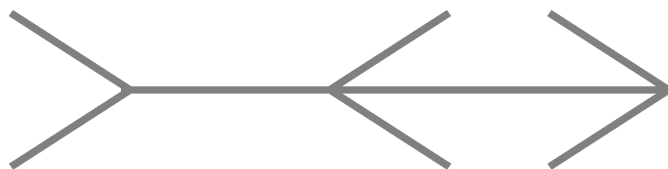


Figure 1

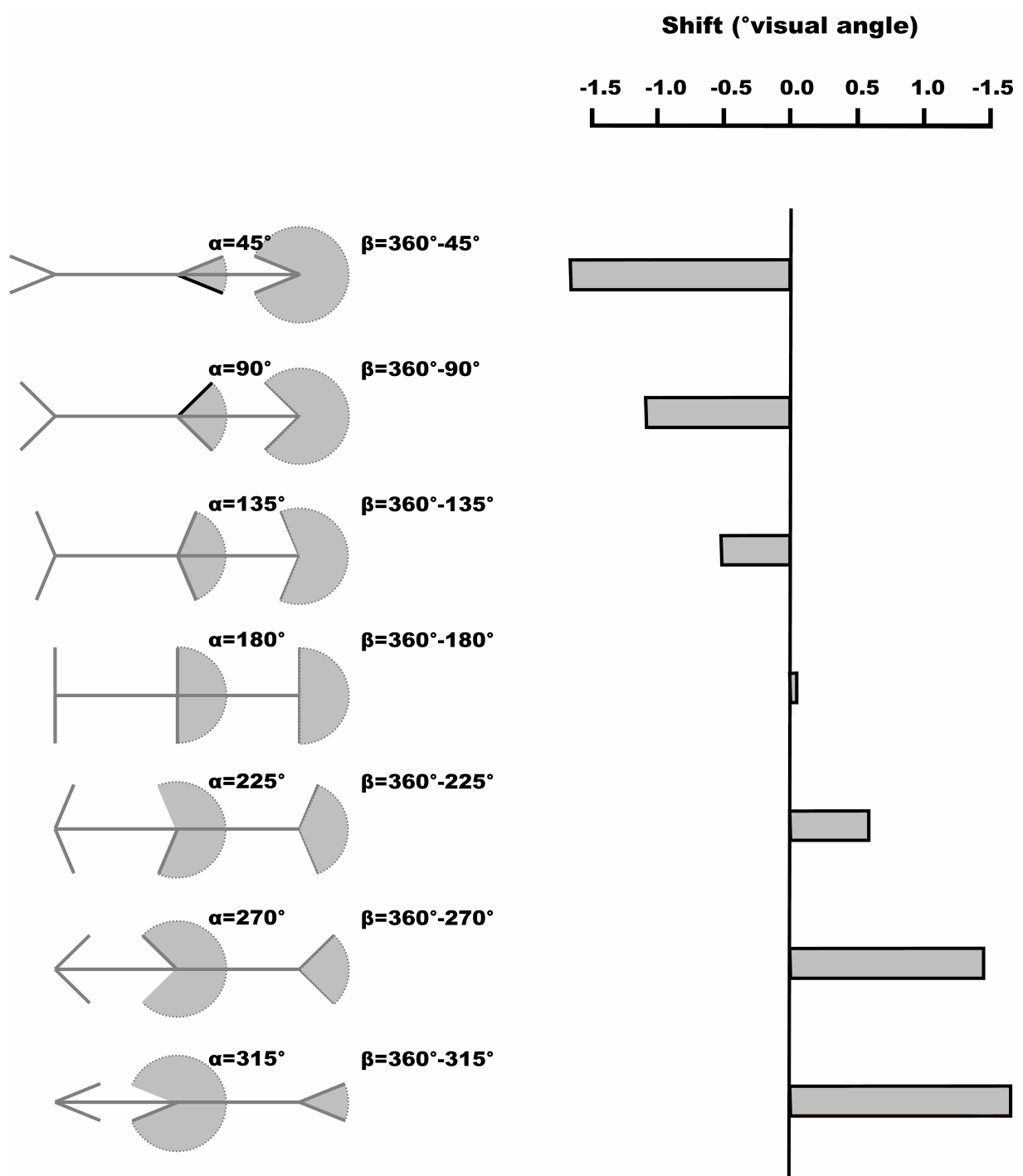


Figure 2

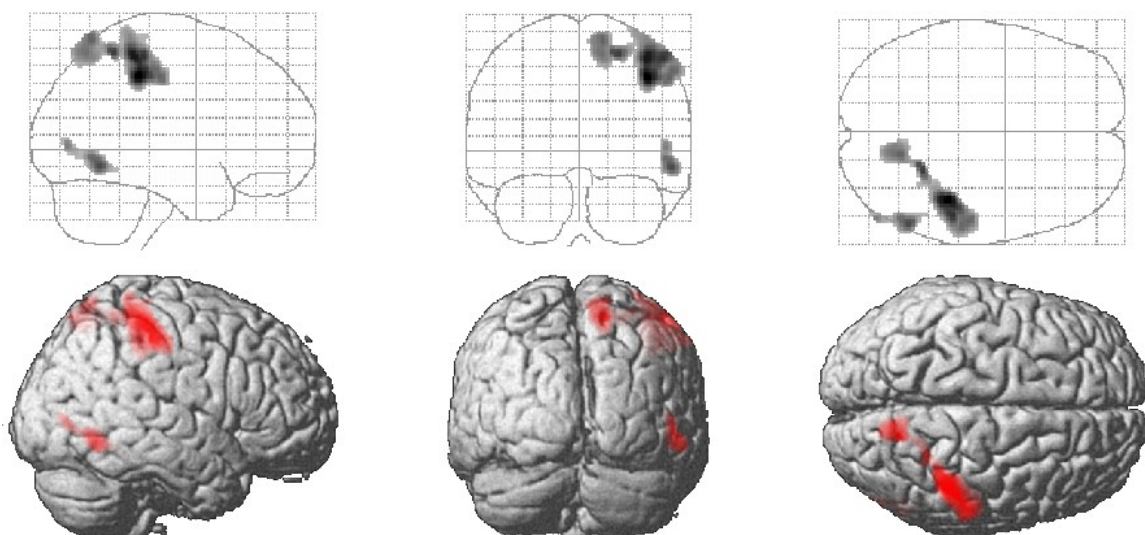


Figure 3

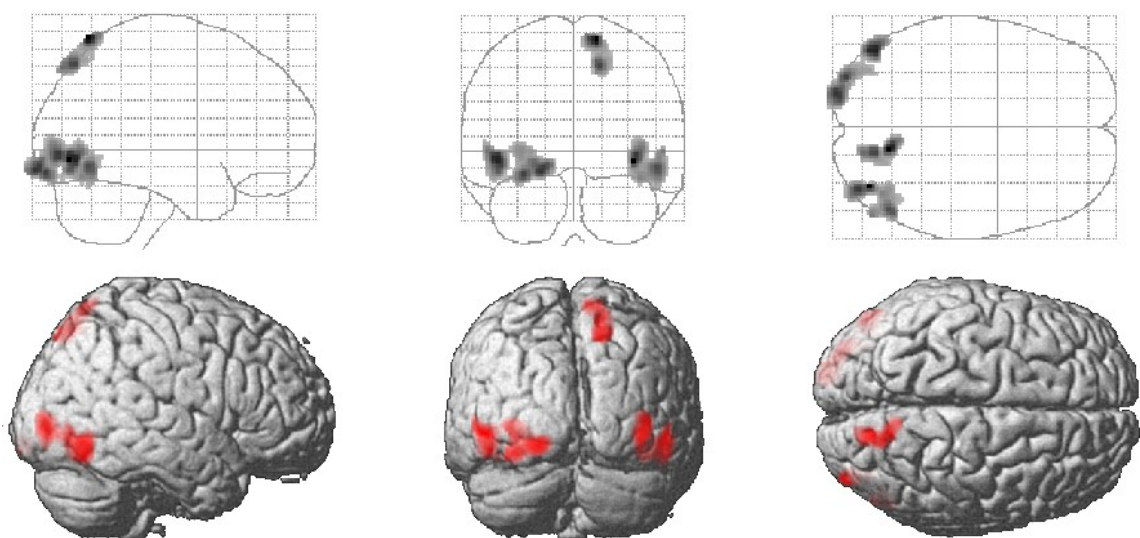


Figure 4

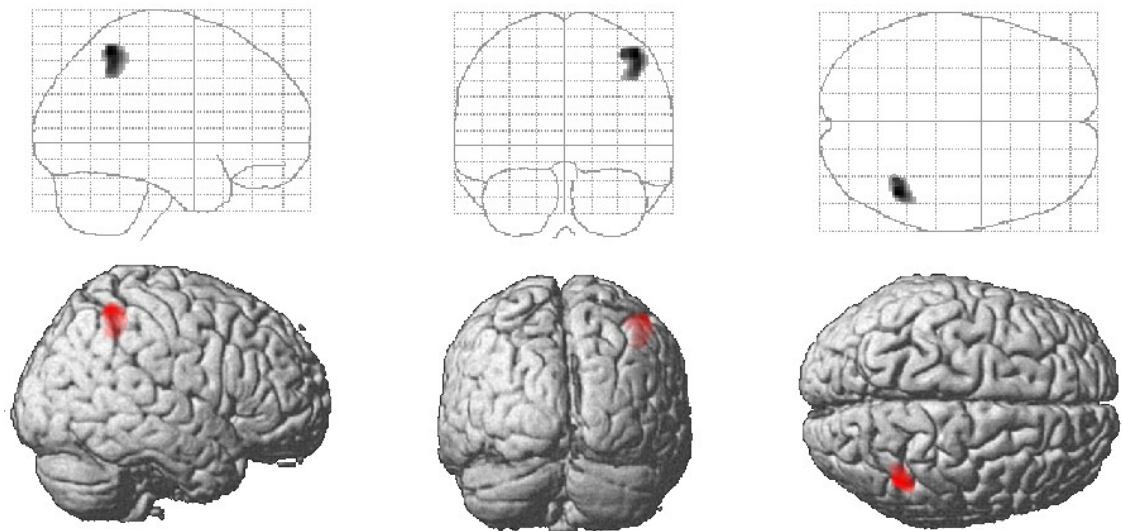


Figure 5