

The Müller–Lyer illusion seen by the brain: An event-related brain potentials study

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Abstract

In two experiments, event-related brain potentials (ERPs) were used to examine the neural correlates of a visual illusion effect in Müller–Lyer illusion tasks (illusion stimuli) and baseline tasks (no-illusion stimuli). The behavioral data showed that the illusion stimuli indeed yielded an illusion effect. Scalp ERP analysis revealed its neurophysiological substrate: the Müller–Lyer illusion tasks (Illusion tasks 1–3) elicited a more negative ERP deflection than did the baseline tasks about 400 ms after onset of the stimuli. Dipole source analysis of the difference wave (Illusion task 2–Baseline task 1) and the original waveforms of the different conditions (Illusion tasks 2 and 3 and Baseline task 2) indicated that the anterior cingulate cortex (ACC)/superior frontal cortex may contribute to the illusion effect, possibly in relation to high-level cognitive control. The results indicated that apparent distortions of the Müller–Lyer illusion might be influenced by top-down control.

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1. Introduction

Optical-geometric illusions are context-induced subjective distortions of visual features, such as the length, size, shape, and direction of one or more of the elements within a visual array. One of the best-known and most extensively investigated geometrical illusions, the Müller–Lyer configuration, in which 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 ($<$ $>$), has fascinated researchers for over 100 years (Valentin and Gregory, 1999).

It is well known that the Müller–Lyer illusion results from interactions between two arrowheads and the line between them. Different explanations for the occurrence of the Müller–Lyer illusion have been advanced. For example, depth theories (misapplied size constancy theory) suggested that an object's apparent size was determined by certain depth cues which

operate neural size-scaling mechanisms directly in some cases (Gregory, 1963; Fisher, 1967; Valentin and Gregory, 1999). According to Gregory, subjective depth impression is automatically induced by the Müller–Lyer figures. That is, the target line with inward-pointing brackets looks longer because we perceive the line as more distant, and vice versa. Assimilation theory (averaging theories) held that the arrowheads interfere with the perceptual system for measuring span of the horizontals, and therefore observers confuse or average the distance between the arrowhead tips (Erlebacher and Sekuler, 1969; Pressey, 1970). Pressey (1970) thought that the length of the central shaft is misperceived because the visual system cannot successfully isolate parts from wholes. In this scenario, the central shaft of the figure with arrows pointing inward is seen as longer because the stimulus is, in its totality, longer. Confusion theory (displaced vertex theory) suggested that the perceptual system miscalculates the location of the arrowhead vertex, displacing it toward the concave side (Chiang, 1968). In particular, our judgment of the position of each end of the shafts is influenced by the arrows around it. Inward-pointing arrowheads shift the apparent shaft end-point outwards relative to the true end-point. Outward-pointing arrowheads cause the apparent end-point to move inwards. Since we misjudge where the ends of the shafts are, we tend to overestimate the length of

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the shaft in the inward-pointing arrows figure, and underestimate its length in the outward-pointing arrows figure.

As for now, the Müller–Lyer illusion has been measured as a function of the shaft length, the gap between the shaft and the apices of the wings, the wing tilt angle and the wing length (Bertulis and Bulatov, 2001). However, a satisfactory and reliable model for the Müller–Lyer illusion has not been found yet. Recently, Howe and Purves (2005) provided a new hypothesis that the standard Müller–Lyer effect and its variants are a result of the fundamentally probabilistic strategy of visual processing that contends with inverse optics problem. They said that “the identical shafts or intervals in Müller–Lyer stimuli appear different in length because the probability distributions of the real-world sources of the lines or intervals, given the contexts provided by the arrowheads or arrow tails, are in fact different” (Howe and Purves, 2005).

Recently, developed brain imaging techniques such as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET) have made it possible for us to precisely record the brain activity associated with many cognitive processes, including visual illusion effects. For example, Lebedev et al. (2001) demonstrated that prefrontal cortex activity can reflect the perception of a visual illusion. In their study, they found a population of cells in the prefrontal cortex that reflected a monkey’s report of displacement (even when wrong) in the displacement illusion task using single cell spikes. Weidner and Fink (2006) investigated the neural mechanisms underlying the Müller–Lyer illusion using fMRI and found that the neural processes associated with the strength of the illusion were located bilaterally in the lateral occipital cortex (LOC) as well as the right superior parietal cortex (SPC). They speculated that illusory line-length information and cognitive set interact in the right intraparietal sulcus (IPS), which suggests that the strength of the illusion selectively alters higher cognitive processes involved in visuospatial judgments. As early as 2004, Predebon (2004) examined the effect of selective spatial attention on the magnitudes of the Müller–Lyer illusion and claimed attentional modulation of illusion magnitudes implicates high-level or cognitive factors in the formation of the illusion.

Although previous studies using functional magnetic resonance imaging had obtained some important and interested findings about the neural mechanism of visual illusion, there are still controversies about the cognitive mechanisms of visual illusion, and the time course of cortical activation cannot be studied with precision. It is known that ERPs may provide a means to evaluate timing of cognitive processes prior to a response. In the ERP technique, recordings are made of the electrical activity of the brain that is time locked to the presentation of an external stimulus. Thus, ERP data allow for more precise statements about the time course of activation during different stages of processing (e.g., low-level visual perception or high-level cognitive control) of the Müller–Lyer illusion. In the present study, the purpose of the study was to investigate spatiotemporal patterns of brain activation during the Müller–Lyer illusion using high-density (64-channel) ERP recordings and dipole source analysis. First, we wanted to find

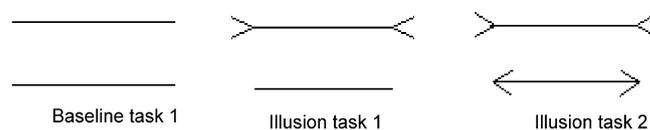


Fig. 1. Stimulus including Baseline task 1, Illusion task 1 (the shaft with inward-pointing arrowheads is seen as longer subjectively) and Illusion task 2 (the shaft with inward-pointing arrowheads is seen as longer subjectively) in Experiment 1.

out which modulations of the ERPs are consistently associated with visual illusion effects by comparing the Müller–Lyer illusion task with the baseline task. Based on previous work and different theories (Lebedev et al., 2001; Predebon, 2004; Weidner and Fink, 2006; Howe and Purves, 2005), we hypothesized that apparent distortions of geometric illusions (the Müller–Lyer illusion) may not depend on basic perceptual principles (low-level visual perception) but be influenced by top-down control. In the present study, the baseline tasks (including the Baseline tasks 1 and 2, see Figs. 1 and 4) which were not involved in context-induced subjective distortions of visual features might have the similar visual processing with the Müller–Lyer illusion tasks, such as primary visual cortex and saccadic eye movement (frontal eye field). Therefore, it could be a better way to investigate spatiotemporal pattern of brain in perception of the Müller–Lyer illusion figure by analyzing the difference wave (illusion tasks–baseline task) and test different theories of visual illusion. Second, high-density ERP recordings and dipole source analysis were used to obtain critical spatiotemporal information for analyzing the functional neuroanatomy of the cognitive processes involved in the illusion, which could validate results of previous studies and allow a more thorough investigation of the brain mechanisms involved. According to our hypothesis, we predicted that the prefrontal cortex or the anterior cingulate cortex might be involved in high-level cognitive control during visual illusions. To the best of our knowledge, this work is the first ERP study to investigate the electrophysiological correlates of the Müller–Lyer illusion.

2. Experiment 1

In this experiment, individuals performed the Müller–Lyer illusion tasks (Illusion tasks 1 and 2, see Fig. 1) and one baseline task (Baseline task 1, see Fig. 1). Subjects were instructed to judge whether a set of presented arrow shafts were the same length. Data from three conditions were considered in the analyses (Illusion task 1 [illusion response]; Illusion task 2 [illusion response]; and Baseline task 1 [correct response]). Electrophysiological data for correct judgment of shaft length in illusion trials were not considered, as there were not a sufficient number of these responses to obtain stable estimates of the ERPs. The experiment was designed to investigate the neural correlates of illusion effects elicited by the Müller–Lyer stimulus. Based on previous work, we expected visual processing of the illusion tasks and the baseline task to activate the occipital extrastriate cortex (Weidner and Fink, 2006; Ffytche and Zeki, 1996) but high-level cognitive processing of

the illusion tasks to activate the prefrontal cortex (Lebedev et al., 2001) or the right intraparietal sulcus (Weidner and Fink, 2006).

2.1. Method

2.1.1. Subjects

Twelve junior undergraduates (6 women, 6 men) aged 21–26 years (mean age, 23.5 years) from Southwest University in China participated in the experiment as paid volunteers. All subjects gave written informed consent, were right-handed, had no current or past neurological or psychiatric illness, and had normal or corrected-to-normal vision.

2.1.2. Stimuli and procedure

The experiment included two versions of the Müller–Lyer illusions (see Fig. 1). Illusion task 1 consisted of a horizontal shaft and another shaft of the same length with two symmetric inward-pointing arrowheads (the two shafts were presented one above the other, with their locations randomized). Illusion task 2 consisted of one shaft with inward-pointing arrowheads and another with outward-pointing arrowheads, both of the same length and presented one above the other with their locations randomized. Baseline task 1 (no-illusion task) consisted of two parallel lines of the same length. The length of all the shafts ranged over 2–4 cm in each trial, the distance between the two shafts was about 1 cm ($1.9\text{--}3.8^\circ$ [horizontal] $\times 0.96^\circ$ [vertical]), and they were displayed in the center of a 17-in. screen.

Subjects were seated in a semi-dark room facing a monitor placed 80 cm from their eyes. They were instructed to rest their right index and right middle finger on the 1 and 2 on the keyboard and were required to press the corresponding keys to indicate whether they judged the set of shafts to have the same length. The experiment was divided into a practice phase and a test phase. When the participant was familiar with the procedure of the experiment, the practice phase was ended. The formal test began with a fixation point followed by a figure with a set of two shafts. The order is as follows: the fixation point appeared between 200 and 400 ms, then the shafts appeared for 1000 ms, and an empty screen appeared for 1000 ms. The formal test consisted of 5 blocks, and every block had 45 judgement trials (15 trials for each task, randomized). Subjects were instructed to avoid blinking and eye movement of any sort and to keep their eyes fixated on the monitor rather than looking down at their fingers during task performance. They were able to rest after finishing each block.

2.1.3. Electrophysiological recording and analysis

Brain electrical activity was recorded 64 scalp sites using tin electrodes mounted in an elastic cap (Brain Product), with the reference on the left and right mastoids. The vertical electrooculogram (EOG) was recorded with electrodes placed above and below the left eye. All interelectrode impedance was maintained below 5 k Ω . The EEG and EOG were amplified using a 0.05–80 Hz bandpass and continuously sampled at 500 Hz/channel for offline analysis.

Eye movement artifacts (blinks and eye movements) were rejected offline and 16 Hz low pass filter was used. Trials with EOG artifacts (mean EOG voltage exceeding $\pm 100 \mu\text{V}$) and those contaminated with artifacts due to amplifier clipping, bursts of electromyographic (EMG) activity, or peak-to-peak deflection exceeding $\pm 100 \mu\text{V}$ were excluded from averaging. According to participants' responses, EEG of "illusion" (the Müller–Lyer illusions tasks), "no-illusion" (Baseline task 1) stimuli was separately overlapped and averaged. The averaged epoch for ERP was 800 ms including a 200-ms pre-stimuli baseline. On the basis of the ERPs grand-averaged map and topographical map, the following 23 electrode points were chosen for statistical analysis: FPz, Fz, Cz, AF3, AF4, F1, F2, F5, F6, C3, C4, FT7, FT8 (13 sites for anterior); Pz, Oz, P1, P2, P5, P6, O1, O2, TP7 and TP8 (10 sites for posterior). Latencies and amplitudes (baseline to peak) of the anterior N1 and P2 were measured separately in the 80–120 and 140–200 ms time windows, respectively, and the posterior P1 and N2 were measured separately in the 80–140 and 140–200 ms time windows, respectively. Mean amplitudes in the time window of 200–600 ms was analyzed using two-way repeated-measures Analyses of variance (ANOVA). The ANOVA factors were task type (Baseline task 1,

Illusion tasks 1 and 2), and electrode site. For all analyses, *p*-values of all main and interaction effects were corrected using the Greenhouse–Geisser method for repeated-measures effects.

2.1.4. Dipole source analysis

Brain Electrical Source Analysis program (BESA, Version, 5.0, Software) was used to perform dipole source analysis. For dipole source analysis, the four-shell ellipsoidal head model was used. In order to explore the generator of the illusion effect and increase the precision of source location, principal component analysis (PCA) was employed in the ERPs difference wave that evoked by Baseline task 1 were subtracted from the ERPs evoked by the illusion stimuli. When the dipole points are determined, software will automatically determine the dipoles location. The relevant residual variance criterion was used.

2.2. Results

2.2.1. Behavioral data

Mean trials for "no-illusion" stimulus (Baseline task 1: participants judged that the set of shafts have the same length) were 71 ± 3 , and mean RTs were 525 ± 60 ms. Mean trials for "illusion" stimulus (participants judged that the set of shafts have the different length) were 47 ± 7 (Illusion task 1) and 59 ± 4 (Illusion task 2). Mean RTs were 567 ± 82 and 571 ± 71 ms. Repeated-measures Analyses of variance for the mean RTs showed that no significant differences were found among the three types of tasks ($F(2,22) = 2.38$, $p > 0.05$), which indicated that participants could react quickly in all conditions. The behavioral data showed that the Müller–Lyer illusion tasks yielded illusion effect as indexed by judging the two straight lines were different in length mostly for illusion tasks than baseline task.

2.2.2. Electrophysiological scalp data

As shown in Fig. 2, the anterior N100, P170 and posterior P120 and N170 were elicited by the baseline task and illusions tasks. The results of the ANOVAs showed that there was no main effect of task type for the anterior N100 and posterior P120 components, while there was a main effect of task type for the anterior P170 ($F(2,22) = 7.47$, $p < 0.01$) and the posterior N170 components ($F(2,22) = 5.43$, $p < 0.05$). Post hoc tests showed that P170 elicited by Illusion tasks 1 and 2 was more positive than did the baseline task ($p < 0.05$), and N170 elicited by Illusion tasks 1 and 2 was more negative than did Baseline task 1 ($p < 0.05$), while the P170 and the N170 elicited by Illusion tasks 1 and 2 were not significantly different.

Repeated-measures ANOVA showed that the mean amplitude between 500–550 and 550–600 ms of illusion tasks was larger than Baseline task 1 on negative orientation ($F(2,22) = 5.53$, $p < 0.05$; $F(2,22) = 4.28$, $p < 0.05$). Further post hoc tests showed that Illusion tasks 1 and 2 elicited a more negative ERP component than Baseline task 1 did in the 500–600 time window ($p < 0.05$). In addition, interaction between task type and electrode site did not reach significance.

2.2.3. Dipole source analysis

As showed in the grand-average ERPs, the waveforms for Illusion tasks 1 and 2 were almost the same. Thus, only the difference wave elicited by Illusion task 2 and Baseline task 1

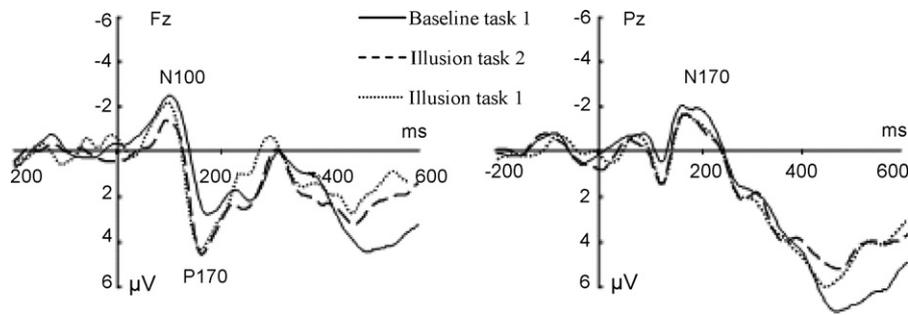


Fig. 2. Grand-average ERPs at Fz and Pz for Baseline task 1, Illusion tasks 1 and 2 in Experiment 1.

was chose for the source analysis using BESA software. PCA was employed in the 100–200 ms time window (P170, N170). Results showed that two principal components were needed to explain 93.8% of the variance in the data. One principal component was needed to explain 83.2% of the variance in the data, and the second component explained 10.6%. Therefore, these two dipoles were fitted with no restriction regarding direction or location. The reconstructed dipole 1 was located near the ACC (BA32: location according Talairach coordinates: $x = 11.2, y = 27.6, z = 27.5$) and dipole 2 located approximately in right occipital gyrus (BA19: $x = 28.1, y = -69.1, z = 27.0$), both revealed maximal dipole moment strength at about 170 ms. This model explained the data best and accounted for most of the variance with a residual variance (RV) of 7.8% at the peak activity of these two dipoles (see Fig. 3). The PCA indicated that two principal components explained 80.2 and 7.9% of the variance in the 500–600 ms time window. Therefore, these two dipoles were fitted with no restriction regarding direction or location. The result indicated that dipole 1 located approximately in the ACC (BA32: $x = 3.8, y = 29.9, z = 20.3$) and dipole 2 located approximately in the medial occipital cortex (BA18: $x = 0.9, y = -88.9, z = -9.8$), both were at the peak activity at about 520 ms. This model explained the data best and accounted for most of the variance with a residual variance of 10.5% (see Fig. 3). The display of the

residual maps showed no further dipolar activity and no further dipoles could be fitted in the investigated time window.

2.3. Discussion

According to the grand-average map, the ERP components elicited by the illusion tasks were obviously different from those elicited by the baseline task. Frontal-central areas, especially the dorsal ACC, were involved in the cognitive processing of the illusion. The Müller-Lyer illusion tasks elicited a larger P170 and N170 than did Baseline task 1. Dipole source analysis of the difference wave (Illusion task 2–Baseline task 1) indicated that two generators localized in the ACC (BA32) and occipital gyrus (BA19) contributed to this effect, and were possibly related to identification and evaluation of the stimulus. Previous studies suggest that the P170 and N170 are related to feature selection and stimulus evaluation in visual tasks (Mangun, 1998; Hillyard and Anllo-Vento, 1998). Carbon et al. (2005) also found that the Thatcher illusion resulted in a larger N170 for upright faces, but a smaller N170 for inverted faces. We know that the eyes and mouth regions are turned upside-down in “Thatcherized” faces. Only when presented upright they are perceived as severely distorted. However, this strong perceptual effect is lost when the whole Thatcherized face

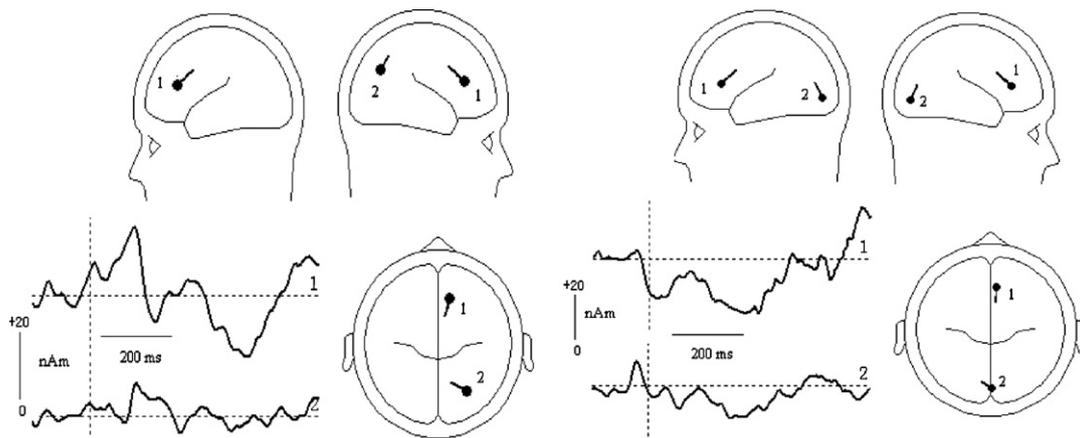


Fig. 3. Results of the dipole source analysis of the difference wave (Illusion task 2 vs. Baseline task 1) in the time range of 100–200 and 500–600 ms in Experiment 1. *Left*: the left-bottom shows the source activity waveforms, whereas the right figure displays the mean locations of the dipole. In the time range of 100–200 ms, the first dipole is located in the anterior cingulate cortex ($x = 11.2, y = 27.6, z = 27.5$) and the second near the right occipital gyrus ($x = 28.1, y = -69.1, z = 27.0$). *Right*: in the time range of 500–600 ms, the first dipole is located approximately in the anterior cingulate cortex ($x = 3.8, y = 29.9, z = 20.3$) and the second near the medial occipital cortex ($x = 0.9, y = -88.9, z = -9.8$).

is inverted. Boutsen and Humphreys (2003) thought that Thatcherization disrupted local configural processing in upright faces and these distortions became invisible when the whole face was inverted, perhaps owing to a failure in configural processing. Investigators (Carbon et al., 2005; Boutsen and Humphreys, 2003) suggested that local feature inversion might affect perceptual processes of the “Thatcherized” faces and modulate processing in the N170. Thus, our result seemingly indicates that the Müller–Lyer illusion tasks (local feature: inward-pointing or outward-pointing arrowheads) are processed differently compared to the baseline task and this difference arises at the initial encoding of the stimulus.

The illusion tasks also elicited a more negative ERP deflection than did Baseline task 1 between 500 and 600 ms. Dipole source analysis of the difference wave (Illusion task 2–Baseline task 1) indicated that two generators localized in the ACC (BA32) and the occipital cortex (BA18) contributed to this effect. Previous studies have indicated that the anterior cingulate cortex (ACC) is critically involved in the central executive control system (Carter et al., 1998; Botvinick et al., 2001). As for now, the anterior cingulate cortex is usually thought of as playing an important role in implementing the processes underlying adjustments of performance control. Moreover, the ACC appears to respond selectively to response conflict, and it serves to trigger compensatory adjustments in (inhibitory) control that are itself assumed to be mediated by other brain areas in the prefrontal cortex (PFC) (Botvinick et al., 2001; Kerns et al., 2004). In Experiment 1, we therefore speculate that the activation of the ACC before subjects press the response button may relate to high-level cognitive control of the Müller–Lyer illusion.

3. Experiment 2

The results of Experiment 1 indicated that both the ACC and occipital cortex were activated by the illusion tasks in the 100–200 and 500–600 ms time windows. Although these results indicate that there may be different neural correlates of perception and high-level cognitive control in the Müller–Lyer illusion task, Experiment 1 has some limitations. For example, from a perceptual and sensory point of view, Baseline task 1 is very different from the other two trial types. There is a difference in average luminance and complexity because the stimuli in Illusion tasks 1 and 2 are composed of central shafts plus inward- or outward-pointing arrowheads while the baseline stimuli do not have arrowheads. Therefore, it is possible that first ERP effects do not result from different perception processing but from subtle differences in the physical properties of the stimuli. In addition, there were no trials in which the simple line was actually longer than the line with the arrowheads in Experiment 1. It may be sufficient for subjects to remember to press the 2 key whenever a stimulus with at least one arrowhead is presented and the 1 key in case of stimuli without arrowheads. It is possible to perform the task perfectly without actually appraising and comparing the line lengths and without experiencing an illusion.

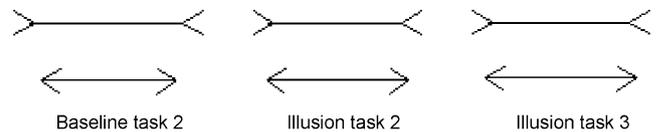


Fig. 4. Stimulus including Baseline task 2, Illusion task 2 (the shaft with inward-pointing arrowheads is seen as longer subjectively) and Illusion task 3 (the two shafts with inward-pointing and outward-pointing arrowheads are seen as the same length subjectively) in Experiment 2.

In order to clarify these questions, it is necessary for us to conduct additional ERP experiments in which both illusory and baseline tasks would contain shafts of different lengths and arrowheads. Under these conditions, very similar pictures would be perceived differently, which allows us to compare illusion versus no-illusion trials for similar picture types. Therefore, we selected Illusion task 2 as one of the stimuli in this experiment. In addition, we devised another illusion task and another baseline task (see Fig. 4). Illusion task 3 shows a shaft with inward-pointing arrowheads and one with outward-pointing arrowheads which appear the same length. Baseline task 2 shows a shaft with inward-pointing arrowheads that is distinctly longer than one with outward-pointing arrowheads. We speculated that differences in the pattern of brain activation observed across these conditions could not be attributed to different physical properties of the stimuli.

3.1. Methods

3.1.1. Subjects

Twelve junior undergraduates (6 women, 6 men) aged 19–23 years (mean age, 21.7 years) from Southwest University in China participated in the experiment as paid volunteers. All subjects had no history of current or past neurological or psychiatric illness, and had normal or corrected-to-normal vision.

3.1.2. Stimuli and procedure

The experiment consisted of two kinds of visual illusions (see Fig. 4). Illusion task 2 had been used in Experiment 1. The two shafts were the same length, but the shaft with inward-pointing arrowheads appeared longer than the one with outward-pointing arrowheads. Illusion task 3 also consisted of one shaft with inward-pointing arrowheads and one with outward-pointing arrowheads (the location of the two shafts was randomized), but the shaft with inward-pointing arrowheads was slightly shorter (about 0.2 mm) than the one with outward-pointing arrowheads so that they appeared to be the same length. Baseline task 2 (no-illusion task) also consisted of one shaft with inward-pointing arrowheads and one with outward-pointing arrowheads, but the shaft with inward-pointing arrowheads was slightly longer (about 0.2 mm) so that subjects could distinguish the length of the two shafts. The length of each shaft was 2, 2.5, or 3 cm, the distance between the two shafts was about 1 cm (1.9–2.8° [horizontal] × 0.96° [vertical]), and they were displayed in the center of a 17-in. screen.

Subjects were seated in a semi-dark room facing a monitor placed 80 cm from their eyes. They were instructed to rest their right index and right middle finger on the 1 and 2 on the keyboard and were required to press the corresponding keys to indicate whether they judged the set of shafts to have the same length. The detailed experimental procedure was similar to the Experiment 1. The formal test consisted of five blocks, and every block had 45 judgement trials (15 trials for each task, randomized). In addition, electro-physiological recording and analyses were also identical to that used in Experiment 1.

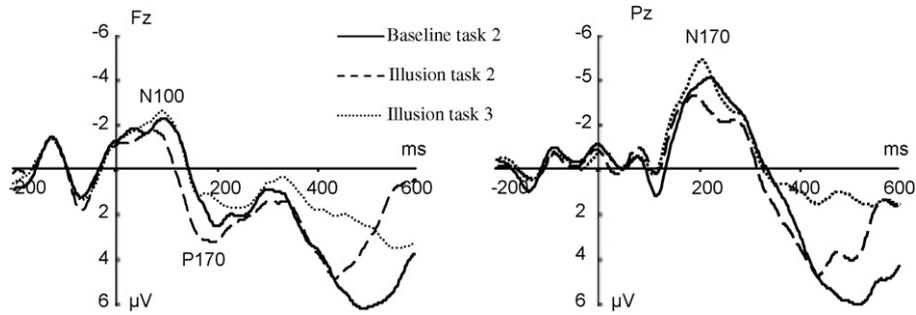


Fig. 5. Grand-average ERPs at Fz and Pz for Baseline task 2, Illusion tasks 2 and 3 in Experiment 2.

3.2. Results

3.2.1. Behavioral data

Mean trials for “no-illusion” stimulus (Baseline task 2: participants judged that the set of shafts have the different length) were 59 ± 6 , and mean RTs were 611 ± 55 ms. Mean trials for “illusion” stimulus were 48 ± 11 (Illusion task 2: participants judged that the set of shafts have the different length) and 63 ± 13 (Illusion task 3: participants judged that the set of shafts have the same length). Mean RTs were 620 ± 47 and 616 ± 65 ms. Repeated-measures Analyses of variance for the mean RTs showed that no significant differences were found among the three types of tasks ($F(2,22) = 0.36, p > 0.05$), which indicated that participants could react quickly in all conditions.

3.2.2. Electrophysiological scalp data

As shown in Fig. 5, the anterior N100, P170 and posterior P120 and N170 were elicited by the baseline task and illusions tasks, similar to results of Experiment 1. The results of the ANOVAs showed that there was no main effect of task type for these components (see Table 1).

Repeated-measures ANOVA showed that there were significant main effects of task type in the time windows of 400–500 and 500–600 ms, $F(2,22) = 5.39, p < 0.05$; $F(2,22) = 5.09, p < 0.05$. Post hoc tests showed that Illusion task 3 elicited a more negative ERP component than Baseline task 2 did in the 400–500 and 500–600 ms time windows ($p < 0.05$; $p < 0.01$), while Illusion task 2 only elicited a more negative ERP component than Baseline task 2 did in the 500–600 time window ($p < 0.01$). The difference between Illusion tasks 2 and 3 was not significant. In addition, the interaction task type and electrode site was significant in these time windows. In other time windows, the results showed that the

main effects of task types and the task type and electrode site interaction were not significant.

3.2.3. Dipole source analysis

For dipole source analysis, the four-shell ellipsoidal head model was used. Firstly, principal component analysis was employed in the grand-average ERPs that evoked by three different conditions. When the dipole points are determined, software will automatically determine the dipoles location. The relevant residual variance criterion was used. As showed in the grand-average ERPs, a late positive component (LPC) was elicited by all three conditions about 350 ms after onset of the stimulus. Thus, we fitted the original waveforms of the different conditions in the time window of 350–600 ms separately in a first step and subsequently compared the source solutions. Firstly, the PCA indicated that only one principal component explained 98.0% of the variance in the time window of 350–600 ms under Baseline task 2 condition. Therefore, one dipole was fitted with no restriction regarding direction or location. The result indicated that this dipole located approximately in the right occipital gyrus (BA19: $x = 13.7, y = -73.1, z = 36.9$), and its strength peaked about 480 ms after stimulus onset. This model explained the data best and accounted for most of the variance with a residual variance of 13.6% at the peak activity of the dipole (see Fig. 6). Secondly, the PCA indicated two principal components explained 88.7 and 8.6% of the variance in the 350–600 ms time window under Illusion task 2 condition. Therefore, these two dipoles were fitted with no restriction regarding direction or location. The result indicated that dipole 1 located approximately in the right occipital gyrus (BA19: $x = 11.1, y = -78.1, z = 38.1$) and dipole 2 located near in the ACC (BA32: $x = 9.6, y = 24.4, z = 41.1$), both were at the peak activity at about 540 ms. This model explained the data best and accounted for most of the variance with a residual variance of

Table 1
Summary of ANOVAS results for the amplitudes and latencies of N120 and P220 in Experiment 2

Time (ms)	Task type		Electrode site		Task type × electrode site	
	F	p	F	p	F	p
N120	0.29	ns	5.84	0.005	1.73	ns
N120	0.73	ns	4.45	0.009	1.09	ns
P220	0.33	ns	4.30	0.01	1.12	ns
P220	2.05	ns	4.25	0.005	1.25	ns

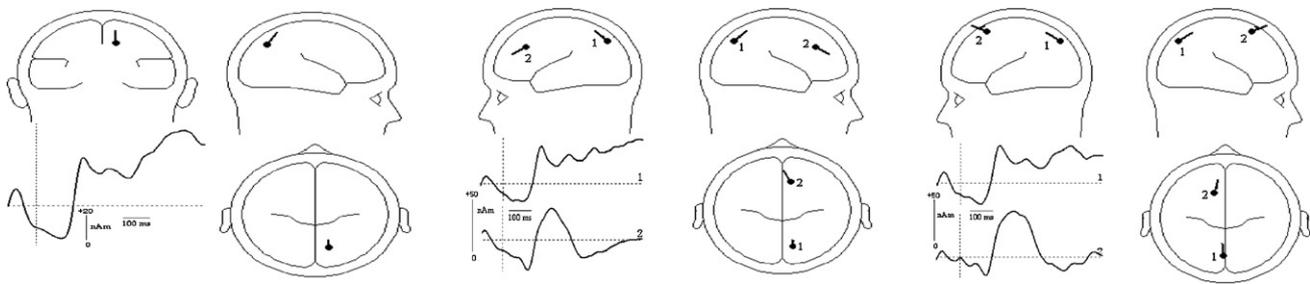


Fig. 6. Results of the dipole source analysis of the original waveforms of the different conditions (Baseline task 2, Illusion tasks 2 and 3) in the time range of 350–600 ms in Experiment 2. The left-bottom of each single image shows the source activity waveforms, whereas the right image displays the mean locations of the dipole. *Left*: under the Baseline task 2 condition, the dipole is located near in the right occipital gyrus ($x = 13.7, y = -73.1, z = 36.9$). *Middle*: under the Illusion task 2 condition, the first dipole is located approximately in the right occipital cortex ($x = 11.1, y = -78.1, z = 38.1$) and the second near the anterior cingulate cortex ($x = 9.6, y = 24.4, z = 41.1$). *Right*: under the Illusion task 3 condition, the first dipole is located approximately in the medial occipital cortex ($x = -1.2, y = -74.3, z = 20.3$) and the second near the superior frontal cortex ($x = -7.4, y = 18.5, z = 67.9$).

10.1% (see Fig. 6). Thirdly, the PCA also indicated two principal components explained 93.2 and 6.1% of the variance in the 350–600 ms time window under Illusion task 3 condition. The result indicated that dipole 1 located approximately in the occipital gyrus (BA19: $x = -1.2, y = -74.3, z = 20.3$) and dipole 2 located near in the superior frontal cortex (BA6: $x = -7.4, y = 18.5, z = 67.9$), both were at the peak activity at about 560 ms. This model explained the data best and accounted for most of the variance with a residual variance of 9.1% (see Fig. 6).

3.3. Discussion

In Experiment 2, we determined that perceptual processing was similar among the three different stimuli (Baseline task 2, Illusion tasks 2 and 3) for the anterior N100 and P170 and posterior P120 and N170 ERP wavelengths. This is likely because all of the presented stimuli were composed of two shafts with inward- and outward-pointing arrowheads. The first ERP effects in Experiment 1 might result from subtle differences in the physical properties of the stimuli due to the arrowheads. In Han's study (Han et al., 2003), they found that the N1 (180–200 ms) was of larger amplitude to the global than local targets, and thought that the enlarged N1 might reflect a general mechanism involved in discrimination processes based on different visual feature dimensions (e.g., Ritter et al., 1983; Vogel and Luck, 2000). This result therefore indicates that perceptual ERP components might be susceptible to stimulus properties (e.g., Busch et al., 2004; Rossion et al., 1999).

The Müller-Lyer illusion probably occurred at a higher cognitive processing level after this initial stimulus processing. As shown by the grand-averaged ERPs, a late positive component (LPC) was elicited by all three conditions 350 ms after onset of the stimulus. The LPC might be an obvious P300 component. In general, P300 latency is thought to represent the relative duration of multiprocess stimulus evaluation/classification operations, and P300 amplitude reflects the amount of attentional resources employed in a given task (Donchin and Coles, 1988; Ilan and Polich, 1999). According to the results of the dipole source analysis of the

original waveforms (LPC) of the different conditions in the 350–600 ms time window, we found that the illusion tasks and Baseline task 2 activated the occipital gyrus (BA19), but Illusion task 2 also induced activation of the ACC (BA32) and Illusion task 3 induced activation of the superior frontal cortex (BA6). The illusion tasks and Baseline task 2 both activated the right occipital gyrus (BA19) which possibly relates to group of the line segments to an integrated figure. Thus, these results indicate that apparent distortions of geometric illusions (the Müller-Lyer illusion) may not depend on low-level visual perception. For the difference waves (Illusion task 2–Baseline task 2 and Illusion task 3–Baseline task 2), we observed a negative component during the 350–600 ms window, which was similar to the results observed in Experiment 1. We thought that the difference wave might be a “true” negativity was hidden in the small positivity of the illusion-condition.

What is more interesting is that another generator of LPC was near the ACC/superior frontal cortex under illusion tasks which might be involved in monitoring and controlling of the visual illusion. Previous studies indicated that the anterior cingulate cortex are involved in action selection based on the expected outcome of an action (Bush et al., 2002; Hadland et al., 2003), integrating information regarding a motor response and its potential outcome (Williams et al., 2004). In Howe's study, they said that “although the discrepancies between the physical measurements of a stimulus and the percepts they elicit may seem ‘maladaptive’ on the face of it, this probabilistic strategy allows routinely successful behavior in typical visual environments” (Howe and Purves, 2005). Previous work had found that high-level or cognitive factors might be involved in the formation of the illusion (Lebedev et al., 2001; Predebon, 2004; Weidner and Fink, 2006). In our study, results also indicate that apparent distortions of the Müller-Lyer illusion may be influenced by high-level cognitive control, which might be involved in the ACC/superior frontal cortex.

4. General discussion

The current experiments were designed to reveal the spatiotemporal pattern of the Müller-Lyer illusion and confirm

activation of brain areas related to it. The results showed that the ERP components elicited by the illusion tasks were different from those elicited by the baseline tasks, and frontal-central areas, especially the ACC/superior frontal cortex, were involved in cognitive processing of the visual illusion. These results support the hypothesis that apparent distortions of the Müller–Lyer illusion may be controlled by high-level cognitive factors.

Although Illusion tasks 1 and 2 elicited a larger P170 in the frontal-central cortex and a larger N170 in the occipito-temporal cortex than did Baseline task 1, we determined that perceptual processing was similar among Baseline task 2, Illusion tasks 2 and 3 for the anterior N100 and P170 and posterior P120 and N170 ERP waveforms. These results confirmed that first ERP effects in Experiment 1 might result from subtle differences in the physical properties of the stimuli due to the arrowheads. They also indicated that the neural correlates of low-level visual processing in the Müller–Lyer illusion tasks are similar to those in the baseline tasks.

In both experiments, the illusion tasks elicited a more negative ERP deflection than did the baseline tasks about 400 ms after onset of the stimuli. Dipole source analysis of the difference wave (Illusion task 2–Baseline task 1) and the original waveforms of the different conditions (Illusion tasks 2 and 3 and Baseline task 2) indicated that generators mainly localized in the ACC/superior frontal cortex contributed to this effect, and are possibly related to high-level cognitive control in the formation of the illusion. Previous work indicates that the ACC has also been shown to be the generator of the midline theta rhythm, an EEG oscillation that is characteristically observed during intense concentration (Gevins et al., 1997). Other studies suggest that the ACC is involved in linking mental effort to the autonomic changes that typically accompany it (Critchley et al., 2003; Walton et al., 2003). Prior research indicates that subjects have significantly shorter reaction times and increased ACC activity during the high effort condition, compared to those found in the relaxed condition (Mulert et al., 2005). These results provide direct evidence for a close relationship between conscious effort and ACC activity. The ACC activity has been described as a critical locus for “conscious effort” in “complex effortful tasks that presumably cannot be performed without conscious guidance” (Dehaene and Naccache, 2001; Mulert et al., 2005). Weidner and Fink (2006) also thought that the magnitude of the illusion can be influenced by top-down control. For example, 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 arrows. The present results, together with the prior findings, suggest that the ACC/superior frontal cortex may be involved in high-level cognitive control arising from the Müller–Lyer illusion as an index of the mental effort it demands (Botvinick et al., 2004).

Assimilation theory (averaging theories) held that the length of the central shaft is misperceived because the visual system cannot successfully isolate parts from wholes, and confusion theory (displaced vertex theory) suggested that we misjudge where the ends of the shafts are, and tend to overestimate or

underestimate the length of the shaft with inward or outward-pointing arrowheads. Obviously, these two theories of visual illusion might be set up on the basis of the view that the basic perceptual principles (low-level visual perception) underlie the apparent distortions. However, according to our results and the prior findings, we thought that apparent distortions of the Müller–Lyer illusion might be influenced by high-level cognitive control, and support the hypothesis that visual perception is a fundamentally probabilistic process that has evolved to contend with the inherent ambiguity of information in retinal stimuli (Howe and Purves, 2005). In a word, in the Müller–Lyer illusion tasks, subjects need much more conscious effort to judge the length of two straight lines according to their experience so as to induce activation of the ACC/superior frontal cortex.

In the present study, the ACC/superior frontal cortex was activated by the Müller–Lyer illusion tasks, as determined by the method of dipole source localization. However, it should be stressed that dipole source analysis is an inverse problem because there is no unique solution. Due to inherent limitations of source localization, the brain areas implicated by source localization are only tentative. Regarding the involvement of brain regions in response to the visual illusion effect, the current results provide only a model rather than empirical data.

5. Conclusion

In the present study, results showed that the Müller–Lyer illusion tasks indeed yielded an illusion effect as indexed by judging the two straight lines are different in length mostly for illusions tasks than the baseline task. Scalp ERP analysis revealed that the Müller–Lyer illusion tasks (Illusion tasks 1–3) elicited a more negative ERP deflection than did the baseline tasks about 400 ms after onset of the stimuli. Results of dipole source analysis indicated that the ACC/superior frontal cortex contributed to the illusion effect, possibly in relation to high-level cognitive control.

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