Cross-modal Processing in the Occipito-temporal Cortex: A TMS Study of the Müller-Lyer Illusion

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Abstract

■ The Müller-Lyer illusion occurs both in vision and in touch, and transfers cross-modally from vision to haptics [Mancini, F., Bricolo, E., & Vallar, G. Multisensory integration in the Müller-Lyer illusion: From vision to haptics. *Quarterly Journal of Experimental Psychology, 63,* 818–830, 2010]. Recent evidence suggests that the neural underpinnings of the Müller-Lyer illusion in the visual modality involve the bilateral lateral occipital complex (LOC) and right superior parietal cortex (SPC). Conversely, the neural correlates of the haptic and cross-modal illusions have never been investigated previously. Here we used repetitive TMS (rTMS) to address the causal role of the regions activated by the visual illusion in the generation of the visual, haptic, and cross-modal visuo-haptic illusory effects, investigating putative modality-specific versus cross-modal underlying processes. rTMS was administered to the right and the left hemisphere, over occipito-temporal cortex or SPC. rTMS over left and right occipito-temporal cortex impaired both unisensory (visual, haptic) and cross-modal processing of the illusion in a similar fashion. Conversely, rTMS interference over left and right SPC did not affect the illusion in any modality. These results demonstrate the causal involvement of bilateral occipito-temporal cortex in the representation of the visual, haptic, and cross-modal Müller-Lyer illusion, in favor of the hypothesis of shared underlying processes. This indicates that occipito-temporal cortex plays a cross-modal role in perception both of illusory and nonillusory shapes. ■

INTRODUCTION

Arrowheads at the ends of a line may affect its estimated length (Müller-Lyer, 1889). Outward-oriented arrowheads bring about an illusory lengthening of it, whereas inward-oriented arrowheads reduce the perceived extent of the segment. The Müller-Lyer illusion and its variants have been extensively investigated in the visual modality, and have been interpreted according to purely visual theoretical frameworks (Coren & Girgus, 1978). The finding that similar illusory effects occur also in touch (for a review, see Gentaz & Hatwell, 2004), even in congenitally blind participants (Heller et al., 2002), challenges these classical visual accounts (Over, 1967; Rudel & Teuber, 1963), opening an ongoing debate as to whether modality-specific or shared processes underlie the visual and haptic Müller-Lyer illusion.

In support of the multisensory hypothesis (shared processes underlying both visual and haptic Müller-Lyer figures), it has been demonstrated that the visual and haptic illusions occur with the same magnitude (Mancini, Bricolo, & Vallar, 2010; Suzuki & Arashida, 1992; Over, 1966), correlate with each other (Frisby & Davies, 1971), and are affected in a similar fashion by a number of experimental manipulations (Millar & Al-Attar, 2002; Over, 1966). Importantly, cross-modal effects have been reported. For example, the decrement of the illusion with practice transfers between the visual and the haptic Brentano variants of the Müller-Lyer figure (namely, a combined form that includes both the inward and the outward configurations; Rudel & Teuber, 1963).

Recently, we showed that the Müller-Lyer illusion may occur within and across modalities (Mancini et al., 2010). We compared unimodal and cross-modal presentations of the Judd variant of the Müller-Lyer figure (namely, a line with two identical arrowheads at its ends; Holding, 1970; Judd, 1899). Neurologically unimpaired participants were required to set a mark at the midpoint of the horizontal shaft. In this task, participants make systematic errors towards the "tail" end (outward-oriented with respect to the shaft). Particularly, in the cross-modal condition, the view of irrelevant arrowheads affects the bisection of an out-of-sight line explored haptically. Crucially, these cross-modal effects occur only when the visual and haptic stimuli are spatially aligned, in line with the spatial effects of multisensory integration described in behavioral and neurophysiological studies (e.g., Gepshtein, Burge, Ernst, & Banks, 2005; Stein, 1998). Experiments using other paradigms, such as same/different (Gallace & Spence, 2005) and adjustment (Walker, 1971) tasks, show similar cross-modal interference of the visual Müller-Lyer illusion on the participant's performance in the tactile modality.

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As for the neural correlates of the visual variants of the Müller-Lyer figure, neuropsychological evidence from brain-damaged patients suggests the crucial involvement of extrastriate visual cortex in the generation of the visual Müller-Lyer illusion (Daini, Angelelli, Antonucci, Cappa, & Vallar, 2002). More recently, an fMRI study (Weidner & Fink, 2007) investigated the hemodynamic response associated to the processing of the Brentano illusion in the visual modality. Weidner and Fink (2007) manipulated parametrically the strength of the perceived illusion by varying the angles of the illusion-inducing fins, comparing a landmark-like judgment task with a luminance control task. Areas that correlated with the strength of the Müller-Lyer illusion were explored by looking at the regressor representing the parametric modulation of the strength of the illusion. Weidner and Fink found bilateral activations in lateral occipital cortex, and in the right superior parietal lobule (superior parietal cortex, SPC). In a successive MEG study, the time course of the processing of the visual Müller-Lyer illusion was investigated (Weidner, Boers, Mathiak, Dammers, & Fink, 2010). An early activation in the visual areas, occurring between 85 and 130 msec after stimulus onset, was found, followed by a later activation (at 195–220 msec) along the ventral visual pathway in right superior temporal cortex; activations also took place in right inferior parietal cortex and in right frontal cortex. Based on these sources of evidence, Weidner et al. suggest that ventral stream areas (lateral occipital and inferior temporal) may be involved in forming object representations, including size-invariant shape, whereas dorsal stream areas (posterior parietal cortex) may subsequently integrate these object representations into spatial frames of reference (Weidner et al., 2010; Weidner & Fink, 2007). Finally, an event-related potential study suggests that higher-level cognitive control, based on activity in the anterior cingulate and in the superior frontal cortices, may contribute to the Müller-Lyer illusory effects (Qiu, Li, Zhang, Liu, & Zhang, 2008).

So far, there is no evidence concerning the neural correlates of haptic and cross-modal visuo-haptic illusory effects. The hypothesis of a multisensory representation of the Müller-Lyer illusion predicts that the brain regions (i.e., occipito-temporal cortex bilaterally and right SPC) activated by the visual illusion in the Weidner and Fink's (2007) study should be involved also in the processing of the haptic and cross-modal illusions. These regions participate in multisensory processing. Neuroimaging studies have shown that SPC is involved in visual (Yantis & Serences, 2003; Corbetta, Shulman, Miezin, & Petersen, 1995) and cross-modal spatial attention and localization (Molholm et al., 2006; Bushara et al., 1999). SPC contributes also to the transformation of multisensory inputs into a common spatial frame of reference (Tanabe, Kato, Miyauchi, Hayashi, & Yanagida, 2005). On the other hand, the lateral occipital complex (LOC) is a visual area implicated in object recognition (Grill-Spector, 2003; Malach et al., 1995), which seems to compute category- and viewpoint-independent shape representations (e.g., Pourtois, Schwartz, Spiridon, Martuzzi, & Vuilleumier, 2009; Kourtzi & Kanwisher, 2001). Crucially, recent neuroimaging studies have highlighted the involvement of this area in tactile processing, with the LOC responding to both familiar and unfamiliar shapes presented not only in the visual but also in the tactile modality (Deshpande, Hu, Stilla, & Sathian, 2008; Peltier et al., 2007; Amedi, Jacobson, Hendler, Malach, & Zohary, 2002; James et al., 2002; Amedi, Malach, Hendler, Peled, & Zohary, 2001). These findings indicate that the LOC may subserve cross-modal processing (Beauchamp, 2005).

The aim of the present study was to explore the involvement of the parietal and (extrastriate) occipital–temporal areas found to be activated by the visual Müller-Lyer illusion (Weidner & Fink, 2007) in both the unisensory (visual and haptic) and the cross-modal (visuo-haptic) processing of this illusory figure. To this aim, we used transcranial magnetic stimulation (TMS), which may provide insight into the causal role of particular regions of the cerebral cortex in specific behaviors (Pascual-Leone, Walsh, & Rothwell, 2000). In particular, low-frequency repetitive TMS (rTMS) can be used to transiently disrupt ongoing neuronal activity in a localized cortical area by briefly inducing an electrical field in the tissue below the magnetic coil (Walsh & Cowey, 2000). Here, low-frequency 1-Hz rTMS was applied over the occipito-temporal or superior parietal cortices, either of the right hemisphere or of the left hemisphere, in two groups of neurologically unimpaired participants. These stimulation sites were selected on the basis of previous neuroimaging evidence, showing the involvement of the left and the right lateral occipital cortices, and right SPC, in the visual processing of the Müller-Lyer illusion (Weidner & Fink, 2007). In the present study, we investigated the role of the above discussed visual and parietal areas in the processing of the Judd variant of the Müller-Lyer illusion, under three conditions of stimulus presentation: unimodal visual, unimodal haptic, and cross-modal visuo-haptic (see Mancini et al., 2010, for a behavioral study). If occipito-temporal cortex is involved in the processing of the Müller-Lyer illusion independent of the modality of the sensory input, low-frequency rTMS over that region would be expected to interfere with the generation of the illusion, reducing illusory effects in each condition of stimulus presentation. As for parietal cortex, an asymmetric effect of rTMS over this region may be predicted. On the basis of the study by Weidner and Fink (2007), rTMS over right SPC should affect the magnitude of the illusion, at least in the visual modality. Instead, left SPC should not be functionally relevant for the present task (Weidner & Fink, 2007): Therefore, it was chosen as a control site for testing the specificity of rTMS stimulation.

METHODS

Participants

Twenty naïve healthy volunteers (12 women, mean age = 25 years, range = 20–40 years) took part in the study. All were right-handed (Oldfield, 1971), and had a normal or corrected-to-normal vision. None of the participants had neurological, psychiatric, or other relevant medical problems or any contraindication to TMS (Rossi, Hallett, Rossini, & Pascual-Leone, 2009). All participants gave written informed consent and received course credits for their participation. The protocol was carried out in accordance with the ethical standards of the Declaration of Helsinki, and was approved by the Ethical Committee of the University of Milano-Bicocca.

Stimuli and Apparatus

Stimuli consisted of three types of black 3-D plastic figures (Figure 1A–C): two illusory figures (leftward outgoing/rightward ingoing fins, which brought about a leftward displacement of the shaft's perceived center; leftward ingoing/rightward outgoing fins, which brought about a rightward displacement of the shaft's perceived center), and one baseline control stimulus (a shaft with vertical terminators). Each stimulus included a horizontal shaft (120 mm long) and two identical terminators, vertical (length = 25 mm; width = 10 mm; thickness = 1 mm) or angled at 45° (length of each fin = 35 mm; width = 10 mm; thickness = 1 mm). All stimuli, both with vertical and angled terminators, were 50 mm high. Each stimulus was glued on the center of a white wooden board (40 × 40 cm). In the bimodal condition, the horizontal shaft was positioned centrally on the backside of the board, and the arrowheads on the frontside in the correspondent positions (Figure 1C).

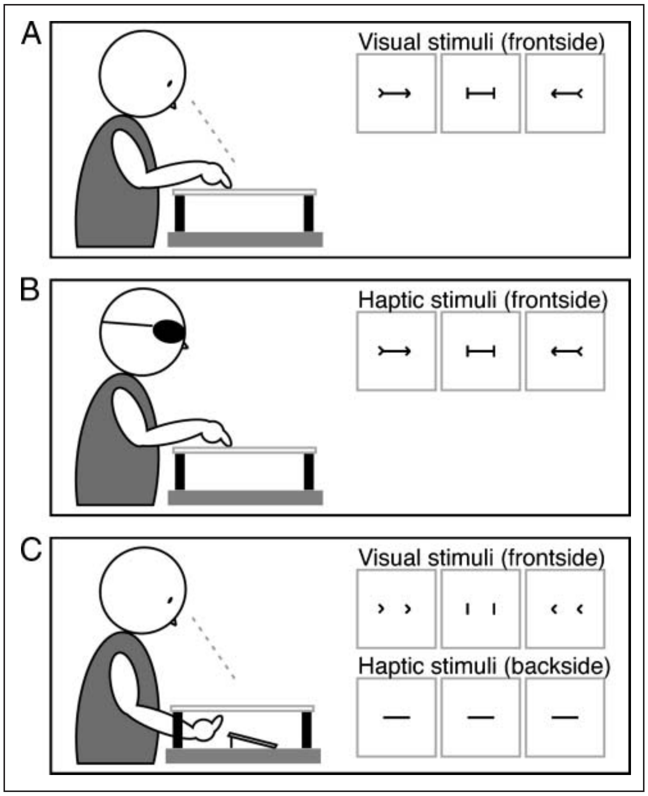

Figure 1. Stimuli and apparatus. Under visual (A), haptic (B), and cross-modal visuo-haptic (C) presentations, three types of stimuli were administered: leftward outgoing/rightward ingoing fins, which brought about a leftward displacement of the shaft's perceived center; a baseline control stimulus with vertical terminators; leftward ingoing/rightward outgoing fins which brought about a rightward displacement of the shaft's perceived center. In the visuo-haptic condition (C), the terminators were glued on the frontside of the board, and the horizontal shaft to be bisected on the backside, in the correspondent positions.

The task was performed in a quiet room with participants being seated in front of a table. Each board was presented individually, with its center aligned with the mid-sagittal plane of the participant's trunk, and placed flat on a wooden support at the height of 12 cm from the table top (Figure 1A–C). In the bimodal condition, a mirror was placed on the table under the board; the mirror reflected the shaft on the backside and was seen only by the experimenter (Figure 1C).

Procedure

Participants were required to bisect with the index finger the horizontal shaft of each stimulus, using either their right or left hand in different groups. Throughout all experimental conditions, participants who were administered a right hemisphere rTMS used the ipsilateral right hand, participants who were administered a left hemisphere rTMS used the ipsilateral left hand. The task was performed under three sensory input conditions, given in different blocks: visual, haptic, or visuo-haptic. The experimenter who administered the behavioral tasks was blind to the TMS experimental condition. In the *visual condition*, participants received instructions to touch the midpoint of the shaft without exploring haptically the stimulus, and to close their eyes immediately after the bisection response, in order to allow the experimenter to measure the bisection error (Figure 1A). In the *haptic condition*, blindfolded participants scanned the shapes (arrowheads and shafts) haptically, using the hand ipsilateral to the hemispheric side of rTMS, and then set the midpoint of the shaft with their index finger (Figure 1B). Each trial started with the experimenter placing the palm of the participant's open hand centrally over the stimulus. The bisection error was measured by means of a ruler. In the *visuo-haptic condition*, participants received instructions to look at the arrowheads on the frontside of the board, simultaneously palpate the shaft glued on the backside of the board with the whole hand, and then set its midpoint using their index finger. Participants did not see their forearm, which was covered by the wooden support (Figure 1C). The experimenter measured the bisection error, with the help of the mirror, by means of a ruler taped close to the shaft. Participants had received instructions to provide their responses as soon and as accurately as possible, without time limits.

The presentation condition (visual, haptic, visuo-haptic) was blocked and counterbalanced across participants and experimental sessions. Rest breaks of approximately 2 min were given between each block. Within each block, the three stimulus configurations (baseline neutral; leftward outgoing/rightward ingoing fins; leftward ingoing/rightward outgoing fins) were repeated randomly six times, for a total of 18 trials per block, and 54 per session. Two practice trials, one baseline and one illusory stimulus selected at random, were administered at the beginning of each block (visual, haptic, or visuo-haptic), and not included in the analyses.

The 20 participants were randomly assigned to one of two groups, right and left hemisphere stimulated, each group comprising 10 participants. Participants performed the tasks using the hand ipsilateral to the stimulated hemisphere, namely, the right hand in the right hemisphere group, and the left hand in the left hemisphere group. For each participant, the experimental task was repeated in three different sessions, given in a counterbalanced order across participants, and performed over different days (the intersession interval was at least 48 hr): a baseline session with no rTMS, and two rTMS sessions (rTMS over occipito-temporal or superior parietal cortex). In both rTMS sessions, the 1-Hz stimulation was applied for 20 min before the participant was tested on the task. The duration of the task was about 13 min, with each experimental session lasting about 33 min.

rTMS

Low-frequency (1 Hz) off-line rTMS was delivered using a Magstim Super Rapid magnetic stimulator (Magstim, Whitland, UK) and a figure-of-eight coil (7 cm diameter). Off-line rTMS may transiently modulate neural excitability, with the net effect being dependent on stimulation frequency. From a physiological point of view, low-frequency rTMS (1 Hz) generally results in inhibition of the stimulated area (Chen et al., 1997). Similar effects have been found also in behavioral experiments (e.g., Bolognini, Miniussi, Savazzi, Bricolo, & Maravita, 2009; Merabet et al., 2004; Knecht, Ellger, Breitenstein, Bernd Ringelstein, & Henningsen, 2003; Pascual-Leone et al., 2000). rTMS was delivered for 20 min at a fixed intensity, 65% of the maximum output of the stimulator. These parameters were compatible with the aim of the present experiment, which was to interfere with the normal functioning of stimulated areas (Bolognini et al., 2009; Bolognini & Maravita, 2007; Cappelletti, Barth, Fregni, Spelke, & Pascual-Leone, 2007; Harris & Miniussi, 2003; Boroojerdi, Prager, Muellbacher, & Cohen, 2000).

The targeted stimulation sites were the occipito-temporal and the superior parietal cortices, using the stereotaxic coordinates of Weidner and Fink (2007) in the right hemisphere in one group of participants, and in the left hemisphere in a second group (see Figure 2). The targeted areas were localized using the SofTaxic Evolution navigator system (Version 1.0; www.emsmedical.net). This system allows the reconstruction of cerebral cortex in Talairach coordinates, with an accuracy of ≈1 cm, on the basis of digitized skull landmarks (nasion, inion, and two preauricular points), and other 30 uniformly distributed points that are mapped on the scalp (3-D Fastrak Polhemus digitizer). An estimation of the cerebral volume of each participant was obtained by "Point-based Warping" to an MRI template

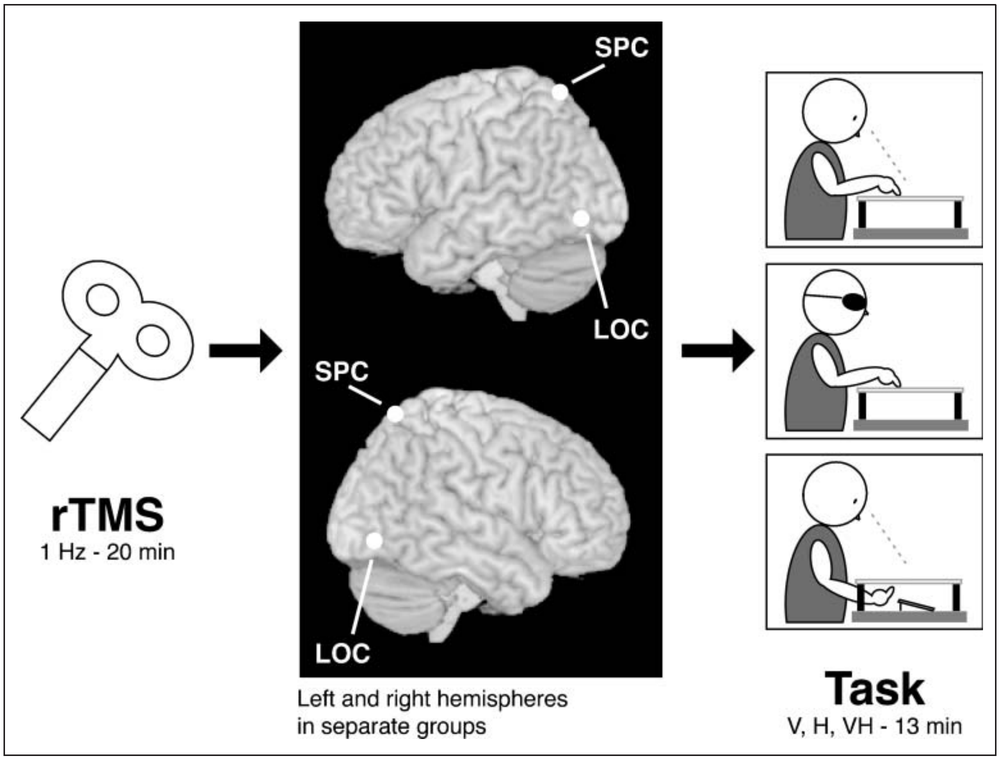

Figure 2. Procedure. Low-frequency rTMS was administered to occipito-temporal cortex (at the level of the LOC) and SPC, separately for the right and the left hemispheres in two different groups of participants. The experimental task was administered and performed with the hand ipsilateral to the stimulated hemisphere. The task was given alone ("no rTMS" condition), and after 20 min of rTMS.

and a 3-D virtual reconstruction based on the points recorded from the subject's scalp. Following this procedure, lateral occipital cortex was localized for each participant with Talairach and Tournoux (1988) coordinates corresponding, on average, to $x = \pm 36, y = -76, z = -1$ (Weidner & Fink, 2007); right/left SPC corresponded, on average, to Talairach coordinates $x = \pm 14, y = -61, z = 66$ (Weidner & Fink, 2007). The choice of these stimulation sites and coordinates (original Montreal Neurological Institute coordinates were converted into Talairach coordinates using SPM5) was based upon a previous fMRI study (Weidner & Fink, 2007), as discussed above. On each session, the correct site was marked on the participant's cap; the coil was positioned on that site, and was supported and held in place by a mechanical device.

Data Analysis

The bisection error (mm) was computed as the difference between the subjective midpoint of the horizontal shaft, marked by each participant, and its objective center; positive values indicated a rightward displacement, whereas negative values indicated a leftward displacement from the objective centre of the line.

Preliminarily, we assessed whether the participant's response was influenced by the hand used to perform the task by conducting an analysis on the corrected illusion errors in each presentation condition, in the "no rTMS" session only (i.e., for each participant, the average bisection error for each of the two illusory stimuli minus the baseline average bisection error in the "no rTMS" session). A repeated measures analysis of variance (ANOVA) was performed with two within-subjects main factors (stimulus: leftward ingoing/rightward outgoing, leftward outgoing/rightward ingoing; modality: visual, haptic, visuo-haptic), and one between-subjects factor (hand: left, right).

The effects of rTMS stimulation on illusion magnitude were then assessed. An illusion magnitude score was computed as follows, individually for each participant and experimental condition: $I = (\text{error}_{\text{right illusion}} - \text{error}_{\text{left illusion}})$, that is, the difference between the bisection errors (mm) in the leftward ingoing/rightward outgoing and the leftward outgoing/rightward ingoing stimuli. Positive values indicated that the illusory effect was present (i.e., the leftward ingoing/rightward outgoing stimulus had been bisected more rightward than the leftward outgoing/rightward ingoing stimulus). Negative values indicated shifts in a direction opposite to that of the expected illusory effect (i.e., the leftward ingoing/rightward outgoing stimulus had been bisected more leftwards than the leftward outgoing/rightward ingoing stimulus). Finally, a 0-score marked a null illusory effect (i.e., the leftward ingoing/rightward outgoing stimulus had been bisected at the same point as the leftward outgoing/rightward ingoing one). The illusion scores were submitted to a repeated measures ANOVA with two within-subjects main factors (session: no rTMS; rTMS: occipito-temporal, superior parietal; modality: visual, haptic, visuo-haptic), and one between-subjects factor (hemisphere/hand: left, right).

Finally, the specificity of the effect of rTMS on illusion processing was assessed by a similar ANOVA performed on the average bisection errors of the baseline stimulus only (vertical terminators).

RESULTS

Cross-modal Judd Illusion

As shown in Figure 3, the expected (see Mancini et al., 2010) illusory effects were present in the "no rTMS" condition; in every modality, stimuli with leftward outgoing/rightward ingoing fins brought about a leftward error, and stimuli with leftward ingoing/rightward outgoing fins a rightward error. The illusory effects were slightly reduced under the cross-modal visuo-haptic presentation, as compared with the unimodal visual and haptic conditions, in line with a previous study using a similar procedure (Mancini et al., 2010).

The ANOVA performed on the corrected bisection errors of the illusory stimuli in the "no rTMS" condition (i.e., illusion − baseline) showed that the main factors of stimulus [$F(1, 18) = 189.66, p < .001, \eta^2 = 0.76$] and of modality [$F(2, 36) = 4.78, p = .014, \eta^2 = 0.01$] were significant, as well as their interaction [$F(2, 36) = 9.26, p = .001, \eta^2 = 0.07$]. Importantly, the main factor of hand was not significant [$F(1, 18) = 2.28, p = .15, \eta^2 = 0.09$], as well as its interactions with the stimulus [$F(1, 18) = 1.21, p = .28, \eta^2 = 0.005$], and the modality [$F(2, 36) = 1.87, p = .17, \eta^2 = 0.001$] main factors. The Hand × Stimulus × Modality interaction was not significant ($F < 1$).

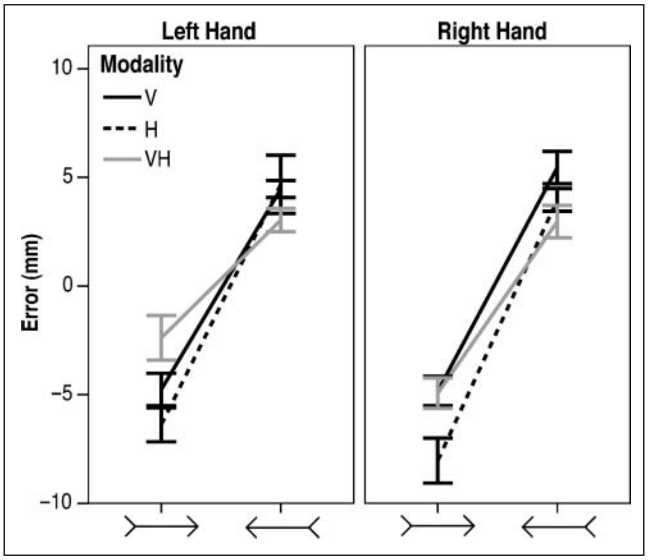

Figure 3. Results: Judd illusion in the "no rTMS" session. Mean bisection error in mm (*SE*), adjusted for the baseline error, by modality (V = visual; H = haptic; VH = visuo-haptic), stimulus type (leftward outgoing/rightward ingoing and leftward ingoing/rightward outgoing fins), and hand (left, right). Negative/positive score: leftward/rightward error.

Bonferroni post hoc comparisons were performed to explore the Stimulus × Modality interaction (see Figure 3). For the stimulus with leftward outgoing/rightward ingoing fins, the differences between the visual and haptic (p = .048), and between the haptic and visuo-haptic presentation conditions (p < .001) were significant; for the stimulus with leftward ingoing/rightward outgoing fins only the difference between the visual and visuo-haptic modalities attained the significance level (p = .024).

Effect of rTMS

The effects of rTMS on the illusion magnitude (i.e., right illusion − left illusion) are shown in Figure 4. Overall, the illusion scores decreased after occipito-temporal rTMS, but not after superior parietal rTMS. The ANOVA on the illusion scores revealed significant effects of the main factors of session [$F(2, 36) = 9.26, p = .001, \eta^2 = 0.07$] and of modality [$F(2, 36) = 20.61, p < .0001, \eta^2 = 0.31$]. Crucially, the interaction between session and modality was not significant [$F(4, 72) = 1.20, p = .32, \eta^2 = 0.01$]. The main effect of hemisphere/hand was not significant [$F(1, 18) = 1.53, p = .23, \eta^2 = 0.01$], as well as its interactions with the main factors of session ($F < 1$) and modality [$F(2, 36) = 1.25, p = .30, \eta^2 = 0.02$]. The Hemisphere/Hand × Session × Modality interaction was not significant [$F(4, 72) = 1.71, p = .157, \eta^2 = 0.01$].

Bonferroni post hoc comparisons on the session factor showed a significant difference between the "no rTMS" condition and the occipito-temporal rTMS (p = .001), with the illusion scores being decreased after occipito-temporal stimulation (mean = 6.83, *SE* = 0.94), with respect to the "no rTMS" condition (mean = 9.32, *SE* = 0.68). Conversely, the difference between the baseline "no rTMS" condition and superior parietal stimulation (mean = 8.67, *SE* = 0.67) was not significant (p = .911), indicating a null effect of superior parietal rTMS on the illusion magnitude. The difference between the superior parietal and occipito-temporal sites of stimulation was also significant (p = .024), with the illusion scores after occipital–temporal rTMS being lower than after superior parietal rTMS. Thus, results highlight an involvement of bilateral occipital–temporal cortex in the processing of the visual, haptic, and visuo-haptic illusion, whereas both right and the left SPC seem to play no relevant role in any presentation condition.[1]

Finally, Bonferroni post hoc comparisons on the modality factor showed that the illusory effects were comparable in size (p = .22) in vision (mean = 8.78, *SE* = 0.78) and in touch (mean = 10.77, *SE* = 0.99), but reduced in the visuo-haptic condition (mean = 5.26, *SE* = 0.77), as compared to both the unimodal visual and haptic presentation conditions (both p < .0001). The reduced illusory effects in the visuo-haptic condition, as compared with the two unimodal conditions, confirm previously reported evidence (Mancini et al., 2010).

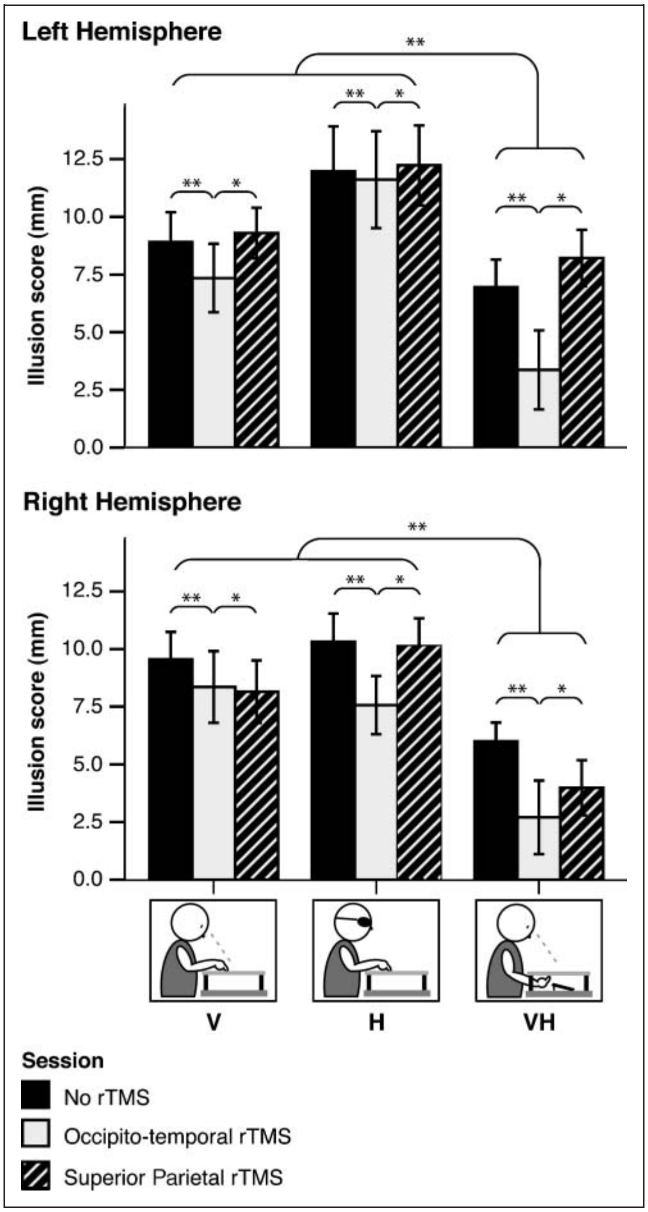

Figure 4. Results: Judd illusion after rTMS interference. Mean illusion scores in mm (*SE*) by modality (V = visual; H = haptic; VH = visuo-haptic), session (no rTMS; rTMS: occipito-temporal, superior parietal), and group (left hemisphere/hand; right hemisphere/hand). The asterisks indicate a significant difference between conditions: *p < .05, **p < .01.

Specificity of the Involvement of Occipito-temporal Cortex in the Cross-modal Judd Illusion

In order to control for the specificity of the effect of rTMS on the illusion, and consequently, to rule out an interpretation in terms of interference with general object-representation processes, an ANOVA on the bisection errors of the baseline stimulus alone (vertical terminators) was performed. Table 1 shows the average bisection error scores for the baseline nonillusory stimulus in the three TMS conditions and in the three input modalities. Importantly, the main factors of session, modality, and their interaction were not

Table 1. Baseline Stimulus: Mean (*SE*) Bisection Error (mm) by Modality (V = Visual; H = Haptic; VH = Visuo-Haptic), Session (No rTMS; rTMS: Occipito-temporal, Superior Parietal), and Group (Left Hemisphere/Hand; Right Hemisphere/Hand)

Modality	*V*	*H*	*VH*
Left Hemisphere/Hand			
No rTMS	−1.20 (0.51)	−1.27 (1.85)	3.82 (1.69)
Occipito-temporal	−0.42 (0.59)	−0.52 (1.56)	4.20 (2.24)
Superior parietal	−1.45 (0.57)	−1.07 (1.19)	4.60 (2.41)
Right Hemisphere/Hand			
No rTMS	0.22 (0.31)	0.98 (0.71)	−4.78 (0.97)
Occipito-temporal	0.82 (0.27)	−0.37 (1.69)	−5.60 (1.45)
Superior parietal	1.00 (0.41)	0.78 (0.88)	−5.52 (1.07)

Negative/positive score: leftward/rightward error.

significant (all $F < 1$). However, the between-subjects factor hemisphere/hand was significant [$F(1, 18) = 4.44$, $p = .049$, $\eta^2 = 0.19$], as the stimulus was bisected more rightward with the left (mean = 0.74, *SE* = 0.71) than with the right hand (mean = −1.39, *SE* = 0.71). The Hemisphere/Hand × Modality interaction was significant [$F(2, 36) = 19.63$, $p < .0001$, $\eta^2 = 0.38$]. Post hoc pairwise comparisons showed a significant difference between the visuo-haptic and the two unimodal presentation conditions, for each hemisphere/hand ($p < .05$); the difference between the two unimodal conditions was not significant. For the left hand, the baseline stimulus was bisected rightward in the visuo-haptic (mean = 4.21, *SE* = 1.49), and leftwards in the visual (mean = −1.02, *SE* = 0.38) and haptic (mean = −0.95, *SE* = 1.12) conditions. On the contrary, for the right hand, the baseline stimulus was bisected leftward in the visuo-haptic (mean = −5.30, *SE* = 1.49), and rightward in the visual (mean = 0.68, *SE* = 0.38) and in the haptic (mean = 0.47, *SE* = 1.12) conditions. Finally, the Hemisphere/Hand × Session, and Hemisphere/Hand × Session × Modality interactions were not significant (all $F < 1$). Overall, these results indicate that the effects of occipito-temporal rTMS were specific for the illusory stimuli.

DISCUSSION

The present study investigated the neural correlates of the Judd illusion, contrasting for the first time visual, haptic, and cross-modal illusory effects in a manual bisection task. We found that rTMS over either left or the right occipito-temporal cortex, at the level of the LOC, interferes with the processing of the unisensory, visual and haptic, and the cross-modal visuo-haptic illusion in a similar fashion. Conversely, rTMS administered over either left or right SPC does not affect illusion scores in any modality. Overall, these findings suggest that the left and right occipito-temporal cortices are causally involved in the processing of the Judd illusion. We show that this visual area, traditionally considered as modality-specific (Grill-Spector, 2003), plays a multisensory role (Lacey, Tal, Amedi, & Sathian, 2009; Beauchamp, 2005), being implicated not only in the visual (Weidner et al., 2010; Weidner & Fink, 2007) but also in the haptic and cross-modal visuo-haptic processing of the illusion.

The main finding of the study is that both the left and the right occipito-temporal cortices are involved in the processing of the Judd variant of the Müller-Lyer illusion. The rTMS interference with the processing of the illusion is not modality-specific, supporting the hypothesis of a multisensory representation of the Müller-Lyer illusion in this region. As far as the visual modality is concerned, these findings are in line with the results of previous neuroimaging studies that used other variants of the visual Müller-Lyer illusion (Weidner et al., 2010; Weidner & Fink, 2007). Here we demonstrate the causal bilateral involvement of occipito-temporal cortex in processing the illusion across different sensory modalities, not only visual but also haptic and cross-modal visuo-haptic.

In this study, the visual and haptic Judd illusions are equally powerful, whereas the cross-modal illusory effects are smaller than the unimodal effects (marginal differences emerged from the analysis in the "no rTMS" condition), in line with recent evidence (Mancini et al., 2010). The decrement of the illusion in the cross-modal condition has been considered the likely marker of the multisensory integration of the visual and haptic components of the stimuli (see Mancini et al., 2010 for discussion). Finally, the occipito-temporal rTMS interference was comparable among the three presentation conditions, in line with the hypothesis of shared processes in the two assessed modalities.

Occipito-temporal Cortex

The mechanisms underlying the processing of the visual Müller-Lyer illusion may be closely linked to those associated with object perception (Weidner et al., 2010). Our findings suggest that the Müller-Lyer illusion may elicit a bias in mechanisms involved in cross-modal shape processing. Within the visual ventral stream, the LOC is an object-selective area that responds to objects not only in vision but also in touch (Deshpande et al., 2008; Peltier et al., 2007; Amedi et al., 2001, 2002; James et al., 2002).

The LOC may build up a multisensory representation of objects (Tal & Amedi, 2009). In particular, a subregion of the LOC, the lateral occipital tactile–visual region (LOtv; Amedi et al., 2001, 2002), contains a modality-independent representation of geometric shape that can be flexibly addressed either bottom–up, from direct sensory inputs, or top–down, from prefrontal and parietal regions, irrespective of the modality of the sensory input, and depending on object familiarity (Deshpande, Hu, Lacey, Stilla, & Sathian, 2010; Lacey et al., 2009). This neural network concerned with multisensory representations of objects might be implicated also in the processing of illusions, such as the Müller-Lyer figure and its variants, within and across different sensory modalities.

It is still controversial whether the LOC's recruitment in haptic shape processing is purely multisensory or is also mediated by visual imagery. The role of visual imagery has been investigated in a series of fMRI studies using connectivity analyses. Particularly, visual imagery may mediate the recruitment of LOC in haptic shape processing of familiar objects, through top–down paths from prefrontal cortex to LOC. Conversely, the unfamiliar shape network is mainly characterized by bottom–up somatosensory inputs to LOC (Deshpande et al., 2010; Lacey, Flueckiger, Stilla, Lava, & Sathian, 2010; Deshpande et al., 2008). Importantly, activation of LOC during haptic shape processing has been demonstrated also in congenitally blind people (Amedi, Raz, Azulay, Malach, & Zohary, 2010; Amedi et al., 2007; Pietrini et al., 2004). This indicates that visual imagery is not an obligatory condition for the haptic recruitment of visual cortex.

As for the Müller-Lyer illusion, tactile illusory effects are preserved in congenitally blind people (Heller et al., 2002), indicating that they are not dependent on visual experience. In addition, recent behavioral results (Mancini et al., 2010) show that the cross-modal transfer of the illusion from vision to haptics depends on the spatial coincidence between the visual and tactile sensory inputs. Particularly, in a cross-modal condition similar to the present one, we varied the horizontal position of the shaft with respect to the arrowheads: It could be shifted in the congruent or incongruent direction of the side expanded by the illusion, with a 25% offset. Only when the visual arrowheads are aligned with the shaft are they able to affect its haptic bisection. The misalignment of the shaft with respect to the arrowheads, even when it is in the direction expanded by the illusion, breaks up the cross-modal transfer of the illusory effects. In line with these findings, spatial coincidence is known to be a relevant factor in multisensory integration (Gepshtein et al., 2005; Stein & Meredith, 1993). The absence of illusory effects for spatially incongruent stimuli suggests that imagery itself cannot explain the influence of the visual illusion on haptic bisection (in particular, the condition where the shaft is shifted in the direction expanded by the visual illusion does not elicit any bisection bias). Instead, the illusory effect is likely to result from the cross-modal combination of the sensory inputs, being dependent on the spatial coincidence between them.

Finally, one more issue is relevant to the interpretation of our data. We aimed at stimulating lateral occipital cortex, shown to be activated by the visual Müller-Lyer illusion in a previous study (Weidner & Fink, 2007). Other areas within occipito-temporal cortex might be also relevant in the processing of the cross-modal variant of the illusion, such as the LOtv, which is activated by haptic shape processing (Amedi et al., 2001, 2002). LOtv is localized slightly more laterally (Talairach coordinates, mean ± *SD*, −45 ± 5, −62 ± 6, −9 ± 3) (Amedi et al., 2001) than the region targeted in the present experiment. The use of group-based coordinates for coil positioning might have reduced the spatial accuracy of our rTMS effects (Sack et al., 2009; Sparing, Buelte, Meister, Paus, & Fink, 2008), hence, resulting in the stimulation of nearby regions of occipito-temporal cortex, such as LOtv. fMRI-guided TMS studies may provide additional information concerning the selective involvement of different regions of occipito-temporal cortex (i.e., LOC vs. LOtv) in the unimodal and cross-modal processing of the illusion.

Parietal Cortex

In addition to lateral occipital cortex, in the study by Weidner and Fink (2007), the visual Müller-Lyer illusion activates also right SPC. This activation may reflect spatial processing, rather than the illusory effects per se, possibly the integration and updating of a size-invariant representation of shape, which is illusory biased, into a spatial reference frame (Weidner & Fink, 2007). In this study, we did not find any significant involvement of SPC in the processing of the illusion, regardless of stimulus modality. Our rTMS study differs from the fMRI experiment by Weidner and Fink in a number of important respects that may have influenced the results. Weidner and Fink used the Brentano variant of the Müller-Lyer illusion and a perceptual judgment task; we used the Judd illusion and a manual bisection task. Importantly, however, there is a convergence as to the cerebral area responsible of the illusory effects in the visual modality, namely, occipito-temporal cortex.

Moreover, in line with our null effect of the superior parietal stimulation, a number of neuropsychological studies show that patients with right parietal cortical lesions exhibit preserved visual illusory effects (Vallar & Daini, 2006). The illusory effects occur independently of the presence of spatial and attentional deficits, such as unilateral spatial neglect. However, when the patients' right-sided posterior parietal lesions extend to the occipital regions, patients show impaired illusory effects (Daini et al., 2002). These findings in brain-damaged patients are consistent with the current results that the stimulation of parietal cortex alone does not elicit significant effects.

It should also be noted that the different physiology of the cortical regions targeted in the present study (i.e., gyral/sulcal geometry with respect to the plane of TMS pulse propagation) could make them not equally susceptible to rTMS interference (Wassermann et al., 2008; Walsh & Cowey, 2000). For all these reasons, the null effect of right superior parietal stimulation should be interpreted with caution. Finally, other multisensory regions in posterior parietal cortex, as the intraparietal sulcus (IPS; Peltier et al., 2007), might play a role.

The bisection of the baseline stimulus with vertical terminators is not affected by any condition of TMS stimulation, indicating that the TMS interference over occipital–temporal cortex is specific for the illusion. Particularly, right superior parietal rTMS does not impair bisection. There is evidence that TMS interference over posterior parietal cortex, of which SPC is a component part, may affect line bisection performance, eliciting a "neglect-like" bias in healthy participants (Oliveri & Vallar, 2009; Fierro et al., 2000; right supramarginal gyrus). Furthermore, neuroimaging activation studies indicate a role of the entire posterior parietal cortex (both the inferior and the superior parietal lobule) in bisection tasks (Ciçek, Deouell, & Knight, 2009; Fink et al., 2000, 2003). However, neuropsychological evidence indicates that damage to SPC is associated with optic ataxia, rather than with unilateral spatial neglect, of which the rightward bias in line bisection is one of the main manifestations (Coulthard, Parton, & Husain, 2006). Finally, anatomoclinical correlation studies in right-brain-damaged patients with spatial neglect indicate that the rightward bias in line bisection is associated with posterior lesions, specifically at the junction between the right middle temporal and the middle occipital gyri (Rorden, Fruhmann Berger, & Karnath, 2006), and lesions to the inferior parietal lobule (Verdon, Schwartz, Lovblad, Hauert, & Vuilleumier, 2010).

In summary, TMS and neuroimaging studies suggest an involvement of posterior parietal cortex (both the inferior and the superior parietal lobule, and the IPS) in line bisection tasks. The available evidence from brain-damaged patients highlights the role of the inferior parietal lobule, in line with the present finding that rTMS interference with SPC does not affect line bisection performance.

Conclusion

The present results indicate the existence of a common multisensory neural substrate of the Judd variant of the Müller-Lyer illusion, showing the critical involvement of occipito-temporal cortex in building up a representation shared by the visual, haptic, and visuo-haptic illusion. These findings indicate that occipito-temporal cortex is implicated in cross-modal shape processing, both of illusory and of nonillusory figures (Amedi et al., 2001, 2002). Growing evidence indicates that this visual region, traditionally considered unisensory, plays a cross-modal role in perception (Kim & James, 2010; Lacey et al., 2009; Beauchamp, 2005). Here we provide a new insight on the multisensory involvement of occipito-temporal cortex in perception, through a classical "optical" illusion.

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Note

1. An inspection of the data (Figure 4) may suggest that in the visual (and the visuo-haptic) conditions, the illusion scores were reduced also after right SPC rTMS, in line with the study by Weidner and Fink (2007). Therefore, in the right hemisphere/hand group, we directly compared, by one-tailed t tests, the illusion scores in the "no rTMS" and in the SPC rTMS sessions, in both the visual and the visuo-haptic presentation conditions; no significant differences were found, for both the visual ($t_9 = 1.660$) and the visuo-haptic ($t_9 = 1.391$) modalities.

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