The Oppel Kundt Illusion is effective in modulating horizontal space representation in humans

THE OPPEL-KUNDT ILLUSION IS EFFECTIVE IN MODULATING HORIZONTAL SPACE REPRESENTATION IN HUMANS

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Summary.—A modified version of the Oppel-Kundt illusion (i.e., a filled space is perceived as more expanded than an empty space of the same length) has been previously employed to distort space representation both in patients with neglect (i.e., failure to report/react to stimuli located in the space contralateral to the brain lesion) and in healthy participants. In those experiments, participants had to bisect or extend horizontal segments on backgrounds of exponentially spaced vertical lines. The exclusive use of visuo-motor tasks, however, did not allow excluding that the results were accounted for by a bias occurring at a response level of stimulus processing rather than by a visual illusion. To address this issue, in addition to a traditional line bisection task, a line length estimation task was employed, which allowed separating response and illusion-related factors. The results demonstrated that performance depended on the visual illusion rather than on a response bias. It was concluded that this version of the Oppel-Kundt illusion can be successfully employed to modulate space representation in humans.

The term geometrical illusion derives from the German "geometrisch-optische täuschung" and describes any misperception of stimulus length, size, shape, or direction due to a non-correspondence between the percept and the actual stimulus. Oppel (1854/1855) originally demonstrated that the visual space enclosed within a series of dots is perceived longer than an empty space of the same dimension (see Fig. 1, upper part). The principle underlying such an illusion, later (Kundt, 1863) called the Oppel-Kundt

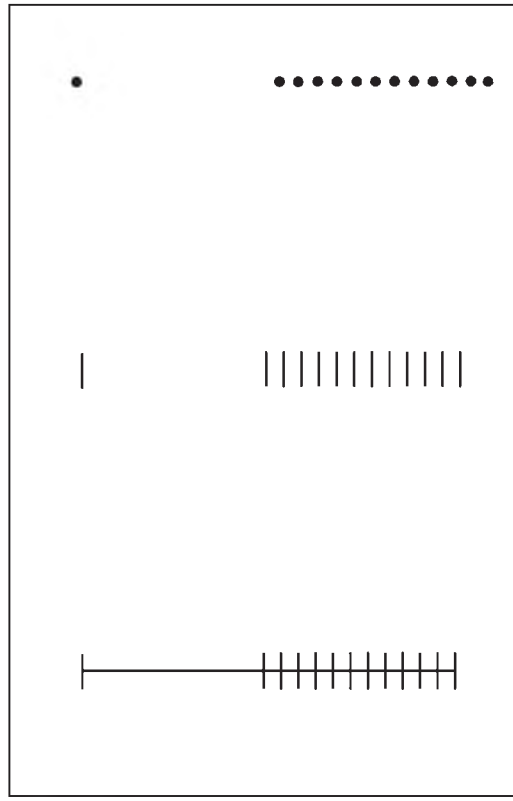

FIG. 1. The Oppel-Kundt illusion. Some examples.

illusion, is also effective when the space is enclosed within vertical lines (Kundt, 1863; Lewis, 1912; Ni, 1934; Coren, Girgus, Ehrlichman, & Hakistan, 1976; see Fig. 1, middle part), for horizontal lines subdivided by vertical lines (Oppel, 1860/1861; Ricci, Calhoun, & Chatterjee, 2000; Ricci, Pia, & Gindri, 2004; see Fig. 1, lower part), and in 3D visual space (Deregowski & McGeorge, 2006). The magnitude of the illusory effect is a function of multiple properties of the stimuli, such as texture and illusory gradient (Giora & Gori, 2010; Wackermann & Kastner, 2010). Interestingly, the principles underlying the illusion are also effective within sensory modalities other than vision, such as haptic (e.g., haptic line bisection; Suzuki & Arashida, 1992) audition (e.g., estimation of time intervals; Russo & Dellantonio, 1989). Additionally, the illusion is effective also across modalities. Gallace and coworkers (Gallace, Auvray, & Spence, 2007), for instance, showed that haptic line bisection in healthy participants is affected cross-modally by varying the visual background that participants viewed.

Ricci and coworkers (Ricci, *et al.*, 2004) developed a modified version of the Oppel-Kundt illusion to modulate space representation in patients with unilateral neglect (i.e., a disorder of contralesional space awareness; see Halligan, Fink, Marshall & Vallar, 2003, for a review) and in healthy participants. The aim of that study was to induce in healthy participants the anisometrical (i.e., non-linear) spatial distortion hypothesized to underlie neglect (Bisiach, Ricci, & Neppi-Mòdona, 1998; Bisiach, Neppi-Mòdona, & Ricci, 2002), and to counteract this distortion in patients. Indeed, according to Bisiach's account, in neglect patients, "the left–right dimension of space representation is settled, as it were, on a logarithmic scale, with compression on the ipsilesional side and expansion on the contralesional side" (Bisiach, Pizzamiglio, Nico, & Antonucci, 1996, p. 855-856). At a perceptual level, this results in an underestimation of contralesional stimuli with respect to ipsilesional ones. Hence, Ricci and coworkers (Ricci, *et al.*, 2004) employed visual backgrounds composed of vertical lines whose distance progressively decreased from one side of the page to the other, according to an exponential function. In this way, they defined filled and empty portions of space by means of non-linearly or anisometrically distributed vertical lines (in the original version of the Oppel-Kundt illusion, space is subdivided into equal, isometric intervals). On the abovementioned visual backgrounds, participants had to perform a line bisection task (i.e., mark the midpoint of a horizontal line) and a line extension task (i.e., extend a horizontal segment leftward or rightward to double its original length). According to the principles underlying the original version of the Oppel-Kundt illusion, the more densely segmented portion of the background was expected to induce perceptual expansion of the line (overestimation of stimulus length) with respect to the less densely segmented portion (underestimation of stimulus length). The authors predicted a displacement of the subjective midpoint and shorter line extensions towards the denser side of the background. The performance of both neglect patients and healthy participants confirmed these predictions. Interestingly, patients with neglect showed an improvement of their rightward bisection bias when the visual illusion induced a perceptual distortion opposite to that hypothesized to underlie neglect (i.e., illusory expansion of left space), whereas healthy participants exhibited a neglect-like bisection bias when the visual illusion induced a perceptual distortion mimicking the one hypothesized to underlie neglect (i.e., illusory contraction of the left space). Subsequent studies, employing similar versions of the Oppel-Kundt illusion, replicated and extended Ricci and coworkers' (Ricci, *et al.*, 2004) findings, namely the displacement of the subjective midpoint towards the denser side of the illusory background in the line bisection task both in neglect patients (Savazzi, Posteraro, Veronesi, &

Mancini, 2007) and healthy participants (Binetti, Aiello, Merola, Bruschini, Lecce, Macci, *et al.*, 2011).

The validity of the above-mentioned findings (Ricci, *et al.*, 2004; Savazzi, *et al.*, 2007; Binetti, *et al.*, 2011) can be challenged by the argument that these tasks do not provide a direct measure of the effects of the illusion because participants do not explicitly judge horizontal lengths. Hence, such tasks do not allow excluding the possibility that participants' performance is strongly driven by a response bias towards the denser side of the background. Indeed, given that stimulus characteristics may automatically draw attention to particular regions of space (see, for instance, Mark, Kooistra, & Heilman, 1988), the side of the background with the highest density of vertical lines might have automatically attracted participants' attention. This, in turn, might have biased participants' motor responses towards this side (see Ricci, *et al.*, 2004, p. 234, and Savazzi, *et al.*, 2007, p. 10, for details on this point).

The present study aims to clarify this issue. To this end, it compares the effect of the above mentioned modified version of the Oppel-Kundt illusion on a traditional line bisection and on the landmark task (Milner, Brechmann, & Pagliarini, 1992; Bisiach, Ricci, Lualdi, & Colombo, 1998), a task conceived to separate perceptual and response-related factors in the estimation of horizontal lengths. Here, participants have to perform a line length estimation task by choosing which of two segments (left or right) composing a pre-bisected line is shorter, in one condition, and longer, in the other. If participants' behavior is driven by the visual illusion, they are expected to choose more often the segment lying on the more sparse side in the Shorter condition, and the opposite segment (lying on the denser side) in the Longer condition. Conversely, if the participants' performance is the consequence of a response bias towards the denser side of the background, they should consistently choose the segment lying on this side independent of task demands.

Method

Participants

Thirty-five right-handed (Oldfield, 1971), randomly chosen, healthy participants participated in this study (16 men, 19 women). In order to compare the results of the present work to those obtained in the aforementioned studies (Ricci, *et al.*, 2004; Savazzi, *et al.*, 2007; Binetti, *et al.*, 2011), participants were selected to be comparable for age and educational level (M age = 69.2 yr., SD = 9.3; M education = 11.1 yr., SD = 4.8). All participants gave their informed consent to participate in the study, which was approved by the local ethical committee.

Stimuli

The visual background consisted of 25 0.5 mm thick and 88.25 mm

long vertical lines parallel to the shorter side of an A4 sheet of paper (printed in black against a white background). Vertical lines were interrupted by a 14 mm high and 297 mm long rectangular empty gap located in the middle of the sheet. In one condition (Uniform Density), the lines were evenly spaced at a distance of 10 mm. This condition served as baseline. In the

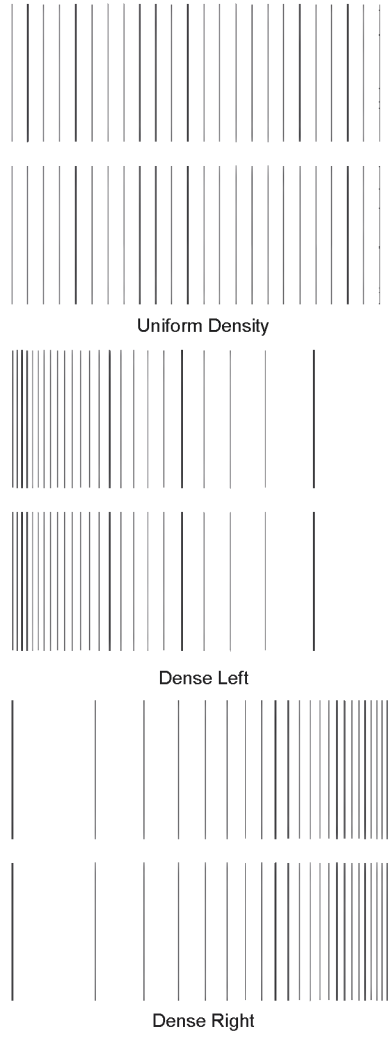

FIG. 2. Backgrounds used in line bisection and the landmark tasks. Uniform Density = evenly spaced vertical lines (baseline); Dense Left = exponentially spaced vertical lines with distances progressively decreasing leftwards; Dense Right = exponentially spaced vertical lines with distances progressively decreasing rightwards.

other two conditions (i.e., Dense Left and Dense Right), they were exponentially spaced with distances progressively decreasing from one side of the page to the other (toward the left in the former and towards the right in the latter, according to the exponential function $Y = e^x$; $x \in [-0.50; 1.9]$ in steps of 0.10 (see Fig. 2). The Dense Left condition was designed to induce an illusory spatial expansion of the left spatial sector and a contraction of the right spatial sector. Conversely, the Dense Right condition was designed to induce the opposite illusion.

Procedures

Line bisection task.—A 200 mm long and 0.5 mm thick horizontal line segment was printed within the rectangular horizontal gap interrupting the vertical background lines. The center of the line segment was displaced leftward or rightward (by 3 mm) of the midpoint of the page to prevent participants from using the background lines as a visual cue to estimate the objective midpoint of the line. Participants were explicitly informed that such a strategy would be misleading and throughout the execution of the task the examiner took care in preventing from participants used this strategy. Participants were given 60 trials (10 repetitions × 3 backgrounds × 2 line positions) in a pseudo-random order (there were no consecutive identical trials). The sheet of paper was centered on the participant's saggittal mid-plane and presented at reaching distance under normal room lighting conditions. The visual angle subtending the line was about 30°. Participants were asked to mark the midpoint of the horizontal line with a pencil.

Landmark task.—The 200 mm long and 0.5 mm thick horizontal line, printed within the rectangular horizontal gap was pre-bisected with a 0.5 mm thick and 4 mm long vertical black line placed to the left or to the right (by 1 or 2 mm) of the objective midpoint or centered on it. As for the line bisection task, the center of the line segment was displaced 3 mm leftward (or rightward) to prevent the use of the background as a visual cue to estimate the segment midpoint. Indeed, participants were informed of the ineffectiveness of the strategy and were controlled during the task. The sheet of paper was centered on the participant's saggittal mid-plane and presented at reaching distance under normal room lighting conditions. The visual angle subtending the line was about 30°. Participants were required to make a binary forced-choice decision (right/left) according to opposing question conditions: in one condition, they had to point with the right hand towards the longer side of the segment (left or right), whereas in the other, they had to point with the right hand towards the shorter side of the segment (left or right). Longer and Shorter question conditions were grouped in four separate blocks following an ABBA order (which was counterbalanced across participants). The overall number

of trials was 120 (2 question conditions × 2 repetitions × 3 backgrounds × 2 line positions × 5 bisector positions). Left and right responses were recorded. The order of the two tasks (i.e., line bisection and landmark task) was counterbalanced across participants.

Statistical Analysis

Line bisection task.—Bisection errors were measured with an approximation to the nearest mm. Positive values were assigned to rightward deviations and negative values to leftward deviations. Measures were distributed normally (Kolmogorov-Smirnov test) and variance was homogeneous (Box's M test). Hence, the authors performed a repeated-measures analysis of variance (ANOVA) with Background (three levels: Uniform Density, Dense Left and Dense Right) as within-subjects factors, and bisection error as the dependent variable. In this task, both the illusory and the response bias interpretations predicted statistically significant bisection errors toward the denser portion of the background.

Landmark task.—For each participant, the proportion of left and right side responses with respect to the bisector positions was estimated by means of a stratified logistic analysis on each combination of Background and Question condition levels. Then the parameters of the logistic function were used to estimate the point of subjective equality (hereinafter PSE) obtained as a 0.5 threshold value of the function, namely the point where the two halves of the segment are subjectively perceived as identical (Kingdom & Prins, 2010). Positive values were assigned to rightward deviations, negative values to leftward deviations. Since measures were distributed normally (Kolmogorov-Smirnov test) and variance was homogeneous (Box's M test), we performed a repeated-measures ANOVA with Background (three levels: Uniform Density, Dense Left, and Dense Right) and Question (two levels: Longer and Shorter) as within-subjects factors, and PSEs as dependent variables (missing values were replaced with the group mean). A statistically significant misplacement of the PSE toward the denser portion of the background, and no Background × Question condition interaction was expected in the presence of an illusory perceptual bias (choosing the segment lying on the more sparse side as shorter, and the one lying on the denser side as longer gives rise to the same PSE). On the other hand, a significant interaction between Background × Question conditions (PSE towards the denser side for the Longer condition and towards the sparse side for the Shorter condition) was expected to be observed in the presence of a response bias.

Results

Line Bisection Task

The ANOVA was significant ($F_{2,68} = 94.73$, $p < .0001$, partial $\eta^2 = 0.74$;

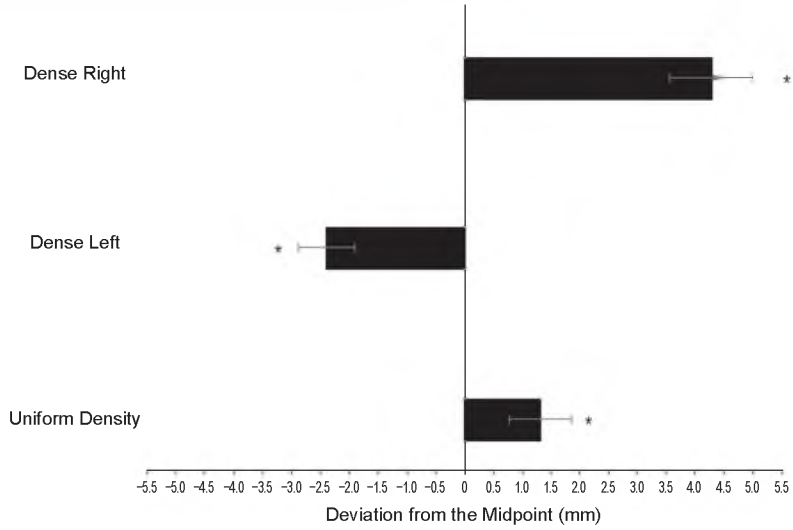

FIG. 3. Line bisection. Mean bisection error in the different Background conditions. Uniform Density = evenly spaced vertical lines (baseline); Dense Left = exponentially spaced vertical lines with distances progressively decreasing leftwards; Dense Right = exponentially spaced vertical lines with distances progressively decreasing rightwards. Positive and negative values indicate, respectively, a rightward and a leftward deviation of the midpoint.

observed power = 1.0). A *post hoc* analysis (Duncan) showed that each condition was significantly different from the others ($p < .0005$). The bisection error was displaced towards the denser side of the Background (Uniform Density: $M = 1.321$ mm, $SE = 0.529$ mm; Dense Left: $M = -2.385$ mm, $SE = 0.474$ mm; Dense Right: $M = 4.321$ mm, $SE = 0.691$ mm). Each condi-

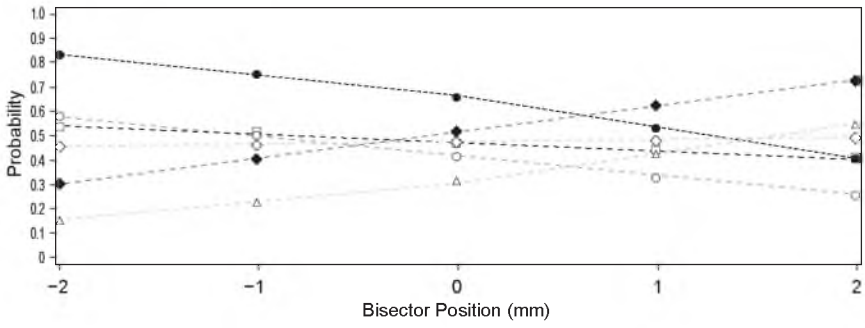

FIG. 4. Landmark task. Psychometric curves fitted according to Background and Question condition levels. Shorter Uniform Density (□); Shorter Dense Left (○); Shorter Dense Right (●); Longer Uniform Density (◇); Longer Dense Left (◆); Longer Dense Right (△).

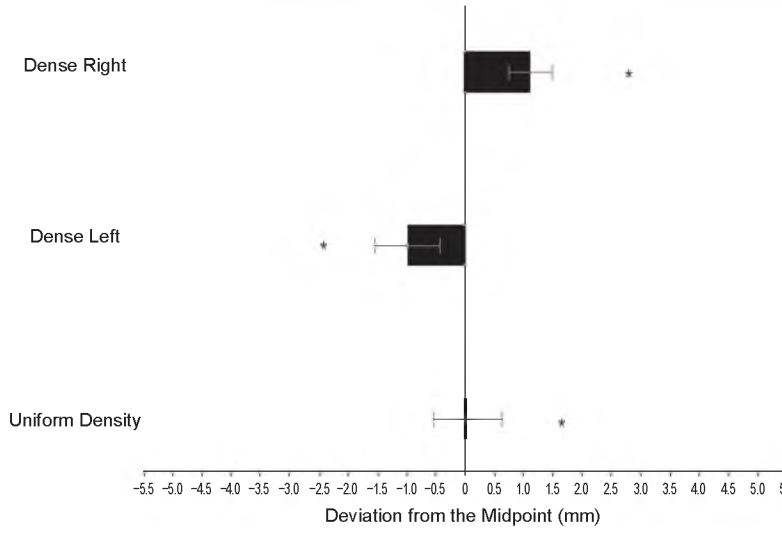

FIG. 5. Landmark task. PSE in the different Background conditions. Uniform Density = evenly spaced vertical lines (baseline); Dense Left = exponentially spaced vertical lines with distances progressively decreasing leftwards; Dense Right = exponentially spaced vertical lines with distances progressively decreasing rightwards. Positive and negative values indicate, respectively, a rightward and a leftward deviation of the midpoint.

tion was also different from the veridical midpoint ($p < .05$). Fig. 3 shows the mean bisection errors (mm) for each Background condition.

Landmark Task

Fig. 4 depicts the psychometric function. In the ANOVA, only the main factor Background was significant ($F_{2,68} = 8.68$, $p < .0005$, partial $\eta^2 = 0.20$; observed power = 0.96). A *post hoc* analysis (Duncan) showed that each condition was significantly different from the others ($p < .05$). The PSE was displaced towards the denser side of the Background (Uniform Density: $M = 0.043$ mm, $SE = 0.41$ mm; Dense Left: $M = -0.968$ mm, $SE = 0.381$ mm; Dense Right: $M = 1.09$ mm, $SE = 0.263$ mm). Dense Left and Dense Right conditions were also different from the veridical midpoint ($p < .05$). Fig. 5 shows the mean PSE (mm) for each Background condition.

DISCUSSION

The present results show that the effects of a variant of the Oppel-Kundt illusion on line length estimations tightly depend on a perceptual illusion of length rather than on a motor response bias. Previous studies have used a modified (i.e., non-linear) version of the Oppel-Kundt illusion in healthy participants and neglect patients to modulate spatial rep-

resentation (Ricci, *et al.*, 2004; Savazzi, *et al.*, 2007; Pia, Folegatti, Guagliardo, Genero, & Gindri, 2009; Binetti, *et al.*, 2011; Pia, Ricci, Gindri, & Vallar, 2012). One of the aims of these studies was to investigate the anisometric spatial distortion thought to underpin spatial neglect (Bisiach, *et al.*, 1996; Bisiach, Ricci, & Neppi-Mòdona, 1998; Bisiach, *et al.*, 2002). Those studies reported that participants mis-bisected horizontal lines towards the denser portion of the background. This result could be interpreted as due to the illusion (inducing line length overestimation in correspondence of the denser side of the background), or to a motor response bias towards this side. To investigate this issue, healthy participants were asked to perform, under the same illusory backgrounds, a traditional line bisection task and a landmark task in which they had to evaluate the horizontal extension of two segments composing a pre-bisected line. Consistent with the abovementioned findings (Ricci, *et al.*, 2004; Savazzi, *et al.*, 2007; Binetti, *et al.*, 2011), participants mis-bisected the lines toward the denser portion of the background, a result consistent with both an illusory and a "bias of response" interpretation. The landmark task disambiguated these alternatives in favor of the illusory interpretation. Indeed, participants judged the segment lying on the denser side as longer and the segment lying on the more sparse side of the background as shorter, rather than consistently pointing towards the denser side independently of task demands. In accordance with this behavior, the PSE calculated from participants' choices was displaced towards the denser side of the background and it was consistent under both task demands.

It is worth noticing that in the landmark task, participants responded with a pointing movement. The theory of separate vision-for-perception and vision-for-action subsystems (Milner & Goodale, 2008) predicts that visually guided actions should be immune from illusions. It is worth noticing, however, that whether this prediction is convincingly supported by experimental results is still controversial (e.g., Carey, 2001; Smeets, Brenner, de Grave, & Cuijpers, 2002). Indeed, some data suggest that illusory effects do not solely depend on response modality (motor tasks as opposed to procedures designed to tap into conscious perception) but, rather, other factors modulate the effect of the illusion on motor responses (Bruno, Bernardis, & Gentilucci, 2008). The current results support this conclusion and are in line with a recent study demonstrating that some system mediating motor activity may remain vulnerable to the Oppel-Kundt illusion (Savazzi, Emanuele, Scalf, & Beck, 2012).

The fact that this illusion is effective in both healthy participants and neglect patients (Ricci, *et al.*, 2004; Savazzi, *et al.*, 2007; Binetti, *et al.*, 2011) adds to previous evidence showing that space representation in the intact brain and in left unilateral neglect possesses similar susceptibilities to

a variety of manipulations. Non-invasive brain stimulation such as transcranial magnetic stimulation can improve neglect and induce neglect-like symptoms in healthy participants (e.g., Fierro, Brighina, Oliveri, Piazza, La Bua, Buffa *et al.*, 2000; Brighina, *et al.*, 2003). Sensory manipulations, for instance, neck-proprioceptive or vestibular stimulations (Karnath, Fetter, & Dichgans, 1996), can improve neglect symptoms and reproduce them in healthy participants. Prism adaptation is known to improve neglect and induce a neglect-like bias in healthy participants (Loftus, Vijayakumar, & Nicholls, 2009). As regards to visual illusions, in addition to the Oppel-Kundt illusion, the Judd and the Brentano variants of the Mueller-Lyer illusion have also been used to alter the metric of space representation in neglect patients and healthy participants (Fleming & Behrmann, 1998; Daini, Angelelli, Antonucci, Cappa, & Vallar, 2002). In these visual illusions, the effect of spatial expansion is obtained by increasing the physical amount of the horizontal stimulus. In other words, the outwards thin side increases the overall horizontal configuration (i.e., the length of the horizontal stimulus toward the outwards thin side). Instead, in the Oppel-Kundt illusion, perceptual modulation of line length is obtained without changing the horizontal physical length of the line. The possibility of influencing the internal spatial representation of stimuli without changing their horizontal physical dimension might provide a valuable tool to study the mechanisms underlying space representation in both the intact and the lesioned brain.

A final relevant point is the possible link between our data and the nature of the anisometrical spatial distortion thought to underlie neglect. As mentioned above, Bisiach and coworkers (Bisiach, Ricci, & Neppi-Mòdona, 1998; Bisiach, *et al.*, 2002) proposed that neglect is caused by a pathological distortion of the representational medium, progressively compressed towards the ipsilesional space and relaxed towards the contralesional one in a logarithmic manner. Indeed, "the distortion underlying neglect and related phenomena has been likened to a pathological (spatial) remapping of an Euclidean onto a logarithmic scale, with spatial expansion on the contralesional and compression on the ipsilesional side, giving rise to something similar to the Oppel-Kundt illusion" (Bisiach, 1997, p. 491). This kind of distortion is mimicked by the Dense Right condition of our experiment on which participants behaved in a qualitatively similar way to neglect patients (showing a small but significant rightward bisection error). Hence, the data support the view that in the intact brain the metric of the representational medium can be distorted similarly to the anisometrical spatial distortion described in neglect (Ricci, *et al.*, 2004; Savazzi, *et al.*, 2007; Binetti, *et al.*, 2011; Savazzi, *et al.*, 2012). However, even though there is a similarity, illusions of length (among which there is the Oppel-Kundt

Illusion) and space anisometry (resultant from lesion-induced alterations of the space processing neural system) are to be interpreted as independent phenomena. Indeed, it is known that they are likely to occur at intermediate and late stages of visual processing (respectively), which have been found to doubly dissociate (Driver, Baylis, & Rafal, 1992; Vecera & Behrmann, 1997; Ricci, Vaishnavi, & Chatterjee, 1999). It has been speculated that the neurophysiological signature of space anisometry might be ascribed to the changes of the response properties of the receptive fields of fronto-parietal neurons surviving the lesion (Bisiach, Ricci, & Modona, 1998): "It might turn out that the characteristics of such neurons, and therefore the metrics of space representation, are contingent upon the equilibrium emerging within a widespread neuronal network from, as it were, a system of functional counterforts. Unilateral brain damage could result in one-sided lack of counterpoise within such a system and lead to skewness of the medium for space representation.

We must acknowledge the main limitation of the present study. The findings are simple and straightforward (i.e., validating a tool to study the mechanisms underlying space representation in humans) and purely behavioral. Hence, further research is necessary to obtain information about the neural mechanisms underlying modulation of space perception through the Oppel-Kundt illusion in the healthy and in the lesioned brain. Results, for instance, should be replicated in patients with visuo-spatial neglect.

REFERENCES

Binetti, N., Aiello, M., Merola, S., Bruschini, M., Lecce, F., Macci, E., & Doricchi, F. (2011) Positive correlation in the bisection of long and short horizontal Oppel-Kundt illusory gradients: implications for the interpretation of the "cross-over" effect in spatial neglect. *Cortex*, 47(5), 608-616.

Bisiach, E. (1997) The spatial features of unilateral neglect. In P. Thier & H-O. Karnath (Eds.), *Parietal lobe contribution to orientation in 3D space.* Heidelberg, Germany: Springler Verlag. Pp. 465-495.

Bisiach, E., Neppi-Mòdona, M., & Ricci, R. (2002) Space anisometry in unilateral neglect. In H. O. Karnath, A. D. Milner, & G. Vallar (Eds.), *The cognitive and neural bases of spatial neglect.* Oxford, UK: Oxford Univer. Press. Pp. 145-152.

Bisiach, E., Pizzamiglio, L., Nico, D., & Antonucci, G. (1996) Beyond unilateral neglect. *Brain*, 119, 851-857.

Bisiach, E., Ricci, R., Lualdi, M., & Colombo, M. R. (1998) Perceptual and response bias in unilateral neglect: two modified versions of the Milner Landmark Task. *Brain and Cognition*, 37(3), 369-386.

Bisiach, E., Ricci, R., & Neppi-Mòdona, M. N. (1998) Visual awareness and anisometry of space representation in unilateral neglect: a panoramic investigation by means of a line extension task. *Consciousness and Cognition*, 7(3), 327-355.

Brighina, F., Bisiach, E., Oliveri, M., Piazza, A., La Bua, V., Daniele, O., & Fierro, B. (2003) 1 Hz repetitive transcranial magnetic stimulation of the unaffected hemisphere ameliorates contralesional visuospatial neglect in humans. *Neuroscience Letters*, 336(2), 131-133.

Bruno, N., Bernardis, P., & Gentilucci, M. (2008) Visually guided pointing, the Muller-Lyer illusion, and the functional interpretation of the dorsal-ventral split: conclusions from 33 independent studies. *Neuroscience and Biobehavioral Review*, 32(3), 423-437.

Carey, D. P. (2001) Do action systems resist visual illusions? *Trends in Cognitive Sciences*, 5(3), 109-113.

Coren, S., Girgus, J. S., Ehrlichman, H., & Hakistan, A. R. (1976) An empirical taxonomy of visual illusions. *Perception and Psychophysics*, 20, 129-147.

Daini, R., Angelelli, P., Antonucci, G., Cappa, S. F., & Vallar, G. (2002) Exploring the syndrome of spatial unilateral neglect through an illusion of length. *Experimental Brain Research*, 144(2), 224-237.

Deregowski, J. B., & McGeorge, P. (2006) Oppel-Kundt illusion in three-dimensional space. *Perception*, 35(10), 1307-1314.

Driver, J., Baylis, G. C., & Rafal, R. D. (1992) Preserved figure-ground segregation and symmetry perception in visual neglect. *Nature*, 360(6399), 73-75.

Fierro, B., Brighina, F., Oliveri, M., Piazza, A., La Bua, V., Buffa, D., & Bisiach, E. (2000) Contralateral neglect induced by right posterior parietal rTMS in healthy subjects. *NeuroReport*, 11(7), 1519-1521.

Fleming, J., & Behrmann, M. (1998) Visuospatial neglect in normal subjects: altered spatial representations induced by a perceptual illusion. *Neuropsychologia*, 36(5), 469-475.

Gallace, A., Auvray, M., & Spence, C. (2007) The modulation of haptic line bisection by a visual illusion and optokinetic stimulation. *Perception*, 36(7), 1003-1018.

Giora, E., & Gori, S. (2010) The perceptual expansion of a filled area depends on textural characteristics. *Vision Research*, 50(23), 2466-2475.

Halligan, P. W., Fink, G. R., Marshall, J. C., & Vallar, G. (2003) Spatial cognition: evidence from visual neglect. *Trends in Cognitive Sciences*, 7(3), 125-133.

Karnath, H. O., Fetter, M., & Dichgans, J. (1996) Ocular exploration of space as a function of neck proprioceptive and vestibular input: observations in normal subjects and patients with spatial neglect after parietal lesions. *Experimental Brain Research*, 109(2), 333-342.

Kingdom, F. A. A., & Prins, N. (2010) *Psychophysics: a practical introduction*. Boston: Academic Press.

Kundt, A. (1863) Untersuchungen über Augenmass und optische Täuschungen [Studies on sound judgment and optical illusions]. *Poggendorff, Amalle*, 120, 118-158.

Lewis, E. O. (1912) The illusion of filled and unfilled space. *British Journal of Psychology*, 5, 36-50.

Loftus, A. M., Vijayakumar, N., & Nicholls, M. E. (2009) Prism adaptation overcomes pseudoneglect for the greyscales task. *Cortex*, 45(4), 537-543.

Mark, V. W., Kooistra, C. A., & Heilman, K. M. (1988) Hemispatial neglect affected by non-neglected stimuli. *Neurology*, 38(8), 1207-1211.

Milner, A. D., Brechmann, M., & Pagliarini, L. (1992) To halve and to halve not: an analysis of line bisection judgements in normal subjects. *Neuropsychologia*, 30(6), 515-526.

Milner, A. D., & Goodale, M. A. (2008) Two visual systems re-viewed. *Neuropsychologia*, 46(3), 774-785.

Ni, C. F. (1934) The effect of combining some geometrical optical illusions. *The Journal of Genetic Psychology: Child Behavior, Animal Behavior, and Comparative Psychology,* 10, 472-476.

Oldfield, R. C. (1971) The assessment and analysis of handedness: the Edinburgh inventory. *Neuropsychologia,* 9(1), 97-113.

Oppel, J. J. (1854/1855) *Jahresbericht des physikalischen Vereins zu Frankfurt a. M.* [*Annual report of the Physical Society of Frankfurt*], 37-47.

Oppel, J. J. (1860/1861) *Jahresbericht des physikalischen Vereins zu Frankfurt a. M.* [*Annual report of the Physical Society of Frankfurt*], 26-37.

Pia, L., Folegatti, A., Guagliardo, M., Genero, R., & Gindri, P. (2009) Are drawing perseverations part of the neglect syndrome? *Cortex*, 45(3), 293-299.

Pia, L., Ricci, R., Gindri, P., & Vallar, G. (2012) Drawing perseveration in neglect: effects of target density. *Journal of Neuropsychology.* DOI:10.1111/j.1748-6653.2012.02034.x. [Epub ahead of print]

Ricci, R., Calhoun, J., & Chatterjee, A. (2000) Orientation bias in unilateral neglect: representational contributions. *Cortex,* 36(5), 671-677.

Ricci, R., Pia, L., & Gindri, P. (2004) Effects of illusory spatial anisometry in unilateral neglect. *Experimental Brain Research,* 154(2), 226-237.

Ricci, R., Vaishnavi, S., & Chatterjee, A. (1999) A deficit of intermediate vision: experimental observations and theoretical implications. *Neurocase,* 5(1), 1-12.

Russo, G., & Dellantonio, A. (1989) Influence of phenomenal time on perceived space. *Perceptual and Motor Skills,* 68, 971-984.

Savazzi, S., Emanuele, B., Scalf, P., & Beck, D. (2012) Reaction times and perceptual adjustments are sensitive to the illusory distortion of space. *Experimental Brain Research,* 218, 119-128.

Savazzi, S., Posteraro, L., Veronesi, G., & Mancini, F. (2007) Rightward and leftward bisection biases in spatial neglect: two sides of the same coin? *Brain,* 130(8), 2070-2084.

Smeets, J. B., Brenner, E., de Grave, D. D., & Cuijpers, R. H. (2002) Illusions in action: consequences of inconsistent processing of spatial attributes. *Experimental Brain Research,* 147(2), 135-144.

Suzuki, K., & Arashida, R. (1992) Geometrical haptic illusions revisited: haptic illusions compared with visual illusions. *Perception and Psychophysics,* 52(3), 329-335.

Vecera, S. P., & Behrmann, M. (1997) Spatial attention does not require preattentive grouping. *Neuropsychology,* 11(1), 30-43.

Wackermann, J., & Kastner, K. (2010) Determinants of filled/empty optical illusion: search for the locus of maximal effect. *Acta Neurobiologiae Experimentalis,* 70(4), 423-434.