



More far is more right: Manual and ocular line bisections, but not the Judd illusion, depend on radial space

Luca Rinaldi^{a,b,*}, Giovanni Bertolini^c, Christopher J. Bockisch^{c,d,e}, Angelo Maravita^{a,b},
Luisa Girelli^{a,b}, Peter Brugger^{c,f}

^a Department of Psychology, University of Milano-Bicocca, Milano, Italy

^b NeuroMI, Milan Center for Neuroscience, Milano, Italy

^c Department of Neurology, University Hospital Zurich, Zurich, Switzerland

^d Department of Ophthalmology, University Hospital Zurich, Zurich, Switzerland

^e Department of Otorhinolaryngology, University Hospital Zurich, Zurich, Switzerland

^f Zurich Center for Integrative Human Physiology, University of Zurich, Switzerland

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ABSTRACT

Line bisection studies generally find a left-to-right shift in bisection bias with increasing distance between the observer and the target line, which may be explained by hemispheric differences in the processing of proximo-distal information. In the present study, the segregation between near and far space was further characterized across the motor system and contextual cues. To this aim, 20 right-handed participants were required to perform a manual bisection task of simple lines presented at three different distances (60, 90, 120 cm). Importantly, the horizontal spatial location of the line was manipulated along with the viewing distance to investigate more deeply the hemispheric engagement in the transition from near to far space. As the motoric component of the manual task producing activations of left premotor and motor areas may be partially responsible for the observed transition, participants were also involved in an ocular bisection task. Further, participants were required to bisect Judd variants of the target lines, which are known to elicit a Müller-Lyer-type illusion. Since the Judd illusion depends on areas in the ventral visual stream, we predicted that line bisections of Judd-type lines would be unaffected by viewing distance. Results showed that manual bisection of simple lines was modulated separately by viewing distance and the hemispace of presentation, with this pattern being similar for ocular bisection. Critically, bisections in the Judd illusion task were not modulated by viewing distance, whether performed by hand or by eye. Overall, these findings support the hypothesis that the right hemisphere plays a dominant role in the processing of space close to the body. They also present novel evidence for a *general* reduction of this dominance at farther distances, whether hand motor actions are involved or not. Finally, our study documents a dissociation between the processing of pure visuospatial information and that of a visual illusion as a function of viewing distance, supporting more generally the dorsal/near space and the ventral/far space segregation.

1. Introduction

The perception of the space surrounding our body is a key aspect for interacting with the external world. In everyday life, we need to perceive the location of our body with respect to an external reference point in order to program actions within a reasonable distance. It has been repeatedly shown that the representation of near, peripersonal, space differs from the representation of farther, extrapersonal, space (for a review see Halligan, Fink, Marshall, & Vallar, 2003). Beyond this representational dissociation, there is now growing evidence showing that different areas of the human brain are responsible for the coding of

near and far space (e.g., Longo, Trippier, Vagnoni, & Lourenco, 2015; Mahayana, Tcheang, Chen, Juan, & Muggleton, 2014; Valdés-Conroy, Sebastián, Hinojosa, Román, & Santaniello, 2014). Evidence for a distinction between near and far space was reported in monkeys with unilateral ablation of area 6 (postarcuate premotor cortex), resulting in a profound neglect of the contralesional near space, whereas ablation of area 8 (frontal eye field) resulted in a neglect of the contralesional far space (Rizzolatti, Matelli, & Pavesi, 1983). A corresponding dissociation was later demonstrated in humans with left visuospatial neglect, a neuropsychological syndrome whereby patients fail to explore the contralateral side of space (Heilman, Watson, & Valenstein, 1993). In

* Corresponding author at: Dipartimento di Psicologia, Università degli Studi di Milano-Bicocca, Piazza dell'Ateneo Nuovo 1, Edificio U6, 20126 Milano, Italy.
E-mail address: luca.rinaldi@unimib.it (L. Rinaldi).

the seminal work by Halligan and Marshall (Halligan & Marshall, 1991), a right-brain damaged patient showed a severe neglect of left near space, but critically, no neglect symptoms were found in far space. Accordingly, it was suggested that parieto-occipital areas of the dorsal visual processing system would be mainly responsible for attending to stimuli in near space, whereas temporo-occipital areas of the ventral visual system would be mainly involved in attention to far space (Halligan & Marshall, 1991; Halligan et al., 2003). Nonetheless, the opposite dissociation, i.e., neglect in far but not near space, has been also reported (Berti & Frassinetti, 2000; Cowey, Small, & Ellis, 1994; Keller, Schindler, Kerkhoff, Von Rosen, & Golz, 2005; Vuilleumier, Valenza, Mayer, Reverdin, & Landis, 1998). Despite some neglect patients not being influenced by viewing distance (e.g., Keller et al., 2005), overall these findings corroborate a fundamental distinction between the neural mechanisms underlying the control of spatial attention in near and far space.

Evidence in support of a near/far space dissociation comes also from studies with healthy individuals. Indeed, the slight leftward bias characterizing the bisection of visual lines, referred to as pseudoneglect (Bowers & Heilman, 1980; Rinaldi, Di Luca, Henik, & Girelli, 2014; for a review see Jewell & McCourt, 2000), is known to be modulated by visual distance (McCourt & Garlinghouse, 2000). While participants show pseudoneglect in near space, a gradual shift of the subjective midpoint to the right of the objective center has been consistently reported with increasing viewing distance (Bjoertomt, Cowey, & Walsh, 2002; Heber, Siebertz, Wolter, Kühlen, & Fimm, 2010; Longo & Lourenco, 2006; Nicholls, Beckman, & Churches, 2016; Varnava, McCarthy, & Beaumont, 2002). Interestingly, the extent of this rightward transition has been taken as an index of plasticity of the near space (Gamberini, Seraglia, & Priftis, 2008; Hunley, Marker, & Lourenco, 2017; Longo & Lourenco, 2006; Lourenco & Longo, 2009). Yet it is worth noting that, along with studies replicating these findings, there are studies that failed to report effects of viewing distance on visuospatial asymmetries (e.g., Cowey, Small, & Ellis, 1999; Thomas & Elias, 2010).

The mechanisms underlying the rightward shift of the bisection bias with increasing viewing distance remain poorly understood. Recently, Longo et al. (2015; see also Longo & Lourenco, 2006) attempted an explanation, by harking back to the activation-orientation hypothesis (Kinsbourne, 1970, 1993; Reuter-Lorenz, Kinsbourne, & Moscovitch, 1990). This account proposes that, during a spatial task, attention is biased towards the contralateral hemispace with respect to the most activated hemisphere (Kinsbourne, 1987). When individuals perform a bisection task, a preferential activation of the right hemisphere would lead to a leftward attentional bias (Bultitude & Davies, 2006; Loftus & Nicholls, 2012). Accordingly, various neuroimaging studies showed an activation of the right posterior parietal cortex (PPC) in different visuospatial tasks (Fink, Marshall, Weiss, Toni, & Zilles, 2002; Foxe, McCourt, & Javitt, 2003). However, as individuals process information at farther distances, the left hemisphere would play a more active role, thus minimizing pseudoneglect and biasing attention to the right hemispace (Longo & Lourenco, 2006; Longo et al., 2015). In support of this hypothesis, right-lateralized negativity over the occipito-parietal scalp induced by a visuospatial attention task has been reported to depend on viewing distance (Longo et al., 2015). A recent study using repetitive transcranial magnetic stimulation (rTMS) on healthy participants reached similar conclusions (Mahayana et al., 2014). These works strengthen previous evidence in support of a segregation between the dorsal stream areas, which would code mainly information in near space, and the ventral stream areas, which would code information in far space (Bjoertomt et al., 2002; Chen, Weidner, Weiss, Marshall, & Fink, 2012; Lane, Ball, Smith, Schenk, & Ellison, 2013; Weiss, Marshall, Zilles, & Fink, 2003; Weiss et al., 2000).

Whereas the right parietal cortex has been considered responsible for the slight leftward advantage in visuospatial attention, the neural mechanisms underlying the processing of visual illusions seems to be located in different areas (reviewed by Vallar & Daini, 2006). Evidence

supporting this distinction comes from studies using the Müller-Lyer illusion and its variants (Müller-Lyer, 1889). In the Müller-Lyer illusion, arrowheads at a line's endings induce a misperception of line length. In particular, inward-oriented arrowheads reduce the perceived length of the line, and outward-oriented arrowheads prolong it. Both neuropsychological (Daini, Angelelli, Antonucci, Cappa, & Vallar, 2002; Mattingley, Bradshaw, & Bradshaw, 1995; Olk, Harvey, Dow, & Murphy, 2001; see also Mancini, Bricolo, Mattioli, & Vallar, 2011) and neuroimaging (Weidner & Fink, 2007) data indicate that bilateral occipito-temporal cortex is involved in the processing that leads to the visual illusion. For instance, visual illusory effects can occur regardless of the presence of spatial attention deficits (Vallar & Daini, 2006). That is, visual illusory effects are preserved in patients with parietal cortical lesions (Vallar, Daini, & Antonucci, 2000), but not in patients where the damage extends to the occipital lobe (Daini et al., 2002). These results were further strengthened by a recent rTMS study on healthy participants, in which rTMS over both the left and the right occipito-temporal cortex interfered with the processing of the visual illusion (as indexed by a bisection paradigm), while superior parietal stimulation had no effect on performance (Mancini, Bolognini, Bricolo, & Vallar, 2011; but see Weidner, Boers, Mathiak, Dammers, & Fink, 2010). This pattern of results indicates that the mechanisms underlying the Müller-Lyer illusion are tightly linked to mechanisms responsible for object perception and, thus, to the ventral visual stream. Dorsal stream areas, would play a secondary role in the processing producing the illusion (Weidner et al., 2010). Hence, the processing of the visual features that produces the illusion is considered to be different from the mechanisms subserving the analysis of veridical visuospatial information. We note that, to the best of our knowledge, no study so far has compared the Müller-Lyer illusion in near and far space. Also, whether the hands and the eyes are similarly affected by the illusion in the bisection task has never been systematically explored. This is probably due to the considerable technical efforts linked to any sophisticated eye-movement measurement as will be outlined in the following paragraph.

Despite their potential explanatory power, eye-tracking methods have rarely been used to investigate visuospatial asymmetries. Eye-tracking allows inferences about the cognitive processes underlying task performance and, importantly, can inform about the focus of participants' attention (Duchowski, 2007). Following this rationale, a few studies have tried to investigate ocular behavior during line bisection-like tasks. However, the use of different experimental procedures led to contrasting results. Some studies described a pseudoneglect for ocular bisection, that is, eye fixations were shifted leftward of the objective midpoint in accordance with the manually produced displacement (Cavérian, Valadao, Hurwitz, Saoud, & Danckert, 2012; Hurwitz, Valadao, & Danckert, 2011). Other authors found that, during line bisection, the eyes deviate slightly to the *right* of the objective center (Elias, Robinson, & Saucier, 2005; Leonards, Stone, & Mohr, 2013). Most of these prior studies did not use line bisection proper, but rather adopted the greyscales task, which requires a forced-choice comparison of the luminance of two overall equiluminant rectangles (Elias et al., 2005; Thomas, Loetscher, & Nicholls, 2014), or the landmark task, which requires a forced-choice comparison of the length of two segments of off-centre prebisected lines (e.g., Thomas, Loetscher, & Nicholls, 2012; see also Nicholls, Hobson, Petty, Churches, & Thomas, 2017). Yet, landmark and bisection tasks measure different aspects of visuospatial attention (Harvey, Milner, & Roberts, 1995), and performances in the landmark and in the greyscale tasks are not only uncorrelated (Heber et al., 2010) but may be characterized by different ocular behaviors altogether (Cavérian et al., 2012). Pseudoneglect, indeed, appears to be a multi-component phenomenon that is strongly dependent on task demands (Learmonth, Gallagher, Gibson, Thut, & Harvey, 2015). Notably, to the best of our knowledge, no study has compared ocular bisection in near and far space. This is likely because most of previous research used screen-based eye-trackers, whose precision and accuracy are dependent on distance. Indeed, these systems

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