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The modulation of haptic line bisection by a visual illusion and optokinetic stimulation

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Abstract. Research has shown that a variety of different sensory manipulations, including visual illusions, transcutaneous nerve stimulation, vestibular caloric stimulation, optokinetic stimulation, and prism adaptation, can all influence people's performance on spatial tasks such as line bisection. It has been suggested that these manipulations may act upon the 'higher-order' levels of representation used to code spatial information. We investigated whether we could influence haptic line bisection in normal participants crossmodally by varying the visual background that participants viewed. In experiment 1, participants haptically bisected wooden rods while looking at a variant of the Oppel – Kundt visual illusion. Haptic-bisection judgments were influenced by the orientation of the visual illusion (in line with previous unimodal visual findings). In experiment 2, haptic-bisection judgments were also influenced by the presence of a leftward or rightward moving visual background. In experiments 3 and 4, the position of the to-be-bisected stimuli was varied with respect to the participant's body midline. The results confirmed an effect of optokinetic stimulation, but not of the Oppel – Kundt illusion, on participants' tactile-bisection errors, suggesting that the two manipulations might differentially affect haptic processing. Taken together, these results suggest that the 'higher-order' levels of spatial representation upon which perceptual judgments and/or motor responses are made may have multisensory or amodal characteristics.

1 Introduction

Neuropsychological evidence from brain-damaged patients has often been used to study the neurological and functional basis of cognitive systems in normal humans (see Vallar 1991). For example, several contemporary accounts of the way in which neurologically normal individuals process spatial information have emerged from the study of patients suffering from unilateral neglect (see Halligan et al 2003; Vallar 2001; for reviews). Brain-damaged patients suffering from visuospatial neglect typically fail to report (and respond to) stimuli presented on the contralesional side of extrapersonal and/or body space (Bisiach and Vallar 2000; Vallar 1998, 2001).

Many researchers have argued that the behavioural correlates of visuospatial neglect may reflect the consequences of a distortion of (or damage to) the neural representations (and perception) of space (Bisiach and Luzzatti 1978; Bisiach et al 1994; Halligan and Marshall 1991; Milner et al 1993; Rizzolatti and Berti 1990; Rizzolatti et al 2000 — see also Pouget and Driver 2000; Pouget and Sejnowski 2001). Bisiach and colleagues (Bisiach et al 1994, 1996, 2002) have argued that such a distortion may actually reflect an anisometry in the neural representation of spatial information. According to this account, the neural medium underlying the representation of space is progressively relaxed as one moves from the ipsilesional to the contralesional side of such a representation (see also Bisiach et al 1998) as a consequence of brain damage. One effect of such a distorted representation is that distances in the contralesional parts of space are represented as being shorter (since they are mapped onto a disproportionately extended medium) than distances in the ipsilesional parts of space.

In support of this theory, it has been shown that patients with left neglect, asked to mark one endpoint of a virtual line, given its centre and the other endpoint, provide a larger estimate when a leftward extension is required than when a rightward extension is required (see Bisiach et al 1994). Moreover, right-brain-damaged patients underestimate the lateral extension of geometrical figures when they are presented in the contralesional side of space, as compared to when they are presented in the ipsilesional side of space (Gallace et al, submitted; Irving Bell et al 1999; Karnath and Ferber 1999; Kerkhoff 2000; Milner and Harvey 1995; cf Geminiani et al 2004). Interestingly, this bias in length perception has been reported with both visual and tactile stimuli, thus suggesting a possible common mechanism underlying the phenomena in different sensory modalities [Pritchard et al (2001)—though see Bisiach et al (2004) for a recent report of a double dissociation between visual and tactile size distortions in a large group of neglect patients].

On the basis of the asymmetries reported in a variety of spatial tasks (see Jewel and McCourt 2000), it seems possible that a similar distortion, although reduced in magnitude and opposite in direction to that affecting neglect patients, might also be present in neurologically normal individuals. Ricci et al (2004) recently used a modified version of the Oppel–Kundt illusion (note that in its classical form this illusion consists of the perception of a filled space as larger than an empty space of equivalent size; see Coren and Girgus 1978; Kundt 1863/2000; Lewis 1912–1913), composed of a number of vertical lines whose spacing decreased progressively from one side to the other, thus inducing a logarithmic anisometry in the perception of visual space. They reported that the line-bisection performance of neurologically normal participants (as well as of neglect patients) was affected by their viewing of this background visual illusion. Ricci et al argued that the visual illusion may have modified the participants' representation of space in a qualitatively similar way to that thought to underlie the syndrome of neglect [compression of the contralesional side of space—see Bisiach et al (1998)].

Research has shown that performance on the line-bisection task can also be influenced by a number of other experimental manipulations, such as viewing the Müller-Lyer visual illusion (Vallar et al 2002), transcutaneous nerve stimulation (Vallar et al 1995), neck muscle vibration (Karnath et al 1993), vestibular caloric stimulation (Karnath et al 2003; Rubens 1985), optokinetic stimulation (Bisiach et al 1996; Vallar et al 1997), and prism adaptation (Girardi et al 2004). It has been suggested that the common factor underlying such experimental manipulations may be that they all affect the 'higher-order' levels of processing required to support an egocentric representation of external space (Nico 1999; Vallar et al 1993).

In the four experiments reported here, we investigated whether the modulation of visual information would also affect the performance of normal participants crossmodally in a haptic line-bisection task. In experiment 1, we modulated the perception of visual space using the Oppel–Kundt illusion (cf Ricci et al 2004), while in experiment 2 we used the optokinetic stimulation induced by the presentation of a moving visual background (cf Na et al 2002; Vallar et al 1997). In experiments 3 and 4, in addition to manipulating the visual display (Oppel–Kundt illusion and optokinetic stimulation), we also modulated the spatial position of the stimuli to-be-scanned in order to investigate the role played by the spatial frame of reference in haptic line bisection.

If such experimental manipulations of visual information, which involve functionally and neuroanatomically distinct neural systems (Daini et al 2002; Dieterich et al 1998), act upon multisensory or amodal higher-order spatial representations (Ladavas et al 1998), then a crossmodal effect of the visual displays on haptic line-bisection performance would be expected. Specifically, according to the visual literature, a left-compressed background or leftward optokinetic movement should result in a leftward bisection error. Similarly, a right-compressed background and rightward optokinetic movement should result in a rightward bisection error (Na et al 2002; Ricci et al 2004). Indeed, for the Oppel–Kundt illusion, the more densely structured portion of the background was expected to induce a perceptual expansion (ie stimulus overestimation) and vice versa for the less densely structured portion of the background. The demonstration of such crossmodal effects would support the existence of a common representation accessed by information from different sensory modalities that may be used to analyse spatial information (Spence and Driver 2004).

2 Experiment 1

2.1 *Methods*

2.1.1 *Participants.* Twenty right-handed participants (twelve female) took part in the experiment as paid volunteers (mean age 23.1 years, range 19 – 30 years). Visual acuity was normal or corrected-to-normal, and all of the participants reported a normal sense of touch. The experiment took approximately 20 min to complete and all the participants received a £5 gift voucher in return for their participation. The experiments in this study were non-invasive and had ethical approval from the Department of Experimental Psychology, University of Oxford. The experiments were also performed in accordance with the ethical standards laid down in the 1964 Declaration of Helsinki.

2.1.2 *Apparatus and materials.* The experiment was conducted in a dark room. The participants were seated comfortably in front of a table, 40 cm from the centre of a 30 cm × 23 cm LCD screen. The screen rested on an opaque black platform mounted 10 cm above the tabletop. The angle between the screen and the table was 30° (see figure 1a). An optical mouse (with the mouse buttons positioned on the participant's left) was placed on the table under the platform, 22 cm from the edge of the table nearest to the participant. In the starting position, the mouse was shifted 3 cm to the right or left side of the screen. Plastic bars were used to constrain the leftward and rightward movement of the mouse across the table, and to prevent any longitudinal movements of the mouse. A 20 cm wooden bar (diameter = 0.7 cm) was placed 1.5 cm in front of the mouse. The centre of the bar was aligned with the azimuthal centre of the screen. The participants were instructed to rest their right hand on the mouse with their thumb on one of the mouse buttons (see figure 1b). Two vertical plastic bars mounted on the top of the mouse constrained the participant's index finger, minimising any change of position of the finger on the mouse during the experiment. The two bars allowed the accurate transmission of any horizontal movement of the finger to the mouse.

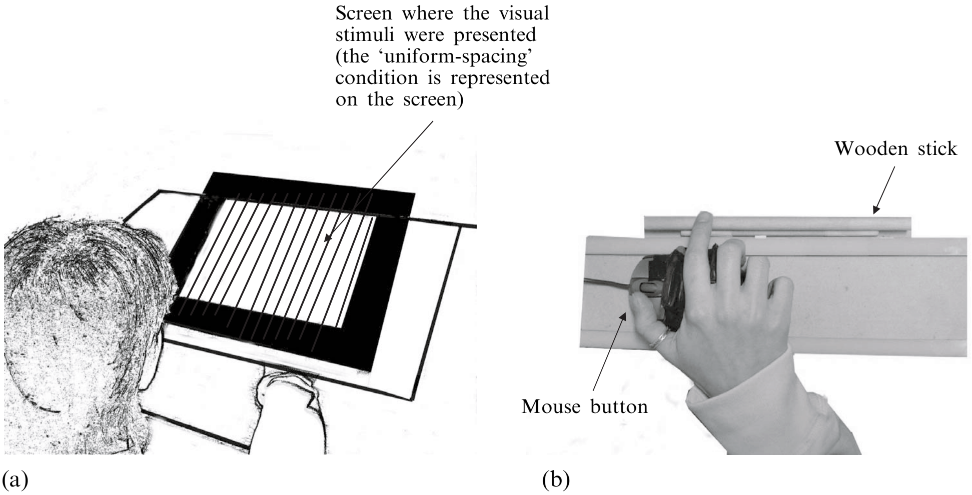

Figure 1. Schematic illustration of the experimental setup used in experiments 1 and 2, showing (a) the position of the participant in front of the screen and (b) the position of the participant's hand on the mouse placed underneath the screen.

The spatial resolution of the mouse was approximately 1 mm. The black platform prevented participants from seeing the mouse and their hands during the experiment.

The participants were instructed to move their hands to the left starting position and then to click the mouse button. A brief tone (400 Hz, duration = 100 ms), delivered via a loudspeaker cone, placed 50 cm from the edge of the table nearest to the participant and horizontally aligned with the middle of the screen, confirmed the registration of the mouse click by the computer. The participants were asked to scan across the wooden stick with the tip of their index finger, to stop at its midpoint, and to click the mouse button again. The participants were also instructed to scan the entire length of the stick at least once (but as many times as they needed) before stopping at its midpoint. A second tone (800 Hz, duration = 100 ms) informed participants that their response had been recorded. No time limit was given for participants to complete the haptic scanning of the stick. Participants were requested to look at the screen throughout each trial (although no fixation point was presented on the screen). They were instructed that the visual information presented on the screen was irrelevant to their task.

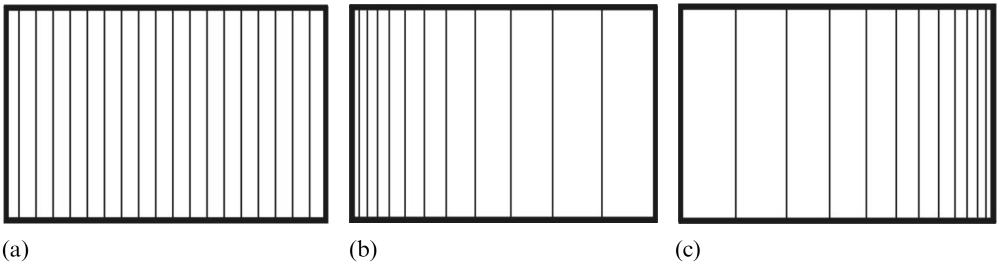

Figure 2. Stimuli presented on the screen in experiment 1 in the three experimental conditions: (a) uniform spacing; (b) left-compressed background; (c) right-compressed background.

Three conditions were presented in experiment 1 (see figure 2). In the uniform-spacing condition (a), a background composed of vertical lines (23 cm long and 0.2 cm thick) spaced 1.5 cm from each other filled the screen. In the left-compressed (b) and right-compressed (c) conditions, the background was composed of vertical lines (23 cm long and 0.2 cm thick) with the space between adjacent lines decreasing progressively from one side of the screen to the other, following the exponential function $y = e^x$; $x \in [-0.50 : 0.207 : 3]$.(1) The distances between the background lines decreased from right to left in the left-compressed condition and from left to right in the right-compressed condition (cf Ricci et al 2004). The position of the lines in the background display was randomly jittered by ±0.5 cm with respect to the centre of the screen on each trial. The order of presentation of the trials was randomised for each participant. 20 trials were presented for each condition, giving rise to a total of 60 trials completed by each participant.

2.2 *Results*

Mean bisection errors, calculated as the shift from the geometrical midpoint of the line, were collected for each condition and for each participant (see figure 3). Shifts to the left of the midpoint are represented by negative values, while shifts to the right are represented by positive values. The bisection error data were submitted to a repeated-measures analysis of variance (ANOVA) with the factor of background (uniform-spacing, left-compressed, and right-compressed) ($F_{2,38} = 4.03$, $p = 0.02$). A Duncan a posteriori test revealed significant differences between the left-compressed and right-compressed conditions ($p < 0.05$), between the right-compressed and uniform-spacing conditions ($p < 0.05$),

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(1) The term 'x' in the function takes all values between -0.5 and 3 at steps of 0.205 [ie -0.5, -0.295, -0.09, etc; cf Ricci et al (2004)].

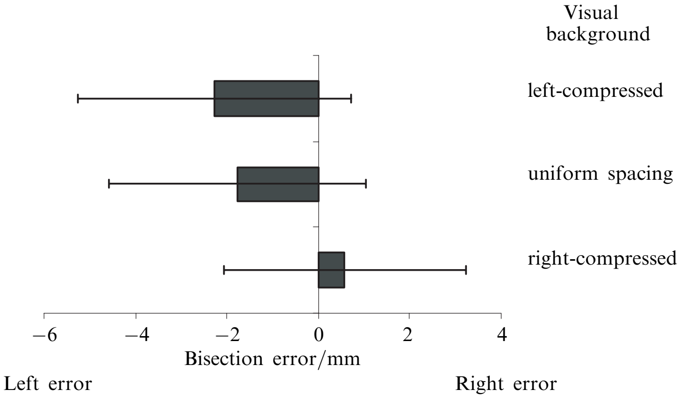

Figure 3. Mean bisection errors as a function of the background presented on the screen during the haptic line-bisection task. Left-compressed condition: background composed of vertical lines spaced with distances that decreased progressively from right to left; uniform-spacing condition: background composed by vertical lines placed 1.5 cm apart; right-compressed condition: background composed of vertical lines spaced with distances that decreased progressively from left to right. Error bars represent the standard errors of the means.

but the difference between the left-compressed and uniform-spacing conditions failed to reach statistical significance ($p > 0.05$, ns). Bisection errors were shifted to the left in the left-compressed condition and toward the right in the right-compressed background condition as predicted. These results appear to confirm (in a crossmodal setting) Ricci et al's (2004) findings, obtained under condition of unimodal visual stimulus presentation. Indeed, as in the present study, they found that participants overestimated line length on the denser side with respect to line length on the expanded side (and vice versa).

2.3 *Discussion*

The results of experiment 1 show that the presentation of irrelevant visual information, consisting of a modified version of the Oppel – Kundt illusion (Bertulis and Bulatov 2001; Kundt 1863/2000; Lewis 1912 – 1913; Ricci et al 2004), can modulate participants' haptic line-bisection judgments in the direction that would be expected on the basis of previous unimodal visual line-bisection data (Ricci et al 2004). In particular, under conditions where the visual information was more densely structured on the left of the display, a leftward shift in haptic line bisection was observed. This suggests that the distorted visual information has access to (and influences) the system used to represent not only visual but also the haptic length of a stimulus.

It should be noted that the magnitude of the crossmodal effect reported in experiment 1 is relatively small (ie the difference between the left-compressed and right-compressed conditions was only 2.8 mm). However, the line-bisection errors reported in previous unimodal visual studies of this illusion have been of a similar magnitude (a left – right orientation difference of 3.2 mm for a 150 mm line in Ricci et al's 2004 study).

3 Experiment 2

It has been suggested that body-centred spatial representations are subserved by redundant and independent subsystems. Optokinetic stimulation, prism adaptation, muscle stimulation, and vestibular caloric stimulation may all influence the computation of spatial information by accessing such representations (Girardi et al 2004; Pizzamiglio et al 1990). In experiment 2, the participants were asked to bisect a line haptically while staring at a visual background that either moved leftward or rightward, or else was stationary. If optokinetic information does indeed impinge on the system used to represent spatial extent independently of the sensory modality of input or output, one might expect there to be an effect of visual stimulation on haptic line bisection. If, however, separate and independent systems are used, or if optokinetic information does not influence such multisensory/amodal systems, then no such crossmodal effect would be expected.

Given the somewhat inconsistent reports regarding the direction of the effects produced by the movement of the visual background on visual line bisection in previous studies (different speeds of movement have been reported to affect the direction of visual bisection in opposite ways—eg Na et al 2002), we thought it prudent to include a unimodal visual version of the line-bisection task in experiment 2, as well as the crossmodal version that was of most interest.

3.1 *Methods*

3.1.1 *Participants.* Fourteen right-handed participants (eight female) took part in the experiment as paid volunteers (mean age 25.3 years, range 21 – 33 years). Visual acuity was normal or corrected-to-normal, and all of the participants reported a normal sense of touch. The experiment lasted approximately 30 min.

3.1.2 *Apparatus and materials.* The experimental setup and procedure were identical to those used in experiment 1 with the following exceptions: A somewhat larger (34 cm wide, 27 cm high) LCD screen was used. The experiment was composed of two blocks of trials, one unimodal and the other crossmodal. In the unimodal block, a horizontal blue line (20 cm long, 2 mm wide) was presented 19 cm from the top of the screen. The centre of the line was aligned with the horizontal midline of the screen. A red bar (2 mm long, 1 mm wide) was superimposed on the left side of the blue line. The position of the red bar on the blue line was controlled by horizontal movement of the mouse across the table. In each trial, the participant had to move the red bar across the blue line and stop at its midpoint. In the crossmodal trials, the participants were instructed to scan a 20 cm long wooden stick placed below the screen (aligned with the centre of the screen) with their index finger and to stop at its midpoint (cf experiment 1). Three experimental conditions were presented: leftward visual movement (a), rightward visual movement (b), and a no-movement control condition (c). In the visual movement conditions, a background composed of vertical bars (27 cm long, 2 mm thick) placed 3 cm from each other, filled the screen. The background either moved leftward (a) or rightward (b) at a speed of 10 cm s^{-1}. In the no-movement condition, a static white background was presented. The background (and the blue line in the unimodal block) was presented on the first click of the mouse and was substituted by a white window after the second mouse click. In order to control for the presence of any possible aftereffects (cf Vallar et al 1997), two different orders of condition presentation were used, counterbalanced across participants: ACBCACBC and BCACBCAC. Ten stimuli were presented in each part of the sequence, giving rise to a total of 80 trials for each participant.

3.2 *Results and discussion*

Mean bisection errors, calculated as the shift from the geometrical midpoint of the stick (haptic) or line (visual), were collected for each block of trials, for each condition and for each participant. Shifts to the left of the geometrical midpoint of the stick/line are represented by negative values, while shifts to the right are represented by positive values. In order to check for the presence of any aftereffect on performance in the no-movement control condition following the background movement conditions, two paired-samples t-tests for the visual and tactile bisection task data were performed on the bisection errors on the no-movement trials following either rightward or leftward movement trials, respectively. These tests revealed no significant difference between the two conditions ($t_{13} = -0.01$, $p = 0.98$, and $t_{13} = -0.29$, $p = 0.77$; for the no-movement conditions following leftward and rightward movement, respectively). Given that bisection errors in the no-movement condition for trials following leftward and rightward movement were not significantly different, a mean of their values was used in the following analysis.

The bisection errors were submitted to a repeated-measures ANOVA with the factors of background (leftward movement, rightward movement, and no-movement), and modality (unimodal: visual bisection with visual background and crossmodal: haptic bisection with a visual background). The analysis revealed a significant main effect of background ($F_{2,26} = 10.10$, $p < 0.001$), but not of modality ($F_{1,13} < 1$, ns), nor any interaction between modality and background ($F_{2,23} = 1.21$, ns). A Duncan a posteriori test revealed significant differences between the leftward and rightward movement conditions ($p < 0.001$) and between the no-movement and rightward movement conditions ($p < 0.01$), but not between the no-movement and leftward movement conditions (see figure 4). The results show a shift in the bisection errors in the direction of the movement presented on the screen independent of the modality (ie haptic or visual) of the bisection task. While the difference between the leftward and rightward movement conditions in the participants' bisection errors appears to be larger for the crossmodal than for the unimodal task (see figure 4), a paired-samples t-test on these measures failed to reveal any significant difference ($t_{13} = -1.21$, ns).

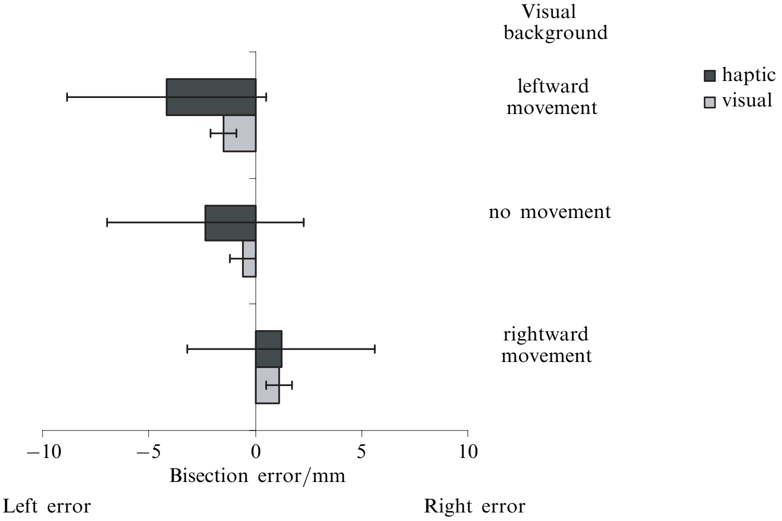

Figure 4. Mean bisection errors as a function of the background presented on the screen during the visual and haptic line bisection in each of the experimental conditions. Background moving leftward, no movement, and background moving rightward. Shifts to the left of the geometrical midpoint of the line/stick are represented as negative values, while shifts to the right are represented as positive values. Error bars represent the standard errors of the means.

The results of experiment 2 show that the presentation of a moving visual background, which is known to elicit horizontal optokinetic movement (Howard 1982; Na et al 2002), influenced participants' judgments of the perceived midpoint of both visually and haptically presented horizontal lines in our neurologically normal participants. Such findings are consistent with the results of experiment 1, and support the view that a common multisensory or amodal system is used to represent spatial information regarding spatial attributes such as length and distance.

It is worth noting that the magnitude of the effect reported in the present experiment, while apparently small (the difference between the leftward and rightward movement conditions was only 1.3% and 2.7% of the line length for the visual and haptic bisection errors, respectively) is in line with previous unimodal studies that have used optokinetic movement (eg leftward – rightward difference of 1.7% of the line length in Na et al 2002).

4 Experiment 3

A large body of research has shown that visual illusions typically do not affect motor behaviour (Aglioti et al 1995; Daprati and Gentilucci 1997; Haffenden and Goodale 1998). Such results have been taken to suggest that the dorsal visual system (thought to process visual information regarding the relative position of objects in space) is immune from illusory effects (see Aglioti et al 1995). However, the question of whether or not illusions affect movement is still controversial, given that a number of researchers have also found illusory motor responses to visual illusions, such as the Müller-Lyer illusion, under certain conditions (Bruno and Bernardis 2003; Elliott and Lee 1995; Gentilucci et al 1996; Meegan et al 2003). For example, it has been reported that the saccades and pointing movements of participants looking at the Brentano visual illusion (a version of the Müller-Lyer illusion in which the wings-in and wings-out parts of the classic illusion are placed end-to-end sharing a central fin; see Gallace and Spence 2005), are affected by the illusion (Grave et al 2006). Therefore, it might be argued that the results observed in experiment 1 were related to an effect of the distorted visual information on participant's pointing movements rather than on a multisensory/amodal representation of space. Indeed, given that the to-be-scanned stick was always aligned with the midline of the screen, the participants could have accomplished the task solely by pointing to the midline of the screen or of their body rather than to the midline of the stick. In order to investigate this possibility, the stick was moved away from the midline of the screen (5 cm to the left or to the right) in experiment 3. If no effect of the illusion were to be found under such conditions this would suggest that the results reported in experiment 1 were primarily related to a motor bias elicited by the Oppel – Kundt illusion in a midline-pointing task, rather than necessarily to a distortion of an amodal/multisensory representation of space

Interestingly, it has long been known in the visual literature that the bisection errors of patients suffering from the 'space-based' form of unilateral neglect are affected by the position of the line, with reference to the midsagittal plane of the body trunk (Heilman and Valenstein 1979; Marshall and Halligan 1990—see also Driver 1998; Tipper and Behrmann 1996; Vallar 1997; for the distinction between object-based and space-based forms of neglect). Specifically, in line-bisection tasks, neglect patients have been shown to commit larger leftward errors (measured in terms of deviations from the objective midpoint of the to-be-bisected line) when the stimuli are presented to the left of a patient's body midline, as compared to conditions in which the stimuli are presented to the right of a patient's body midline (Heilman and Valenstein 1979; Marshall and Halligan 1990; Vallar et al 2000). Following on from these observations, it might be thought that if a modulation of the bisection error of the participants in our tactile bisection task is influenced by the spatial position of the stimuli (with reference to the body midline), this would suggest that a space-based, rather than an object-based, frame of reference and/or representation is more involved in the task. Indeed, no modulation of participants' performance as a function of the position of the stimuli presented would be expected if a purely object-based representation were to be used to perform the bisection task. It is important to note here that the tactile errors when bisecting wooden sticks made by neurologically normal participants are based on a space-based rather than object-based frame of reference (Gallace and Spence, submitted).

Moving the stimuli away from the body midline may therefore also provide information regarding the frame of reference affected by the manipulation of the visual information upon the tactile task (see Gallace and Spence, submitted).

4.1 *Methods*

4.1.1 *Participants.* Twenty right-handed participants (ten female) took part in experiment 3 as paid volunteers (mean age 26.3 years, range 20 – 33 years). The experiment lasted approximately 20 min.

4.1.2 *Apparatus and materials.* The experimental setup and procedure were identical to those used in experiment 1 with the following exceptions: two blocks of trials were used. In the left-alignment block of trials, the position of the to-be-scanned stick was moved 5 cm to the left of the participant's body midline. In the right-alignment block of trials, the position of the to-be-scanned stick was moved 5 cm to the right of the participant's body midline. The order of presentation of the two blocks of trials was randomised between participants.

4.2 *Results and discussion*

The mean bisection errors were collected for each block of trials, for each condition, and for each participant exactly as in experiment 1 (see figure 5). The bisection errors were then submitted to a repeated-measures ANOVA with the factors of background (uniform spacing, left-compressed, and right-compressed), and spatial position (left and right). The analysis revealed a significant main effect of spatial position ($F_{1,19} = 9.64$, $p = 0.005$), but no main effect of background ($F_{2,36} < 1$, ns), nor any interaction between background and spatial position ($F_{2,36} < 1$, ns). The participants' bisection errors were shifted to the left of the veridical midpoint when the stick was placed on the right of the body midline and to the right of the veridical midpoint when the stick was placed on the left of the participant's body midline.

The results of experiment 3 showed absolutely no effect of the Oppel – Kundt illusion on participants' tactile line-bisection performance when the to-be-scanned stick was moved away from the body midline. The results also showed that the tactile mean

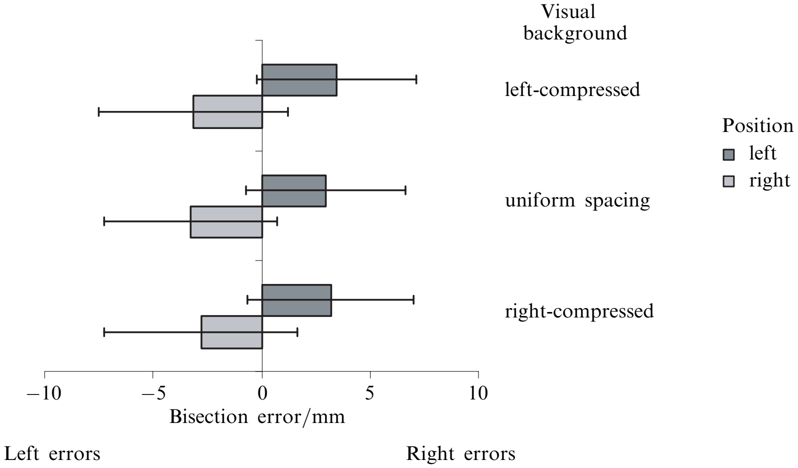

Figure 5. Mean bisection errors as a function of the background presented on the screen and of the position of the stick to-be-scanned (left or right with respect to the participant's body midline) during haptic line bisection. Left-compressed condition: background composed of vertical lines spaced with distances that decreased progressively from right to left; uniform-spacing condition: background composed of vertical lines placed 1.5 cm apart; right-compressed condition: background composed of vertical lines spaced with distances that decreased progressively from left to right. Error bars represent the standard errors of the means.

bisection errors were shifted toward the participants' midline regardless of which visual background was presented. Taken together, these results suggest that the participants in experiment 1 may have pointed to the midline of the screen (or of their body), rather than to the middle of the stick. It therefore appears clear that the results of experiment 1 were primarily related to an effect of the visual illusion over a midline pointing task rather than to a distortion of an amodal/multisensory spatial representation caused by the presentation of the visual information.

The fact that bisection errors were affected by the position of the stimuli across the horizontal dimension of space also suggests that an egocentric (ie centred on the participants' body midline), rather than allocentric (ie centred on the stick to be scanned, regardless of its position in space with respect to the observer's midline) frame of reference was used by the participants in order to perform the task (Gallace and Spence, submitted; Heilman and Valenstein 1979; Marshall and Halligan 1990; Vallar et al 2000). Indeed, it should be noted that no effect of the spatial position would be expected if the length of the stick were to be represented solely on the basis of an object-centred frame of reference.

5 Experiment 4

In order to assess which frame of reference was responsible for the effect reported in experiment 2, we instructed the participants in experiment 4 to scan the stick placed on the right and left of their body midline while watching a visual moving background (just as in experiment 2).

5.1 *Methods*

5.1.1 *Participants.* The same twenty right-handed participants who took part in experiment 3 also took part in experiment 4. The experiment lasted approximately 20 min.

5.1.2 *Apparatus and materials.* The experimental setup and procedures were identical to those used in experiment 2 with the following exceptions: two blocks of trials were used. In the left-alignment block, the position of the stick to-be-scanned was moved 5 cm to the left of the participant's body midline. In the right-alignment block, the position of the to-be-scanned stick was moved 5 cm to the right of the participant's body midline. The order of presentation of the two blocks of trials was randomised across participants. The participant performed only the haptic line-bisection task (ie we did not perform the visual bisection task included in experiment 2).

5.2 *Results and discussion*

The mean bisection errors were collected for each block of trials, for each condition, and for each participant, just as in experiment 3 (see figure 6). In order to check for the presence of any aftereffect on performance in the no-movement control condition following the background movement conditions, two paired-samples t-tests for the left and right position of the display were performed on the bisection errors obtained in the no-movement trials following either rightward or leftward movement trials. These tests revealed no significant difference between the two conditions ($t_{13} = -0.891$, $p = 0.389$, and $t_{13} = 0.365$, $p = 0.72$ for the right and left spatial position of the display, respectively).

The bisection errors were submitted to a repeated-measures ANOVA with the factors of background movement (leftward, rightward, and none), and spatial position (left and right). The analysis revealed a significant main effect of spatial position ($F_{1,19} = 26.38$, $p < 0.0001$), and a significant main effect of background movement ($F_{2,38} = 6.71$, $p = 0.003$). The interaction between background movement and spatial position just failed to reach statistical significance ($F_{2,38} = 2.79$, $p = 0.073$). The participants' bisection errors were shifted leftward when the stick was placed to the right of the body midline

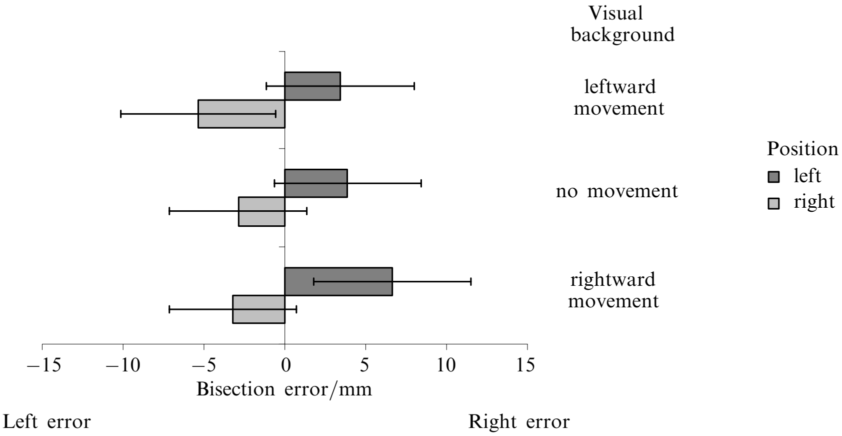

Figure 6. Mean bisection errors as a function of the background presented on the screen and of the position of the stick to-be-scanned (left or right with respect to the participant's body midline) during the visual and haptic line bisection in each of the experimental conditions: background moving leftward, no movement, and background moving rightward. Shifts to the left of the geometrical midpoint of the line/stick are represented as negative values, while shifts to the right are represented as positive values. Error bars represent the standard errors of the means.

and rightward when the stick was placed to the left of the participant's body midline, just as in experiment 3. A Duncan a posteriori test on the factor of background revealed a significant difference between leftward and rightward movement conditions ($p = 0.001$), and between the rightward movement and no-movement conditions ($p = 0.05$), but not between the leftward movement and no-movement background conditions ($p = 0.11$), just as in experiment 2.

The results of experiment 4 therefore showed a significant effect of the visual background on the haptic bisection task, confirming the findings reported earlier in experiment 2. Specifically, the participants' bisection errors were shifted toward the direction of the visual movement presented on the screen. Moreover, the results of experiment 4 also showed a modulation of the effect as a function of the spatial position of the stick. In particular, the mean bisection errors in all background conditions were shifted leftward when the stick was placed on the left side of space, and rightward when the stick was placed on the right side of space (mean shift from the veridical centre of the stick of ±5.1 mm; note that in experiment 3 the mean shift was of ±3.1 mm, suggesting a slightly larger size of the effect of spatial position in experiment 4 as compared to experiment 3). These data confirm previous findings on the effect of the spatial position of the stimuli on the bisection errors of both neurologically normal participants and neglect patients (Heilman and Valenstein 1979; Marshall and Halligan 1990; Sampaio and Philip 1991; Vallar et al 2000—see also Jewel and McCourt 2000). The results of our final experiment also suggest that the frame of reference used by the participants when performing the haptic bisection task was not object-based (cf Gallace and Spence, submitted). Indeed, no modulation of participants' performance as a function of the position of the stimuli presented was expected if a purely object-based representation was used to perform the bisection task.

6 General discussion

The results of the four experiments reported here provide the first empirical demonstration that the Oppel–Kundt visual illusion and optokinetic stimulation can both influence haptic line bisection crossmodally. These results suggest that different visual manipulations might influence the amodal/multisensory systems used to consciously represent external space and/or to organise movements toward a certain spatial location.

In the classic Oppel – Kundt illusion (Bertulis and Bulatov 2001; Lewis 1912 – 1913), a filled space is perceived as being larger than an empty space of equivalent size. In the modified version of the illusion used here, the distances between the horizontal bars decreased progressively from one side of the display to the other, producing a progressive anisometry in the perception of space (cf Ricci et al 2004). Ricci et al reported that performance in both visual line-bisection and visual line-extension tasks were influenced by this manipulation of the visual background. In their line-extension task, the participants were required either to bisect or to extend a line segment leftward or rightward in order to double its original length. Shorter extensions and a smaller shift in bisection errors toward the denser side of the display were made by neurologically normal participants (as well as by the neglect patients in their study). Ricci et al claimed that the modified version of the Oppel – Kundt illusion influenced the representation of space by inducing a perceptual expansion in the more densely structured region of the display.

The results of experiment 1 show that this version of the Oppel – Kundt visual illusion can also crossmodally influence participants' judgments of the midpoint in a 'haptic' line-bisection task. However, the results of experiment 3 showed no effect of the illusion on the haptic bisection task when the position of the stick was not aligned with the participants' body-midline. These data would therefore appear to suggest that the most likely interpretation for the illusory effect found in experiment 1 is that the visual background influenced participants' pointing behaviour (toward their body-midline), rather than the representation of space used for the bisection task itself. This would offer further support for the view that visual illusions also affect representations that are used for the execution of motor commands (Bruno and Bernardis 2003; Elliott and Lee 1995; Gentilucci et al 1996; Meegan et al 2003). It would be useful in future research to address the effect of visual illusions on haptic tasks by using different procedures in order to isolate the role played by motor control and that played by perceptual factors.

It has been proposed that the posterior parietal cortex combines information from different sensory modalities in order to create a common representation of extrapersonal space [Andersen et al (1997); Critchley (1966); Graziano (2001); Mountcastle et al (1975); Pouget and Driver (2000); Spence and Driver (2004)—see also Pouget and Sejnowski (2001) for a computational model of spatial representation in humans]. It has also been suggested that the neurological substrate of such a representation might be related to neurons with spatially congruent receptive fields for stimuli presented in different sensory modalities (Andersen et al 1997; Pouget and Driver 2000). The results of the four experiments reported here support, from a behavioural perspective, the claim that a common representation, accessed by different sensory modalities, may be used to compute spatial information regarding the length of a stimulus (Jonides et al 1982). Note also that it has been suggested that such a representation might be part of the circuit responsible for organising movements toward specific locations in space (Graziano 2001; Rizzolatti et al 2000). Following on from these observations, it therefore appears possible that the difference between the results obtained with the Oppel – Kundt visual illusion and those obtained with optokinetic movement might be related to two alternative loci of the effects. Specifically, while optokinetic movement might act upon a more perceptual part of this circuit, the Oppel – Kundt visual illusion might act more upon the motor-related component of the circuit instead.

Optokinetic movement produces ocular nystagmus, a reflex that helps to keep the position of the retinal image constant when the body moves (Howard 1982). It is by means of such a mechanism that optokinetic stimulation appears to influence the processing of information regarding egocentric space (Pizzamiglio et al 1990). It has been reported that when neurologically normal participants are instructed to walk in a straight line in an optokinetic drum, their walking trajectories deviate in the direction of rotation (Brecher et al 1972). The ability of normal participants to orient a line placed straight ahead has also been shown to be affected by the rotational movement. Similarly, Pizzamiglio et al (1990) reported that line-bisection errors were shifted in the direction of a background of dots moving leftward or rightward (see also Karnath 1996; Na et al 2002). Optokinetic stimulation has also been used to temporarily remove some of the symptoms of patients affected by spatial disorders such as hemineglect and extinction (Nico 1999; Pizzamiglio et al 1990). The results of these studies therefore strengthen the suggestion that the information mediated by optokinetic stimulation also affects computations regarding the position of the body in space (Pizzamiglio et al 1990; Vallar et al 1997—cf Figliozzi et al 2005).

Nico (1999) reported that a background of leftward moving dots significantly improved the performance of a group of brain-damaged patients suffering from extinction in detecting 'tactile' stimuli presented simultaneously to both hands. This finding suggests that visual stimulation can affect the higher-order levels of processing involved in the representation of contralesional space [cf Bottini et al (2005) for a demonstration of an ameliorative effect of left caloric vestibular stimulation on right hemianaesthesia in neurological patients]. The results of experiments 2 and 4, showing an effect of optokinetic stimulation on the judgments of the midpoint of a haptically explored line by neurologically normal participants, both support and extend this view. Taken together, the results of three out of the four experiments reported here (experiments 1, 2, and 4) highlight the effectiveness of two quite different modulations of background visual information on haptic line-bisection performance (see also Gallace and Spence 2005).

Girardi et al (2004) recently reported that manipulating visual information by means of prism adaptation (see also Rossetti et al 1998) can influence both the visual and haptic exploration of a circle by neurologically normal participants. The results of Girardi et al's study therefore also support the view that a common higher-order amodal, multimodal, or noetic (cf Girardi et al 2004) representation might be used in order to compute spatial information (see also Spence and Driver 2004).

Interestingly, the results of experiment 4, showing a modulatory effect of the spatial position from which the stimuli were placed on the participants' bisection errors, suggest that the representation affected by the visual background was not based on an object-based frame of reference, but rather on a space-based or body-centred frame of reference (see also Gallace and Spence, submitted). Indeed, if an object-based representation of the stick had been affected by the presence of the illusion, no modulatory effect of the position of the stimuli across the participants' body midline would have been expected (Heilman and Valenstein 1979; Marshall and Halligan 1990; Vallar et al 2000).

It is worth noting here that the effects of the visual background on the haptic bisection task reported in experiments 1, 2, and 4 were not completely symmetrical. Specifically, participants' mean bisection errors were significantly different from the control condition only when a rightward movement or a right-compressed background were presented on the screen but not when a leftward movement or a left-compressed background were presented. These results differ from those obtained by Ricci et al (2004) where a symmetrical effect of the visual illusion on the visual bisection task was found both in patients affected by neglect and in neurologically normal participants [though see Daini et al (2002) for an asymmetrical effect of the Brentano illusion on the visual bisection of patients affected by spatial neglect].

A possible explanation for this asymmetry in the results regards the capability of the amodal/multisensory representation of space being influenced by different experimental manipulations. Indeed, it may be plausible to think that such a representation is already asymmetrical in nature and that one part of it might be more easily disrupted than the other. The well-known phenomenon of 'pseudoneglect' [this term is attributed to the frequently reported behaviour of normal participants who tend to bisect lines to the left of their veridical centre—see Jewel and McCourt (2000) for an extensive review], and the frequently reported asymmetry in the damage of spatial behaviour caused by the neglect syndrome [neglect affecting the left side of space is far more frequent than neglect affecting the right side of space—see Vallar (2001) for a review] provide examples in support of this view. Therefore, an asymmetry in the underlying representation used to compute the length and position of the stimuli might be the cause of the asymmetry in the results reported in experiments 1 and 2. A more parsimonious interpretation of this asymmetry relates to the role played by the variance of participants' responses (that was higher in the haptic than in the visual task) that might have masked any effect of rightward movement or right-compressed backgrounds on the haptic bisection errors.

Given the proven effectiveness of sensory modulations, such as visual illusions, transcutaneous nerve stimulation, vestibular caloric stimulation, optokinetic stimulation, and prism adaptation, in temporarily removing the symptoms of hemispatial neglect, it will clearly be of interest in future research to study the effect of the Oppel – Kundt illusion and optokinetic stimulation on performance on a haptic bisection task in brain-damaged patients suffering from spatial disorders, by using both perceptual and motor tasks. If the spatial representations damaged in certain patients (Bisiach et al 1996) have multisensory/amodal characteristics, then some beneficial effects of stimulation in one sensory modality on performance for stimuli presented in the other modality should be expected (Nico 1999).

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