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Brief article

# Left to right: Representational biases for numbers and the effect of visuomotor adaptation

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## Abstract

Adaptation to right-shifting prisms improves left neglect for mental number line bisection. This study examined whether adaptation affects the mental number line in normal participants. Thirty-six participants completed a mental number line task before and after adaptation to either: left-shifting prisms, right-shifting prisms or control spectacles that did not shift the visual scene. Participants viewed number triplets (e.g. 16, 36, 55) and determined whether the numerical distance was greater on the left or right side of the inner number. Participants demonstrated a leftward bias (i.e. overestimated the length occupied by numbers located on the left side of the number line) that was consistent with the effect of pseudoneglect. The leftward bias was corrected by a short period of visuomotor adaptation to left-shifting prisms, but remained unaffected by adaptation to right-shifting prisms and control spectacles. The findings demonstrate that a simple visuomotor task alters the representation of space on the mental number line in normal participants.


*Keywords:* Mental number line; Mental representation; Space; Visuomotor adaptation; Perception

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## 1. Introduction

Patients with right parietal damage and unilateral neglect exhibit a perceptual deficit for the left (contralesional) side of physical space (Heilman, Watson, & Valenstein, 1993). As a result, for line bisection tasks, neglect patients bisect the line far to the right of its true centre. Unilateral neglect is not restricted to stimuli that are physically present and also occurs for mental imagery (Bartolomeo, Bachoud-Lévi, Azouvi, & Chokron, 2005) and mental representations of numbers. The mental number line is thought to have a left-to-right organization whereby low and high numbers are represented in the left and right sides of space, respectively (Dehaene, Bossini, & Giraux, 1993). As a result, when judging the distance between two numbers, left neglect patients misplace the midpoint to the right (i.e. toward the higher number) – analogous to their rightward misbisection of physical lines (Vuilleumier, Ortigue, & Brugger, 2004; Zorzi, Priftis, Meneghello, Marenzi, & Umilta, 2006; Zorzi, Priftis, & Umilta, 2002; but cf. Dorrichi, Guariglia, Gasparini, & Tomaiuolo, 2005).

While left neglect patients misbisect mental and physical lines to the right, normal participants demonstrate a leftward bias (Nicholls, Bradshaw, & Mattingley, 1999; Nicholls & Loftus, 2007). This leftward bias reflects pseudoneglect, a phenomenon that causes the leftward stimulus properties to be overestimated relative to those on the right (Bowers & Heilman, 1980). Pseudoneglect manifests itself on physical line bisection tasks, where the perceived midpoint of a line is shifted left of the true midpoint (Jewell & McCourt, 2000; McCourt, 2001), but is also observed for judgments of luminance (Mattingley, Bradshaw, Nettleton, & Bradshaw, 1994; Nicholls et al., 1999; Nicholls, Mattingley, Berberovic, Smith, & Bradshaw, 2004), size and numerosity (Nicholls et al., 1999). Leftward biases have also been observed for the mental representation of stimuli, such as the recall of familiar scenes (McGeorge, Beschin, Colnaghi, Rusconi, & Della Sala, 2007), mental alphabet lines (Nicholls & Loftus, 2007) and mental number lines (Longo & Lourenco, 2007).

The clinical symptoms of neglect can be ameliorated through adaptation to right-shifting prisms, improving performance on a wide range of visuospatial tasks (Frassinetti, Angeli, Meneghello, Avanzi, & Làdavas, 2002; Pisella, Rode, Farnè, Tilikete, & Rossetti, 2006) including explicitly spatial tasks such as physical line bisection (Rossetti et al., 1998) and non-explicitly spatial tasks such as temporal order judgments (Berberovic, Pisella, Morris, & Mattingley, 2004) and mental imagery (Rode, Rossetti, & Boisson, 2001). Rossetti et al. (2004) found that left neglect for the mental number line was improved by adaptation to right-shifting prisms, leading them to suggest that adaptation alters higher-level representations of space.

Wearing right-shifting prisms causes objects to appear to the right of where they actually are, so that when the wearer first points to an object, they miss to the right. Subsequent movements must be adapted if they are to be accurate, a complex process known as ‘prism adaptation’ (PA), which involves two key components – ‘strategic control’ and ‘spatial realignment’ (Redding, Rossetti, & Wallace, 2005). Strategic control is a short-term process whereby initial reaching errors are rapidly detected and reduced. Spatial realignment involves a shift of sensory–motor reference frames so that the felt and seen positions of the moving limb are congruous (Redding & Wallace, 1997). Negative aftereffects (i.e. pointing errors in the direction opposite to the prismatic shift following removal of the prisms) are thought to reflect the amount of spatial realignment that has occurred (Rossetti et al., 1998; Redding & Wallace, 2006), and can be observed within a 5-min PA session (Pisella et al., 2006).

Although the precise mechanism by which PA moderates left neglect remains unclear, it is thought that PA promotes the realignment of dysfunctional spatial maps. Adaptation to right-shifting prisms shifts biased egocentric spatial reference frames to the neglected side, correcting the dysfunctional calibration of the task-work space (Redding et al., 2005; Redding & Wallace, 2006; Rossetti et al., 1998). Left-shifting prisms do not affect bisection judgments (Rossetti et al., 2004, 1998), suggesting that there is an inherent asymmetry in the mechanisms that link PA and spatial cognition, which causes the two hemispheres to be differentially engaged during adaptation (Colent, Pisella, Bernieri, Rode, & Rossetti, 2000; Vallar et al., 1999).

The dramatic effect of PA on neglect patients with disordered spatial maps raises the intriguing possibility that PA also affects normal spatial maps in the intact brain. This issue has been investigated to some extent in studies investigating the effect of prisms on line bisection. Adaptation to left-shifting prisms elicits a rightward shift of midpoint in normal participants (Berberovic & Mattingley, 2003; Colent et al., 2000), whereas right-shifting prisms have no effect (Colent et al., 2000; Michel et al., 2003; but cf. Rossetti et al., 1998). While these studies show that prisms affect the perception of a stimulus, they do not demonstrate that this effect goes beyond relatively low-level congruencies in the mapping of the stimulus with reference to body coordinates and/or the response. In the present study, we sought to demonstrate that PA affects high-order mental representations of space where there are no physical sensory/motor congruencies. The mental number line was explored using low and high numbers, which are known to induce pseudoneglect (Longo & Lourenco, 2007). Given that neglect and pseudoneglect are thought to reflect the operation of a common set of cognitive and neural mechanisms (McCourt & Jewell, 1999; Nicholls et al., 2004) we expected our pseudoneglect study to yield a similar (but mirror-reversed) pattern of results relative to the neglect literature (e.g. Rossetti et al., 2004). Participants completed a mental number line task before and after PA that shifted the visual scene 15° to the left or to the right. In light of the asymmetrical effects of PA reported by Berberovic and Mattingley (2003), we expected left-shifting prisms to reduce pseudoneglect for mental number lines whereas right-shifting prisms should have no effect.

## 2. Methods

### *2.1. Participants*

Thirty-six undergraduate students participated in the study (eight male, mean age 23.1 years). All had normal vision and were right-handed, as confirmed by the Edinburgh Handedness Inventory (Oldfield, 1971).

## 2.2. Apparatus, stimuli, & procedure

Participants completed the tasks in the following order: (i) a pre-adaptation number line task; (ii) visuomotor adaptation to either a 15° leftward or rightward lateral shift, or to control spectacles with no lateral shift; (iii) a post-adaptation number line task identical to the pre-adaptation task; (iv) visuomotor de-adaptation. Twelve participants were adapted to left-shifting prisms, twelve to right-shifting prisms and twelve participants were 'adapted' to the control spectacles. Within each group, six participants saw the number triplets presented in ascending order and six in descending order.

### 2.2.1. Number line task

The stimuli were two-digit number triplets, composed of a red inner number and two yellow flanker numbers. Twelve sets of flankers were used (41_83, 44_86, 47_89, 21_63, 24_66, 27_69, 21_73, 24_76, 27_79, 31_83, 34_86, & 37_89). The flankers in the first and second half of the list were separated by numerical lengths of 42 and 52, respectively. The inner number was shifted by 5 or 9 points below or above the true arithmetic centre. The true arithmetic centre of a number triplet was never presented. There were 144 trials, which included three repetitions of the factorial combinations of flanker set (12) and inner number shift (+5, −5, +9, −9). Participants were seated in front of a 365 mm (height) × 275 mm (width) computer monitor and all numbers were presented along their midline at eye level. A chin rest maintained head position at 500 mm from the monitor. Participants made a single-interval two alternative forced-choice discrimination stating which of two outer (flanker) numbers was furthest away (numerically) from the inner number. Participants were instructed not to perform any arithmetic. Pre-tests revealed the presentation period of 1 second per number discouraged participants from counting. Participants completed three identical blocks of 48 trials and six practice trials (Fig. 1).

### 2.2.2. Visuomotor adaptation

Immediately following the pre-adaptation number line task, PA was commenced. Participants wore a pair of Cebe™ binocular prisms (mounted in spectacle frames) which produced a 15° leftward or rightward lateral shift in the visual scene. Covers attached to the nasal and temporal areas of the frames obstructed any undistorted areas. The control group wore a pair of +1.5 diopter spectacles. Although these spectacles induced a small perceptual distortion, they did not laterally shift the visual scene. A shelf positioned immediately below the participant's chin ensured they could not see the start position of their hand or the first half of their pointing movement. There were two 15 mm yellow targets located on the table, 350 mm (in a straight line) away from the start position, 150 mm to the left or right of the midline. Participants began each trial with the index finger of their right hand placed on the start position, located 10 mm from the edge of the table along their midline. Participants pointed with their right index finger to the left or right target as quickly and accurately as possible. Participants were asked not to perform any corrective movements and to leave their index finger in its final pointing position before being

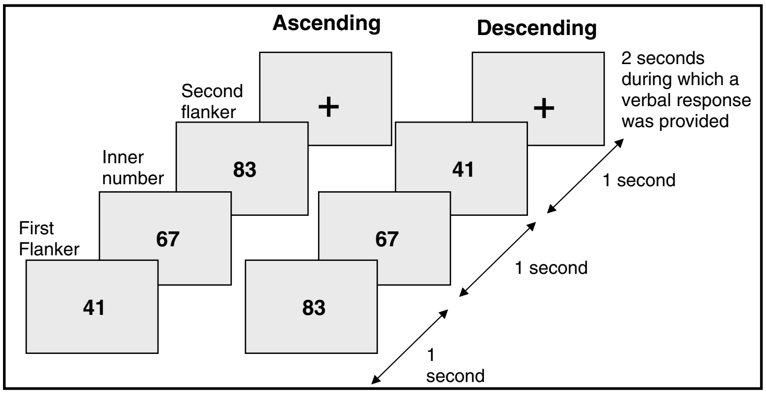



Fig. 1. Schematic representation of the two presentation modes. Each number was presented in the centre of the monitor for 1-s and replaced by the next number in the sequence. There was a 2-s interval between trials, during which participants fixated a central cross and provided a verbal response.

instructed to return to the start. Participants performed 50 pointing movements to each target in a random order. Adaptation was deemed to have occurred when the pointing was accurate. The adaptation phase lasted approximately 15 min and all participants in the study were adapted within the required 50 pointing movements. Following PA, the prisms/spectacles were removed and participants kept their eyes closed and remain still. When instructed, participants opened their eyes and performed the number line task again. Two measurements of the lateral displacement of the index finger from each target were taken on the first and last trial of this phase.

### *2.2.3. Visuomotor de-adaptation*

To assess whether PA was maintained, participants pointed once to each target without wearing the prisms/spectacles. To overcome the effects of PA, participants then performed pointing movements until they were accurate. Two measurements of the lateral displacement of the index finger from each target were taken on the first and last trial of this phase.

## 3. Results

### *3.1. Visuomotor adaptation*

All participants successfully adapted within 50 pointing trials. To establish whether participants in the left-shifting and right-shifting prism conditions adapted equally, the distance by which the finger missed the target was measured at the start of the adaptation phase (i.e. the first pointing movement made whilst wearing the prisms) and at the start of the de-adaptation phase (the first pointing movement made without the prisms – post-adaptation). These measurements provide an index of (i) pre-adaptation pointing error and (ii) post-adaptation negative aftereffects. An ANOVA, conducted on absolute reaching error (i.e. direction was not coded), with direction of prism shift (left, right), target (left, right) and pointing task (pre-adaptation, post-adaptation) as within-subject factors revealed no main effects (all $ps > .05$). Inspection of the relative data (where direction is coded) demonstrated rightward negative aftereffects ($M = 6.01$ mm, $SD = 2.31$) for the left-shifting group and leftward negative aftereffects ($M = 6.33$ mm, $SD = 2.32$) for the right-shifting group. A correlation was performed on the left-shifting group, where an effect of PA was predicted. There was no evidence that participants with stronger negative aftereffects showed greater change in their number line bias ($r = -.296$, $p = .350$).

### 3.2. Response bias

Response bias was calculated by subtracting the number of left responses from right responses and converting the result into a percentage. Response bias scores ranged from −100% (complete leftward bias) to +100% (complete rightward bias). The data for each group (control, left-shifting, right-shifting) were analyzed separately using an ANOVA with pre/post adaptation (pre-adaptation, post-adaptation), number line length (42, 52), block (1, 2, 3) and inner number shift (−9, −5, +5, +9) as within-subject factors and presentation order (ascending, descending) as a between-subjects factor. Effect sizes are expressed as partial $\eta^2$ values.

### 3.3. Control (no lateral shift)

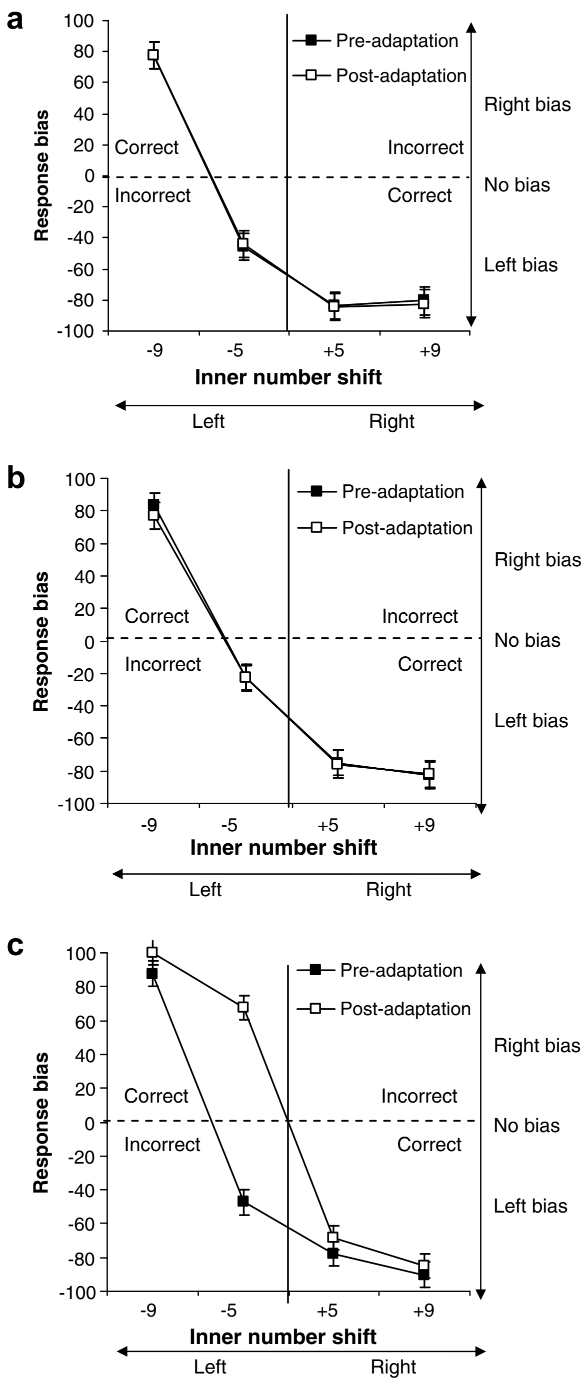
There was a main effect of inner number shift ($F(3,33) = 87.352$, $p < .001$, $\eta^2 = .897$). Fig. 2a illustrates a rightward bias for inner number shifts of −9 and a leftward bias for all other inner numbers. There was a non-significant trend for a stronger leftward bias in the descending compared to ascending condition ($F(1,11) = 4.966$, $p = .051$). No other main effects or interactions were significant.

### 3.4. Right-shifting prisms

There was a main effect of inner number shift ($F(3,33) = 163.123$, $p < .001$, $\eta^2 = .942$). Fig. 2b reveals a rightward bias for inner number shifts of −9 and a leftward bias for all other inner numbers. There was a non-significant trend for a stronger leftward bias in the descending compared to ascending condition ($F(1,11) = 6.428$, $p = .080$). No other main effects or interactions were significant.

### 3.5. Left-shifting prisms

There was a main effect of inner number shift ($F(3,33) = 342.079$, $p < .001$, $\eta^2 = .972$). Fig. 2c illustrates a rightward bias for inner number shifts of −9 and a leftward bias for all other inner number shifts. There was also a main effect of pre/post adaptation ($F(1,11) = 37.513$, $p < .001$, $\eta^2 = .790$) and an interaction between inner number shift and pre/post-adaptation ($F(3,33) = 43.149$, $p < .001$,


a
b
c
Response bias
Pre-adaptation
Post-adaptation
Right bias
No bias
Left bias
Correct
Incorrect
Inner number shift
-9
-5
+5
+9
Left
Right

$\eta^2 = .812$). As Fig. 2c illustrates, the leftward bias in the −5 condition became a rightward bias (i.e. participants were now correct) following adaptation. There was a non-significant trend for a stronger leftward bias in the descending compared to ascending condition ($F(1,11) = 4.072$, $p = .071$). No other main effects or interactions were significant.

## 4. Discussion

Like Longo and Lourenco (2007), participants overestimated the leftward space on the mental number line – consistent with the effect of pseudoneglect. The fact that such a bias is observed for mental representations such as numbers (Göbel, Calabria, Farnè, & Rossetti, 2006; Longo & Lourenco, 2007) and letters (Nicholls & Loftus, 2007) suggests that pseudoneglect occurs independently of stimulus input. While pseudoneglect for physical lines may be related to left-to-right eye movements (Chokron, Bartolomeo, Perenin, Helft, & Imbert, 1998; Manning, Halligan, & Marshall, 1990), this explanation cannot account for biases in mental representations. Instead, the leftward bias may be related to the brain regions associated with the task. The posterior parietal cortex (PPC) in the right hemisphere has been implicated in the manifestation of both pseudoneglect (Göbel et al., 2006) and the mental number line (Hubbard, Piazza, Pinel, & Dehaene, 2005). While theories of attentional bias, such as Kinsbourne's (1970, 1993) orientational bias model typically relate to physical perceptual asymmetries, they are also relevant to representational asymmetries (Bisiach & Vallar, 1988). Thus, increased activation of the right hemisphere may generate an attentional bias toward the left side of the representation. The right hemisphere's role may have been particularly strong in the descending condition where the unusual number format placed extra demands on mental imagery. The asymmetry could operate on the mental representation at an early stage – such as an asymmetry in the construction of mental images (Bisiach & Vallar, 1988). Alternatively, the asymmetry could reflect the operation of an 'internal eye', which scans from left-to-right or asymmetries in the availability of the mental image (Kinsbourne, 1987).

Pseudoneglect for the mental number line was overcome by adaptation to left-shifting prisms, but was unaffected by the same level of adaptation to right-shifting prisms. The asymmetric effect of prisms is consistent with previous studies with normal participants (Berberovic & Mattingley, 2003; Colent et al., 2000; Michel et al., 2003) and in neglect populations (Frassinetti et al., 2002; Rossetti et al., 2004). Unlike previous studies, which used physical line bisection (e.g. Berberovic & Mat-

Fig. 2. Mean responses bias (with ±SE bars) for pre and post adaptation across the four inner number shifts. Correct and incorrect responses are indicated within each of the quadrants. Data are shown for the: (a) control (no shift), (b) right-shift and (c) left-shift conditions. *T*-tests comparing each of the data points with zero revealed a significant difference in all conditions ($p < .001$). Post-hoc tests with Bonferroni corrections revealed the rightward bias in the −9 condition was significantly different to the leftward bias in the −5 condition in all three graphs (all adjusted $ps < .001$)

tingley, 2003), an effect of PA occurred for mental representations of stimuli that were not physically present. The effect of PA therefore cannot reflect low-level remapping of the stimulus with reference to body coordinates and/or the response. Instead, the data demonstrate that the sensory–motor realignment associated with PA affects higher-order representations of stimuli.

The effect of PA on the mental number line may be mediated by the differential hemispheric activation of the hemispheres. If increased right hemisphere activation produces an attentional bias toward the left side of the mental number line, then increased left hemisphere activation may rebalance this attentional asymmetry. The improvement of left neglect is associated with increased neuronal activity in the right cerebellum and right PPC (Lauté et al., 2006; Pisella et al., 2005), suggesting that cerebellar and PPC function is lateralized *ipsilateral* to the direction of prism displacement (Pisella et al., 2005). For normal participants, PA engages the two hemispheres differently (Berberovic et al., 2004; Clower et al., 1996; Inoue et al., 2000; Michel et al., 2003). Inoue et al. (2000) found increased activation of the left supplementary motor area and left dorsal premotor cortex during the later stage of adaptation. Furthermore, PA leads to the selective activation of the PPC *contralateral* to the reaching limb (Clower et al., 1996). In the context of the present findings, activation of the left PPC during PA may rebalance a leftward attentional bias on the mental number line.

An alternative explanation is that external and internal spatial representations are directly linked, so that a shift of attention in one leads to a shift of attention in the other. Perceiving numbers causes shifts in covert spatial attention and signals a link between internal and external representations of space (Fischer, Castel, Dodd, & Pratt, 2003). Hubbard et al. (2005) suggested that the lateral (LIP) and ventral (VIP) intraparietal regions form a neurological link between internal and external representations of space. These regions contain number-sensitive neurons (Dehaene, Molko, Cohen, & Wilson, 2004) and are involved in the construction of a multi-sensory representation of external space (Pouget, Deneve, & Duhamel, 2002). Moreover, neurons in area LIP are involved in the programming of overt and covert shifts of spatial attention (Corbetta & Shulman, 2002). Hubbard et al. (2005) suggested that shifts in attention on the mental number line produces shifts of attention in area LIP, resulting in a shift of attention in external space. We suggest this link may be bi-directional and that shifts of attention in external space produce shifts of attention in area LIP, leading to a shift of attention on the mental number line. The neural basis of this bi-directional flow of information has yet to be established in humans, although studies of Macaques reveal that areas LIP and VIP are connected by a dense network of bidirectional neurons (Lewis & Van Essen, 2000).

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