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Note

Eye rotation does not contribute to shifts in subjective straight ahead: Implications for prism adaptation and neglect

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ABSTRACT

Prism adaptation has received much attention in recent years as a potential method for the rehabilitation of visual neglect. Recent theories as to the underlying mechanisms include oculomotor resetting and pathological realignment of subjective straight ahead (SSA). Typical prism adaptation procedures involve both ocular rotation and manual correction making the precise mechanisms and contribution of these to the amelioration of neglect difficult to determine. This experiment separated the contributions of ocular rotation and manual error reduction to SSA realignment in normal participants by shifting the eye alone, the hand alone or both together. Rotating the eye alone did not contribute to SSA realignment whereas shifting the hand did.

1. Introduction

Despite its apparent simplicity, prism adaptation (PA) remains an important tool for research into one of our most fundamental brain functions providing an observable insight into the remarkable plasticity of the human motor system. Prism lenses displace visual information reaching the eye such that participants wearing prisms initially misreach to visual targets in the direction of visual displacement. Healthy participants easily adapt to this and very rapidly become accurate, but when the prisms are subsequently removed the aftereffects of adaptation causes misreaching in the opposite direction. This aftereffect is most commonly measured either by visual open-loop pointing (VOL) (the target is visible, but the hand is not) or indication of subjective straight ahead (SSA) (pointing straight ahead of the nose/body midline with the eyes closed).

Prism adaptation has received much attention in recent years as a potential method for the rehabilitation of visual neglect (see Luauté, Halligan, Rode, Rossetti, & Boisson, 2006 for a review). Neglect is a frequent behavioural outcome following right hemisphere stroke in which patients fail to respond appropriately to left-sided events or stimuli, often ignoring them altogether (Heilman & Valenstein, 1979). For neglect patients, the aftereffect of rightward PA improves performance on a range of behavioural measures, from line bisection to wheelchair navigation (Jacqui-Courtois, Rode, Pisella, Boisson, & Rossetti, 2008; Rossetti et al., 1998). Some studies in normal participants have shown that mild neglect-like symptoms can be induced by adaptation to leftward displacing prisms, causing participants to bisect lines slightly to the right of centre for example (e.g. Michel et al., 2003). Despite the excitement caused by its apparent success, the precise mechanisms underlying the amelioration of neglect by PA are not fully understood while doing so would provide a major benefit for patient rehabilitation strategies. Two recent theories include oculomotor resetting and a pathological shift in subjective straight ahead.

Serino et al. (Angeli, Benassi, & Ladavas, 2004; Serino, Angeli, Frassinetti, & Làdavas, 2006; Serino, Bonifazi, Pierfederici, & Làdavas, 2007) suggest that the improvement in neglect symptoms following prism adaptation might occur as a result of what they term oculomotor resetting. By this account, a leftward deviation of the eye is prompted by the incremental leftward deviations of the arm that occur during prism exposure. According to this theory, having missed the target to the right on the first trial, patients must correct their reaches further and further leftward until accuracy is achieved. Because the eye and hand are yoked during goal-directed reaching (e.g. Carey, Coleman, & Della Sala, 1997; Fisk & Goodale, 1985; Jackson, Newport, Mort, & Husain, 2005), the eye also deviates leftwards—potentially ameliorating scanning behaviour and prompting leftward orienting of attention. Thus, leftward reduction of reaching error during prism exposure promotes leftward deviation of the oculomotor system, which, in turn, improves leftward performance on a number of measures of neglect after exposure.

At first sight, however, this idea seems slightly at odds with typical prism exposure behaviour in which the eyes deviate in the same

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direction as the prism displacement both during and after adaptation (i.e. rightwards with rightward displacing prisms). This occurs because the asymmetric rightward eye posture required to fixate targets when wearing rightward prisms (a central target will appear to the right of straight ahead) produces lasting changes in the posture of the eyes due to muscle potentiation, causing aftereffects in visual straight ahead (VSA) that match the direction of the prism deviation (Paap & Ebenholtz, 1976) [VSA is usually tested by having participants verbally adjust a visual stimulus until it is perceived to be straight ahead]. Thus, prisms usually cause the eye to deviate rightwards (during and after rightward prism exposure), but the oculomotor resetting theory suggests that manual realignment during prism exposure prompts the eyes to reorient leftwards after prism exposure.

Serino et al. (2006, 2007) highlighted the importance of patients' ability to reduce pointing error during adaptation (without error reduction the eye cannot follow the hand leftwards). They found that the ability to reduce pointing error correlated with improved performance on neglect measures, but that the manual aftereffect (measured by VOL) did not. However, Sarri et al. (2008) observed that it is the SSA aftereffect, and not VOL, that is most strongly correlated with neglect improvement. SSA indication is typically abnormal in neglect patients, erring substantially rightward, and is one of the more common symptoms of this multifaceted syndrome (Karnath, 1997). It is noticeable that the SSA aftereffect is also pathologicalally large in neglect patients (Rossetti et al., 1998; Sarri et al., 2008). Interestingly, shift in SSA is traditionally a measure of proprioceptive (or head–hand) realignment following prism adaptation and is not normally associated with visual (head–eye or eye–hand) realignment. Thus, on the one hand Serino and colleagues champion resetting of the visual system while Sarri et al. champion a resetting of the proprioceptive system.

One of the difficulties with traditional prism adaptation is that it is difficult to dissociate the contributory effects of eye rotation and perceived limb displacement. When (for example) rightward prisms are worn the eyes must be rotated rightwards of a target in order to fixate it. The felt position of the hand, however, is not displaced (and is usually not visible at its starting position). Visual and proprioceptive maps are therefore in misalignment, causing reaches to be inaccurate in the direction of the prism deviation/eye rotation. Reach direction errors only become apparent when the hand (subject to the same visual displacement) appears towards the end of the movement. Separating the relative contributions of these processes has proven difficult using traditional methods because vision of the target (causing eye rotation) and vision of the limb (providing error feedback) are both subject to the same prismatic perturbation. The sensorimotor realignment processes that ultimately lead to the SSA aftereffect might therefore involve the realignment of sensory information relating to perceived limb position, eye position or both. The current experiment aimed to test the relative contributions of ocular rotation and limb realignment to SSA by using a combination of prism goggles and a novel camera system (dubbed MIRAGE) to provide displacement of the hand alone, the eyes alone or both hand and eyes together. Displacing the hand alone required error reduction to correct limb direction, without an accompanying ocular deviation, while displacing the eyes alone provided ocular deviation that was yoked to limb direction without requiring proprioceptive limb realignment.

In this experiment all perturbations were leftwards as this direction is most commonly associated with the simulation of neglect in normals (opposite to the direction employed in neglect studies using prisms; thus a leftward perturbation should produce reaching errors that are leftward during adaptation and rightward immediately afterwards). If the eyes are prompted to orient rightwards due to yoking with rightward manual error reduction in response to a leftward prismatic displacement of limb position then a significant rightward shift in visual straight ahead should be observed following prism adaptation (BS condition). In addition, if it is the ocular yoking of corrective hand movements that stimulates oculomotor resetting, then the same phenomenon should be observed when the arm is required to make incremental corrections, but in the absence of the eye rotation caused by prism lenses (HS condition). If, however, a shift in subjective straight ahead is the key to the improvement in neglect performance, and this, in turn, is prompted by manual correction then a significant rightward SSA (rather than VSA) deviation should be observed following both the HS and BS conditions, but not following ocular rotation alone (ES condition). Finally, the relative contributions of eye rotation and perceived limb displacement to shifts in subjective straight ahead should be observable through differences in rightward SSA shift

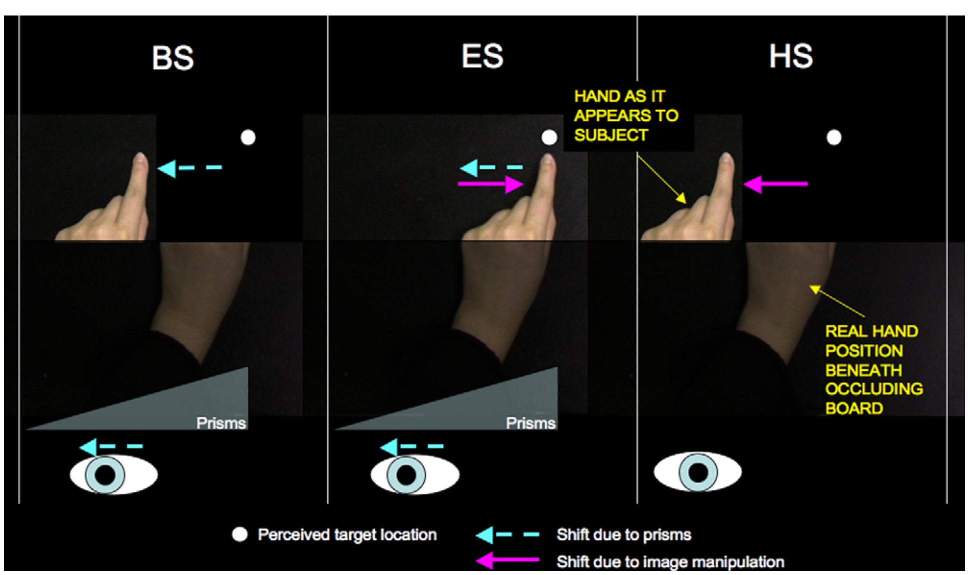

Fig. 1. Right panel: HandShift (HS) condition. Participants wore zero dioptre prisms and the image of the hand was shifted leftward. Middle panel: EyesShift condition. Participants wore leftward displacing prism goggles, but the image of the hand was shifted rightwards by an equal and opposite amount. Left panel: BothShift condition. Participants wore leftward displacing prism goggles and the image was not subject to a lateral shift. Note: in the BS and ES conditions the perceived target location is 20 dioptres to the left of its actual location, whereas in the HS condition the perceived and actual locations are the same.

between the HS and ES conditions. All of these predictions were tested directly using a series of a priori pair-wise contrasts that compared pre- and post-exposure performance on SSA, VSA and error reduction in each of the three conditions.

2. Methods

2.1. Participants

Twelve volunteers from Nottingham University took part in the study (mean age 23.2 (S.D. 2.9)). All had normal or corrected to normal vision, were right handed and were naive as to the purpose of the experiment. All gave informed consent and the study was approved by the local ethics committee.

2.2. Materials

Participants viewed real-time video of their hand and arm from the same perspective as if viewing the actual hand in the following manner. Participants sat at a table and looked down into a mirror suspended horizontally 320 mm above the table top. A further 320 mm above the mirror was a 28 in. 2.8 GHz iMac computer positioned so that the screen was reflected in the mirror. Live video images of the participant's moving hand were captured and displayed via the iMac at 60 Hz by a Basler A601F firewire CCD camera. The location of the camera and angles of the viewing mirror were such that real-time images of the participant's reaching movements reflected in the mirror appeared in the same spatial location as the actual movements and appeared from the same perspective as if viewing the hand directly. The delay between image capture and display was <17 ms and extensive pilot work showed that this discrepancy went undetected. Captured images could be displayed raw, or manipulated by in-house software. Image manipulation involved performing a lateral shift of the hand to the left or right as required by the visual condition. Position data from a Polhemus Liberty motion tracking sensor (sampling at 60 Hz) attached to the index finger were used to calculate the lateral shift of the visual image and to record finger position for the calculation of reach handpaths. Head movements were restricted by a chinrest and the head faced straight ahead throughout all three conditions.

2.3. Experimental procedure

In the exposure condition participant's made 80 left-handed reaches from a proprioceptively defined start point positioned on the leading edge of the table. For each trial a white circular target appeared in a pseudorandom location within a boundary 180–220 mm forward and 50 mm either side of the start location. The hand was only visible for the last third of the reach and a time-constraint was imposed such that vision of the hand and target disappeared after 750 ms. Reaches not completed within this time window were discarded. In the HandShift (HS) condition participants wore zero dioptre Fresnel prisms and the image of the hand was shifted left laterally by the equivalent of 20 dioptre (~11°) leftward displacing prisms. Thus, the eyes were not rotated, but the apparent position of the hand was perturbed leftwards. In the EyesShift (ES) condition participants wore 20 dioptre leftward displacing prisms, but the image of the hand was shifted rightwards by the equivalent of 20 dioptre rightward displacing prisms. Thus, the eyes were rotated leftwards, but, due to the equal and opposite effects of the prism goggles and image shift, the apparent position of the hand was not perturbed from its real position. In the BothShift (BS) condition participants wore 20 dioptre leftward displacing prisms and the image was not subjected to a lateral shift. Thus, the eyes were rotated and the apparent position of the limb was perturbed by the same amount (see Fig. 1). Note that only the hand, and not the target, was subject to image manipulation. All perturbations were leftwards as this direction is most commonly associated with the simulation of neglect in normals.

The three conditions were conducted on consecutive days in order to minimise carry-over effects and the order of completion was counterbalanced between participants. At the beginning of each session was a practice block consisting of 20 unperturbed trials in order to acclimatise to the timing of reaches and the general set up (seeing their own hand in the mirror). Participants also performed pre- and post-exposure tests of subjective straight ahead, which involved indicating where the participant perceived to be directly in alignment with their mid-sagittal axis by extending the finger and arm fully with the eyes closed, and visual straight ahead, which involved instructing the experimenter to move a visual stimulus that randomly appeared from either the left or right until it was perceived to be straight ahead. The pre- and post-tests were each performed four times.

3. Results

Mean SSA and VSA direction errors (in degrees) for pre- and post-exposure tests for each participant were calculated and a priori pair-wise comparisons were conducted between the pre- and post-exposure scores for each visual condition. Mean end-point errors were for the first four and second four reaches in the exposure phase for each participant were also calculated and a priori pair-wise comparisons were conducted between the 1st and 2nd bins for each visual condition. Due to recording errors the data for two participants were lost for the VSA condition. The mean baseline errors for SSA and VSA across all three conditions were −2.9° (range 1.2) and 0.7° (range 2.6) respectively.

3.1. After effects

The planned comparisons revealed significant SSA aftereffects in the direction opposite to the experimental perturbation for

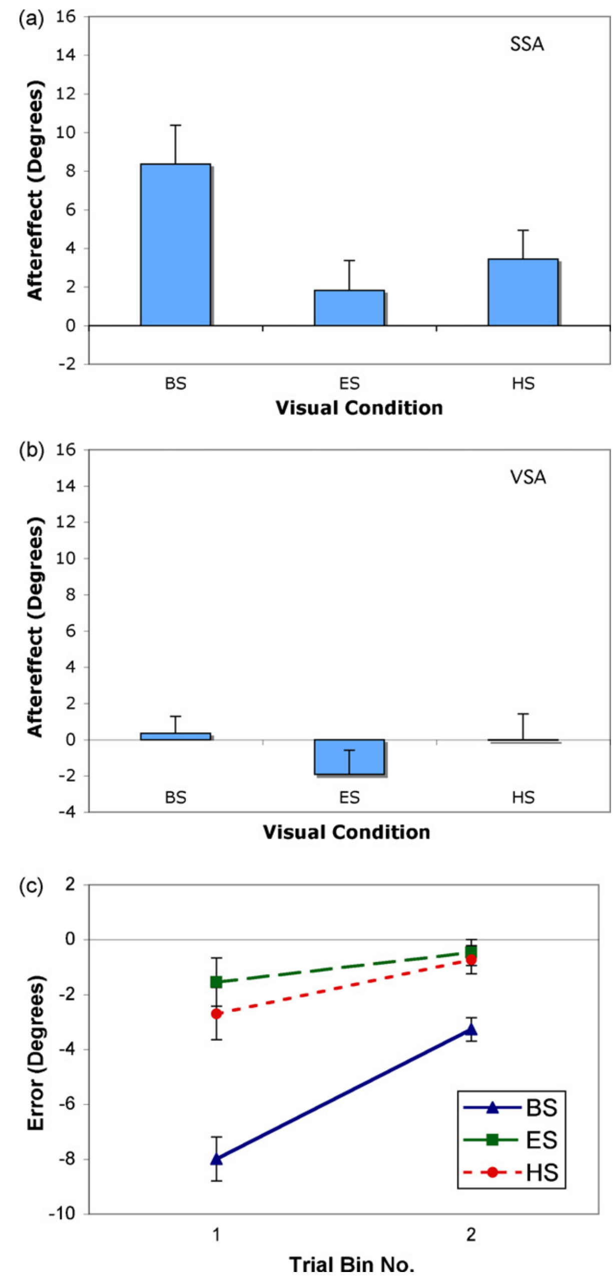

Fig. 2. Mean aftereffect (in degrees) in each visual condition for (a) SSA and (b) VSA trials. For the purpose of these figures the aftereffect has been calculated as the pre-exposure error minus the pre-exposure error. Positive values represent rightward deviation from true straight ahead; (c) mean pointing error (in degrees) in each visual condition for the first 8 trials with each bin containing four trials. HS and BS showed significant error reduction between bins 1 and 2 whereas ES did not. Positive values represent rightward error. Error bars represent SE.

the BS and HS conditions (min: $F(1,11) = 5.754$, $p < .05$), but not the ES condition ($F(1,11) = 1.621$, $p = .2162$) (Fig. 2a); and a significant VSA aftereffect for the ES condition ($F(1,9) = 6.839$, $p < 0.05$), but not the BS or HS conditions (max: $F(1,9) = 0.239$, $p = 0.63088$) (Fig. 2b).

3.2. Error reduction

Planned comparisons for error reduction between the first and second bins revealed significant reduction for the BS and HS conditions (min: $F(1,11) = 10.850$, $p < .005$), but not for the ES condition ($F(1,11) = 3.056$, $p = 0.0944$) (Fig. 2c).

4. Discussion

Perturbing either the hand alone or the hand and eyes together resulted in significant error reduction and significant SSA aftereffects, whereas rotating the eye alone did not (Fig. 2a). Conversely, rotating the eye alone resulted in a significant VSA aftereffect, but shifting the perceived position of the hand did not (Fig. 2b). These results have implications for theories of prism adaptation and the mechanisms underlying the amelioration of neglect. The mechanisms by which low-level adaptation to prisms affects high-level spatial awareness are not fully understood, but recent theories include oculomotor resetting (e.g. Serino et al., 2006) and a pathological leftward deviation of subjective straight ahead (Sarri et al., 2008). Changes in SSA, however, are theoretically independent from the modification of a visually based coordinate system. SSA is measured in the absence of vision and is most likely the result of realignment of the felt position of the limb (Redding & Wallace, 1990) whereas oculomotor resetting involves leftward deviations of the eye and is thought to originate in the yoking of the rotated eye position to leftward limb movements (Serino et al., 2006). In the current study eye rotation and visually perceived limb displacement were examined in isolation under identical adaptation procedures. Rotating the eye alone while pointing to visually defined targets did not induce a significant change in SSA while displacement of the hand alone did.

In Serino et al.'s account, a key component of oculomotor resetting is error reduction because it displaces the arm (and the yoked eyes) leftwards. Those authors measured error reduction as the difference between the means of 30 pre-exposure and 90 exposure trial blocks whereas in the current study error reduction was measured as the reduction of pointing error within a single block of trials. In the two conditions that required error reduction (BS and HS), participants showed significant improvement in accuracy within a single block (Fig. 2b) as well as significant SSA aftereffects. No error reduction was necessary in the ES condition because reaches were accurate from the outset due to the equal and opposite displacement of the prisms and computer image. However, not only were the eyes deviated leftwards in the ES condition (in order to fixate the target), reaches were also directed leftwards (towards fixation), yoking the two together from the first trial. In spite of this asymmetric exercise of both limb and eye, ocular deviation was not sufficient to produce the changes in SSA that are normally associated with neglect improvement. Ocular deviation was, however, sufficient to produce a deviation of visually perceived straight ahead in the same direction as the ocular rotation.

Hatada, Rossetti, and Miall (2006) demonstrated that VSA and SSA aftereffects are dissociable in that they decay at very different rates, with VSA decaying within hours and SSA sometimes lasting for days. It has long been established that VSA and SSA are separable components, but the relationship between these two and the ocular and manual components of manual prism adaptation has not yet been explored. Although the eyes are usually closed during tests of SSA, it is possible that information regarding the position of the eyes in the head is used when calculating straight ahead. The current experiment demonstrates that eye rotation during adaptation does not, on its own, significantly modify the sense of subjective straight ahead. However, it is interesting to note that the BS condition SSA aftereffect is considerably larger than the HS aftereffect and also larger than the combined HS and ES conditions. Furthermore, there is a noticeable absence of a VSA aftereffect in the BS condition, despite the inclusion of eye rotation in that condition. Clearly, there is something different about the combined effects of ocular and perceived limb perturbation under prism conditions. Perhaps, when both eye and limb shift are present at the same time the weighting given to each source of error by the CNS is skewed in favour of limb error, with that error perhaps being the most apparent.

The results of this experiment demonstrate that eye rotation without error reduction (ES condition) does not produce SSA aftereffects, but that error reduction both with (BS) and without eye rotation (HS) does, which suggests that error reduction may be the crucial PA component that modifies SSA. If oculomotor resetting is responsible for neglect amelioration then perhaps it occurs after exposure, and not during as suggested by Serino and colleagues, and it is the leftward post-exposure reaches that drag the eyes leftwards and encourage leftward scanning or orienting of attention. It is clear from this experiment that should ocular resetting occur, it cannot be not a direct result of prism exposure itself, but must be a byproduct of proprioceptive realignment of the limb. Redding and Wallace (2006) suggest that the amelioration of neglect by PA is brought about by the realignment of a dysfunctional sensorimotor reference frame. The current results suggest that this realignment may primarily be proprioceptive in nature and may result in the pathological shift in SSA associated with neglect recovery.

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References

Angeli, V., Benassi, M. G., & Ladavas, E. (2004). Recovery of oculo-motor bias in neglect patients after prism adaptation. *Neuropsychologia*, *42*, 1223–1234.

Carey, D. P., Coleman, R. J., & Della Sala, S. (1997). Magnetic misreaching. *Cortex*, *33*, 639–652.

Fisk, J. D., & Goodale, M. A. (1985). The organization of eye and limb movements during unrestricted reaching to targets in contralateral and ipsilateral space. *Experimental Brain Research*, *60*, 159–178.

Hatada, Y., Rossetti, Y., & Miall, R. C. (2006). Long lasting prism adaptation after effects reveal that shifts in vision and proprioception are independent. *Experimental Brain Research*, *173*, 415–424.

Heilman, K. M., & Valenstein, E. (1979). Mechanisms underlying hemispatial neglect. *Annals of Neurology*, *5*(2), 166–170.

Jackson, S. R., Newport, R., Mort, D., & Husain, M. (2005). Where the eye looks, the hand follows: Limb-dependent magnetic misreaching in optic ataxia. *Current Biology*, *15*(1), 42–46.

Jacqui-Courtois, S., Rode, G., Pisella, L., Boisson, D., & Rossetti, Y. (2008). Wheel-chair driving improvement following visuo-manual prism adaptation. *Cortex*, *44*(1), 90–96.

Karnath, H. O. (1997). Spatial orientation and the representation of space with parietal lobe lesions. *Philosophical Transactions of the Royal Society of London, Series B*, *352*, 1411–1419.

Luauté, J., Halligan, P., Rode, R., Rossetti, Y., & Boisson, D. (2006). Visuo-spatial neglect: A systematic review of current interventions and their effectiveness. *Neuroscience & Biobehavioral Reviews*, *30*(7), 961–982.

Michel, C., Pisella, L., Halligan, P. W., Luaute, J., Rode, G., Boisson, D., et al. (2003). Simulating unilateral neglect in normals using prism adaptation: Implications for theory. *Neuropsychologia*, *41*, 25–39.

Paap, K. R., & Ebenholtz, S. M. (1976). Perceptual consequences of potentiation in extraocular muscles: An alternative explanation for adaptation to wedge prisms. *Journal of Experimental Psychology: Human Perception and Performance*, *2*, 457–468.

Redding, G. M., & Wallace, B. (1990). Effects on prism adaptation of duration and timing of visual feedback during pointing. *Journal of Motor Behavior*, *22*, 209–224.

Redding, G. M., & Wallace, B. (2006). Prism adaptation and unilateral neglect: Review and analysis. *Neuropsychologia*, *44*(1), 1–20.

Rossetti, Y., Rode, G., Pisella, L., Farnè, A., Li, L., Boisson, D., et al. (1998). Prism adaptation to a rightward optical deviation rehabilitates left hemispatial neglect. *Nature*, *395*, 166–169.

Sarri, M., Greenwood, R., Kalra, L., Papps, B., Husain, M., & Driver, J. (2008). Prism adaptation aftereffects in stroke patients with spatial neglect: Pathological effects on subjective straight ahead but not visual open-loop pointing. *Neuropsychologia*, *46*(4), 1069–1080.

Serino, A., Angeli, V., Frassinetti, F., & Làdavas, E. (2006). Mechanisms underlying neglect recovery after prism adaptation. *Neuropsychologia*, *44*, 1068–1078.

Serino, A., Bonifazi, S., Pierfederici, L., & Làdavas, E. (2007). Neglect treatment by prism adaptation: What recovers and for how long. *Neuropsychological Rehabilitation*, *17*, 657–687.