Published in final edited form as:

Neuropsychologia. 2014 April ; 56: 418–427. doi:10.1016/j.neuropsychologia.2014.02.012.

Adaptation to Leftward-shifting Prisms Enhances Local Processing in Healthy Individuals

Scott A. Reed and Paul Dassonville

Department of Psychology and Institute of Neuroscience, University of Oregon, Eugene, Oregon, USA

Abstract

In healthy individuals, adaptation to left-shifting prisms has been shown to simulate the symptoms of hemispatial neglect, including a reduction in global processing that approximates the local bias observed in neglect patients. The current study tested whether leftward prism adaptation can more specifically enhance local processing abilities. In three experiments, the impact of local and global processing was assessed through tasks that measure susceptibility to illusions that are known to be driven by local or global contextual effects. Susceptibility to the rod-and-frame illusion – an illusion disproportionately driven by both local and global effects depending on frame size – was measured before and after adaptation to left- and right-shifting prisms. A significant increase in rod-and-frame susceptibility was found for the left-shifting prism group, suggesting that adaptation caused an increase in local processing effects. The results of a second experiment confirmed that leftward prism adaptation enhances local processing, as assessed with susceptibility to the simultaneous-tilt illusion. A final experiment employed a more specific measure of the global effect typically associated with the rod-and-frame illusion, and found that although the global effect was somewhat diminished after leftward prism adaptation, the trend failed to reach significance ($p = .078$). Rightward prism adaptation had no significant effects on performance in any of the experiments. Combined, these findings indicate that leftward prism adaptation in healthy individuals can simulate the local processing bias of neglect patients primarily through an increased sensitivity to local visual cues, and confirm that prism adaptation not only modulates lateral shifts of attention, but also prompts shifts from one level of processing to another.

Keywords

prism adaptation; local processing; global processing; hemispatial neglect; illusions

Address correspondence to: Paul Dassonville, Ph.D., Department of Psychology, 1227 University of Oregon, Eugene, OR 97403, 541–346–4956, prd@uoregon.edu.

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1. Introduction

Hemispacial neglect is a neuropsychological disorder typically resulting from lesions to the right temporo-parietal cortex, and characterized by deficits in attending to stimuli in the hemispace contralateral to the lesion (Vallar & Perani, 1986; Heilman, Watson, & Valenstein, 1985). Neglect patients have also been shown to have a larger-than-normal local processing bias in tasks that pit local and global contextual cues against each other (Delis, Robertson, & Efron, 1986; Robertson, Lamb, & Knight, 1988; Bultitude, Rafal, & List, 2009). For example, a bias toward local or global information can be inferred through performance on tasks which require a response to Navon letter stimuli, in which large letters (i.e., the global form) are composed of smaller letters (i.e., the local form; Navon, 1977). In contrast to the more efficient processing of the global form typically seen in healthy individuals, neglect patients exhibit more efficient (Robertson et al., 1988) and accurate processing (Delis et al., 1986) of the local form. This suggests that the deficits of attentional guidance associated with neglect affect not only lateral shifts of attention, but also shifts from one level of processing to another. The local processing bias demonstrated in neglect patients with right temporo-parietal lesions is also consistent with neuroimaging studies that have shown hemispheric asymmetries in processing local and global visual information. Specifically, left temporo-parietal areas (Robertson & Lamb, 1991) and the left inferior occipital cortex (Fink, Halligan, Marshall, Frith, Frackowiak, & Dolan, 1996; Fink, Halligan, Marshall, Frith, Frackowiak, & Dolan, 1997) have been shown to be preferentially activated in tasks that require visual processing of local information, while right temporo-parietal areas (Robertson & Lamb, 1991) and the right lingual gyrus (Fink et al., 1996; Fink et al., 1997) have been shown to be more involved during tasks that require visual processing of global information. Although severe right hemisphere damage has been demonstrated to cause deficits in both global and local levels of visual processing (Peru & Chelazzi, 2008), neglect cases following right hemisphere damage more typically result in deficits in global processing while local processing is preserved (Delis et al., 1986; Robertson et al., 1988; Bultitude et al., 2009).

Many of the symptoms exhibited by neglect patients can be ameliorated by having the patient adapt to prismatic lenses that displace the visual field to the right (Rode, Klos, Courtois-Jacquín, Rossetti, & Pisella, 2006). For example, reductions in neglect symptoms following rightward prism adaptation have been observed for tasks involving line bisection (Rossetti, Rode, Pisella, Farné, Li, Boisson, & Perenin, 1998; Pisella, Rode, Farné, Boisson, & Rossetti, 2002), shape cancellation (Rossetti et al., 1998; Serino, Bonifazi, Pierfederici, & Ladavas, 2007), body orientation judgments (Gossmann, Kastrup, Kerkhoff, López-Herrero, & Hildebrandt, 2013), visual search (Saevarsson, Kristjánsson, Hildebrandt, & Halsband, 2009), haptic exploration (McIntosh, Rossetti, & Milner, 2002), straight-ahead pointing (Pisella et al., 2002), and attentional disengagement from ipsilesional hemispace (Schindler, McIntosh, Cassidy, Birchall, Benson, Ietswaart, & Milner, 2009). In addition, Bultitude, Rafal, and List (2009) demonstrated that adaptation to rightward-shifting prisms ameliorates the local processing bias of neglect patients. Interestingly, prism adaptation – in this case, adaptation to prismatic lenses that displace the visual field to the left – can also cause healthy individuals to exhibit neglect-like visuospatial and visuomotor effects. For

example, leftward adaptation causes healthy individuals to show a rightward bias in line bisection tasks, similar to the bias seen in neglect patients (Colent, Pisella, Bernieri, Rode, & Rossetti, 2000; Michel, Pisella, Halligan, Luaute, Rode, Boisson, & Rossetti, 2003). Leftward adaptation has also been shown to cause neglect-like biases in haptic exploration (Girardi, McIntosh, Michel, Vallar, & Rossetti, 2004), posture (Michel, Rossetti, Rode, & Tilikete, 2003), spatial remapping (Bultitude, Van der Stigchel, & Nijboer, 2013), and locomotor tasks (Michel, Vernet, Courtine, Ballay, & Pozzo, 2008).

Despite an increasing number of studies that have demonstrated neglect-like effects after leftward prism adaptation in healthy individuals, only one study to date has examined how adaptation affects local and global processing in healthy individuals. Specifically, Bultitude and Woods (2010) measured local and global interference in Navon stimuli (Navon, 1977) in a sample of healthy individuals before and after leftward and rightward adaptation. Prior to adaptation, participants exhibited the typical global advantage in that they were faster to respond to the global form of the Navon stimulus, and experienced greater global interference when responding to the local form than vice-versa. Following adaptation to leftward-shifting prisms, this global advantage was eliminated, primarily through a significant reduction in the magnitude of global interference (a smaller increase in the magnitude of local interference was not significant). These findings would seem to suggest that leftward adaptation simulates the local processing bias of neglect by reducing global processing rather than enhancing local processing abilities. However, such an interpretation of reaction times to Navon stimuli can be problematic, given that the magnitude of the local and global interference effects can each be affected by modulations of global and local processing; for example, global interference can be diminished either due to a decrease in global processing abilities, or through an enhancement of local processing abilities that make them less susceptible to interference from global incongruencies.

The purpose of the current study was to determine whether the local processing bias caused by adaptation to left-shifting prisms in healthy individuals is brought about by enhanced local processing abilities, diminished global processing abilities, or a combination thereof. In three experiments, local and global processing was assessed through tasks that measured susceptibility to illusions that are known to be driven by local or global contextual effects, and therefore provide a more direct measure of sensitivity to local and global visual cues beyond that of reaction time in the Navon task. In the first experiment, we assessed the effects of prism adaptation on susceptibilities to the rod-and-frame illusion, using frame sizes thought to disproportionately modulate the global and local effects. The results of this experiment suggested that leftward adaptation is capable of enhancing local processing, but leaves global processing unaffected. A second experiment confirmed that leftward adaptation enhances local processing, as evidenced by an adaptation-related increase in susceptibility to a simultaneous-tilt illusion. In a final experiment, the effect of adaptation on global processing was further tested by assessing its influence on a sensorimotor task that is selectively sensitive to the global visuovestibular effects that typically underlie the perceptual phenomena associated with the large frame rod-and-frame illusion. In sum, the results of these experiments indicate that adaptation to left-shifting prisms simulates the local processing bias of neglect predominantly through the enhancement of local processing abilities, with very little, if any, accompanying diminishment of global processing abilities.

2. Experiment 1

The rod-and-frame illusion (Fig. 1), in which a tilted frame causes an enclosed line to appear to tilt in the opposite direction (Witkin & Asch, 1948), seems particularly well-suited to assess global and local levels of processing, as the illusion is known to be disproportionately caused by both global and local contextual effects as a function of the size of the surrounding frame. Specifically, when the illusion is driven by a large inducing frame, the tilt of the frame produces a visuovestibular distortion in the observer's frame of reference, such that the perception of vertical is tilted in the same direction as the frame (Ebenholtz & Benzschawel, 1977; Sigman, Goodenough, & Flanagan, 1979; Cian, Esquivie, Barraud, & Raphel, 1995). This global visuovestibular distortion in the observer's frame of reference causes the rod within the frame to appear tilted in the opposite direction (Ebenholtz & Benzschawel, 1977; Spinelli, Antonucci, Goodenough, Pizzamiglio, & Zoccolotti, 1991; Zoccolotti, Antonucci, Goodenough, Pizzamiglio, Spinelli, 1992). In contrast to this global distortion of the observer's egocentric reference, a different mechanism is responsible for a subjectively-similar perceptual phenomenon associated with a small inducing frame. This second mechanism involves low-level orientation contrast effects (Goodenough, Olman, Sigman, Rosso, & Mertz, 1979; Wenderoth & Johnstone, 1987; Cian et al., 1995; Spinelli, Antonucci, Daini, & Zoccolotti, 1995) brought about by the mutual inhibition of neurons that encode the orientations of the rod and the edges of the frame in early visual areas (Blakemore, Carpenter, & Georgeson, 1970; Carpenter & Blakemore, 1973; Spinelli et al., 1995; Poom, 2000; Chen, 2005). Smaller frame sizes tend to produce greater orientation contrast effects due to the increased proximity of the rod and frame (Coren & Hoy, 1986; Zoccolotti, Antonucci, & Spinelli, 1993). It has been suggested that the local orientation contrast effects typically outweigh the global distortions of vertical when the size of the frame has a visual angle of 10° or less (Spinelli et al., 1991), but small contrast effects may still be present for larger frames (Goodenough et al., 1979), and small distortions in perceived vertical may still occur for smaller frames (Gogel & Newton, 1975, Zoccolotti et al., 1993; Cian et al., 1995).

In Experiment 1, we assessed the effects of left- and right-shifting prisms on the magnitude of the rod-and-frame illusion brought about by small and large inducing frames. The effects of prism adaptation were measured and verified with an open-loop pointing task to subjective straight-ahead before and after prism adaptation, and after the final assessment of the rod-and-frame illusion. An increase in illusion susceptibility with small frames would be expected after adaptation if the effect of the adaptation were an enhancement of local processing. A decrease in susceptibility with large frames would be expected if adaptation diminishes global processing. No significant change in rod-and-frame susceptibility is predicted for participants who undergo adaptation to the rightward-shifting prisms, as past research has found that, although rightward adaptation is able to ameliorate many of the symptoms exhibited by neglect patients, its effect on visuospatial performance in healthy individuals is asymmetrically weaker, and in some cases null (Colent et al., 2000).

2.1. Methods

2.1.1. Participants—Forty-one participants (23 males, 18 females) were recruited from the University of Oregon Human Subjects Pool and participated in the experiment in exchange for course credit. All participants had normal or corrected-to-normal vision and had no known neurological deficits. The mean age of the sample was 20 years ($SD = 3.7$). All participants provided informed consent in accordance with the guidelines of the University of Oregon Institutional Review Board.

2.1.2. Rod-and-frame Procedure—Participants were seated with the head stabilized in chin and forehead rests, and the eyes 86 cm from a semi-translucent screen measuring 102 cm by 136 cm (Polacoat Ultra projection screen with a DA-100 diffusion coating, Da-Lite, Warsaw, IN, USA). Stimuli were back-projected (Marquee 8500 projector, with custom-fit HD145 lenses, Electrohome, Niagara Falls, ON, CAN) onto the screen in a darkened room. The rod-and-frame stimuli were red in color and consisted of a circular fixation point (0.5° of visual angle) that was intersected by a rod measuring 6.9° of visual angle in length, with a width of 0.2° (Fig. 1). Surrounding the rod was either a small or large square frame (8.6° or 35.9° on a side, respectively) with a stroke width of 1.0° and a rotational tilt of either -15° (counterclockwise) or 15° (clockwise).

At the onset of each trial, a fixation point appeared at eye level in the center of the screen. After acquiring fixation, participants initiated subsequent events by pressing the space bar on a keyboard. A tilted frame (-15 or 15° from vertical) would then appear on the screen, followed after 200 ms by a tilted rod ($-6, -4, -2, -1, 0, 1, 2, 4$, or 6° from vertical). After an additional delay of 300 ms (i.e., 500 ms after trial onset), all stimuli were extinguished simultaneously. Participants were asked to judge whether the rod was tilted counterclockwise or clockwise, and to indicate the response by pressing either the F or J key, respectively, on the keyboard. There were 10 trials for each combination of frame tilt, frame size, and rod orientation, with 360 trials total. Before the experimental session began, participants were allowed to gain experience in the task without being exposed to the rod-and-frame illusion itself by completing 18 practice trials that lacked the frame.

Perceptual reports for each frame tilt were quantified by fitting a psychometric function to the proportion of “clockwise” responses in order to derive the point of subjective equality (PSE) – the orientation of the rod reported to be rotated clockwise and counterclockwise with equal likelihood – using the equation:

$$\text{proportion “clockwise” responses} = e^{((\text{rodtilt}-\text{PSE})/\tau)} / (1 + e^{((\text{rodtilt}-\text{PSE})/\tau)})$$

where *rodtilt* was the orientation of the rod, *PSE* was the point of subjective equality, and *tau* was the space constant of the psychometric function. Rod-and-frame susceptibility was operationalized as one-half of the difference in the PSEs for the clockwise and counterclockwise frame tilts, with higher values indicating greater susceptibility to the local and global effects that drive the illusions.

2.1.3. Prism Adaptation Apparatus and Procedure—Participants made pointing movements of the hand to three targets while wearing prism glasses (15D Deluxe Prism Training Glasses, Bernell, Mishawaka, IN, USA) that displaced the visual field 15° to the

right (20 participants) or left (21 participants). The three targets (1° diameter) were positioned at arms' length, 30.5 cm above the table's surface, -11° , 0° , and 11° from the participant's midsagittal plane. An opaque black cloth covered most of the distance between the participant's chest and the targets, such that the participant was unable to view the starting position of the hand and limb (see Redding & Wallace, 1997a, for the importance in preventing visual feedback of the starting location during prism adaptation). In addition, the cloth prevented visual feedback of the hand and limb during the pointing movement, except for the final 2.5 cm of the movement (i.e., the tip of the index finger of the outstretched hand). Pointing movements were synchronized with a metronome set to 0.5 Hz to ensure rapid, evenly paced pointing movements. Starting with the dominant hand (as determined by the participant's self-report), participants performed a block of 25 movements to the center target, followed by separate blocks of 25 pointing movements to each of the left, center, right and center targets (5 blocks total). Participants then switched to the nondominant hand and performed a similar series of blocks, then repeated the process again with each hand for a total of 20 blocks. Participants were allowed to rest their arms for 10 seconds after each block, with the adaptation procedure lasting approximately 20 minutes. This extended adaptation procedure, with 250 adaptation trials for both the dominant and nondominant hands, was used to ensure that participants were thoroughly adapted to the prisms.

As a way of assessing the effects of prism adaptation, participants made 10 open-loop pointing movements (i.e., while wearing a blindfold) to subjective straight-ahead immediately before and after adaptation, and then again at the end of the experiment to verify that participants were still adapted to the prisms. Participants pointed using the dominant hand with the index finger extended, and the experimenter recorded the location of the finger on a mounted ruler to the nearest 0.5 cm. The visual angle of the mean pointing error for 10 trials constituted measurement of the subjective straight-ahead.

2.1.5. General Procedure—Participants completed the experimental tasks in the following order: 1) pre-adaptation assessment of rod-and-frame susceptibility, 2) pre-adaptation assessment of subjective straight-ahead, 3) prism adaptation, 4) post-adaptation assessment of subjective straight-ahead, 5) post-adaptation assessment of rod-and-frame susceptibility, and 6) post-task assessment of subjective straight-ahead. The entire session lasted approximately 1 hr.

2.2. Results

2.2.1. Prism Adaptation—Prior to adaptation, no significant difference was found in subjective straight-ahead between the left- and right-shifting prism groups ($t(39) = .52$). A repeated-measures factorial ANOVA was conducted on the reports of subjective straight-ahead, with Prisms (between-subjects variable: left-shifting vs. right-shifting) and Session (within-subjects variable: pre-adaptation, post-adaptation, post-task) factors (Fig. 2). A significant interaction was found between Prisms and Session ($F(2,78) = 30.23$, $p < .001$), and paired-samples t -tests confirmed significant adaptation to the prisms. Specifically, for the left-shifting prism group, subjective straight-ahead was significantly shifted to the right ($t(20) = -2.27$, $p < .05$) from pre-adaptation to post-adaptation, while for the right-shifting prism group it was shifted to the left ($t(19) = 8.10$, $p < .001$). Importantly, no significant

difference was found in subjective straight-ahead between post-adaptation and post-task assessments for either prism group (left-shifting group: $t(20) = .50$; right-shifting group: $t(19) = .51$), indicating that the participants were still adapted to the prisms at the end of the experiment.

2.2.2. Rod-and-frame Susceptibility—The magnitudes of illusion susceptibility in the different experimental conditions are reported in Table 1. Prior to prism adaptation, initial tests across all participants confirmed that the small and large frames were capable of inducing an illusion of rod tilt, with the rod perceived as being tilted in a direction opposite the frame by 2.31° ($SD = 1.55^\circ$; $t(40) = 9.52$, $p < .001$) and 1.47° ($SD = 1.06^\circ$; $t(40) = 8.81$, $p < .001$), respectively. Additionally, prior to adaptation, no significant difference was found in rod-and-frame susceptibility between the left- and rightshifting prism groups for either the small ($t(39) = .92$) or large frames ($t(39) = -.15$).

A $2 \times 2 \times 2$ repeated-measures factorial ANOVA was conducted for Prisms (between-subjects variable: left-shifting vs. right-shifting), Frame Size (within-subjects variable: small vs. large), and Session (within-subjects variable: pre- vs. post-adaptation), with rod-and-frame susceptibility (one-half of the difference in PSE with clockwise- and counterclockwise-tilted frames) as the dependent variable. A significant main effect was found for Frame Size ($F(1,39) = 49.33$, $p < .001$) in that participants were more susceptible to the illusory effects of the small frame ($M = 2.37^\circ$, $SD = 1.37^\circ$) compared to those of the large frame ($M = 1.47^\circ$, $SD = 1.01^\circ$). No other main effects were significant. Among the possible interactions, only a significant effect was found between Prisms and Session ($F(1,39) = 7.42$, $p = .01$). For the left-shifting prism group, a paired-samples t-test demonstrated that overall rod-and-frame susceptibility significantly increased ($t(20) = 2.32$, $p < .05$) from pre-adaptation ($M = 1.79^\circ$, $SD = 1.05^\circ$) to post-adaptation ($M = 2.05^\circ$, $SD = .83^\circ$), while no significant change in susceptibility was found ($t(19) = -1.49$) for the right-shifting group from pre-adaptation ($M = 1.99^\circ$, $SD = 1.43^\circ$) to postadaptation ($M = 1.85^\circ$, $SD = 1.15^\circ$). Although there was a trend for the increase in susceptibility due to leftward adaptation to be larger with small frames (Fig. 3a) than with large frames (Fig. 3b), the three-way interaction between Prisms, Session, and Frame Size was not significant ($F(1,39) = 1.63$, $p = .21$).

2.3. Discussion

Experiment 1 examined the effects of leftward and rightward adaptation on susceptibility to two versions of the rod-and-frame illusion: a large frame version thought to be driven primarily by a global distortion of the observer's egocentric reference frame, and a small frame version primarily driven by local contrast effects brought about by the inhibitory interactions of neurons in early visual processing. Given that previous studies of prism adaptation in healthy individuals have typically shown only leftward adaptation to cause a modulation of the balance between global and local processing (Bultitude & Woods, 2010), it was expected that the same would be true in the present study. Furthermore, if leftward adaptation specifically causes a reduction in the use of global cues (as was suggested by Bultitude & Woods, 2010), it was hypothesized that this would result in a decreased susceptibility to the rod-and-frame illusion, particularly for the large frame version.

Alternatively, if leftward adaptation results in an increased reliance on local cues, it was hypothesized that there would be an increased susceptibility to the illusion, which would be somewhat more prominent for the small frame version. The results of Experiment 1 confirmed that only leftward adaptation resulted in a modulation of rod-and-frame susceptibility. This modulation took the form of an increase in susceptibility, and the somewhat larger effect for the small frame version of the illusion might suggest that the effect was brought about by a heightened sensitivity to the local contrast effects that drive the illusion. However, this modulation by frame size did not reach significance.

Given our prediction that an adaptation-related increase in local processing effects would cause a greater modulation of susceptibility to the illusion for small frames compared to that of large frames, our hypothesis was only partially supported. However, it should be reemphasized that the dissociation between the local and global mechanisms that drive the small and large frame versions of the illusion are not complete. Indeed, previous studies have shown that the mechanisms differ in a graded fashion (Goodenough et al., 1979; Spinelli et al., 1991; Gogel & Newton, 1975; Zoccolotti et al., 1993; Cian et al., 1995). That is, while the effect of large frames is thought to be driven primarily by global distortions of the egocentric reference frame, local contrast effects still play some role (and vice-versa for small frames). If this is the case, an adaptation-related increase in local contrast effects could be expected to magnify the susceptibility to both frame sizes, as was seen in Experiment 1. To avoid this confound between local and global effects, we performed a second experiment that assessed the effects of prism adaptation on susceptibility to an illusion thought to be driven exclusively by local processes.

3. Experiment 2

To confirm that leftward prism adaptation specifically affects local processing, we performed a second experiment to assess the effects on the simultaneous-tilt illusion (Fig. 4), in which the perceived orientation of an inner array of lines is influenced by the orientation of an outer array of tilted lines (Gibson, 1937). This effect is thought to be driven solely by local contrast effects in early visual processing causing a perceptual repulsion of the lines' orientations (Poom, 2000). If adaptation to left-shifted prisms enhances local processing, as suggested by the results of Experiment 1, then susceptibility to the simultaneous-tilt illusion should show a significant increase from pre- to post-adaptation.

3.1. Methods

3.1.1. Participants—Thirty-nine participants (22 males, 17 females) were recruited from the University of Oregon Human Subjects Pool for participation in Experiment 2, and all received course credit for their participation. All participants had normal or corrected-to-normal vision and no known neurological deficits. The mean age of the sample was 21.8 years ($SD = 5.1$). All participants provided informed consent in accordance with the guidelines of the University of Oregon Institutional Review Board.

3.1.2. Simultaneous-tilt Procedure—The equipment used to display the simultaneous-tilt stimuli was identical to that used in Experiment 1. Stimuli (Fig. 4) were red in color and comprised an inner circular grating of parallel bars (8.4° outer diameter, with a square wave

grating of .83 cycles/°) surrounded by an outer annulus of a similar grating (13.2° diameter). The outer grating was tilted either -15 or 15° from vertical, while the inner grating was tilted -4, -3, -2, -1, 0, 1, 2, 3, or 4° from vertical. Participants were instructed to direct their gaze to a fixation point that was present at the beginning of each trial, and to maintain this gaze location throughout the task. After acquiring fixation, participants pressed the spacebar on the keyboard to initiate the trial and trigger the onset of the outer grating. The inner grating appeared 200 ms later and remained on screen for 300 ms, at which point both the inner and outer grating disappeared. After stimulus offset, participants indicated whether the inner grating was rotated counterclockwise or clockwise by pressing either the F or J key, respectively. There were 10 trials for each combination of the 9 possible rod orientations and the 3 tilt conditions of the outer grating (clockwise tilt, counterclockwise tilt, or no outer grating), with 270 trials total. Before the experimental session began, participants were allowed to gain experience in the task without being exposed to the illusion itself by completing 9 practice trials with stimuli that only included the inner grating.

As in Experiment 1, susceptibility to the simultaneous-tilt illusion was quantified as one-half of the difference in the PSEs calculated separately for the clockwise- and counterclockwise-tilted outer gratings. Because the participants' responses for trials with no outer grating provided no information on the susceptibility to the illusion, those responses were not considered further.

3.1.3. Prism Adaptation—The apparatus and procedure for prism adaptation were the same as those used in Experiment 1, with 20 participants adapted to left-shifting prisms and 19 participants to right-shifting prisms.

The effect of adaptation was measured by having participants make 10 open-loop pointing movements to subjective straight-ahead. In order to obtain measurements of prism adaption with greater precision, a real-time motion tracking system (miniBIRD 800, Ascension Technology Corporation, Shelburne, VT, USA) was used to measure the participants' pointing movements with an accuracy of 1.8 mm. Before the first open-loop pointing movement was made, the miniBIRD sensor was placed on the tip of the participant's nose and its location recorded to mark the horizontal reference point for straight ahead (the miniBIRD transmitter was mounted in front of and to the left of the participant, but was obscured from the participant's view). The sensor – small and light enough so as not to systematically affect the pointing movements – was then attached to the tip of the participant's index finger on the dominant hand. After each pointing movement, the participant made a verbal indication of when they believed their index finger was pointing straight ahead (with full extension of the arm), and the experimenter made a keypress to record the location of the sensor. Participants made 10 pointing movements to subjective straight-ahead both before and after adaptation.

3.1.4. General Procedure—Participants completed the experimental tasks in the following order: 1) pre-adaptation assessment of simultaneous-tilt susceptibility, 2) pre-adaptation assessment of subjective straight-ahead, 3) prism adaptation, 4) post-adaptation assessment of subjective straight-ahead, and 5) post-adaptation assessment of simultaneous-

tilt susceptibility. The entire session lasted approximately 1 hr. Given that the magnitude of the sensorimotor after effects of adaptation did not differ in the post-adaptation and post-task assessments in Experiment 1 (demonstrating that these effects lasted beyond the duration of the illusion task, Figure 2), we chose to include only the pre-adaptation and post-adaptation assessments in Experiments 2 and 3, eliminating the post-task assessment.

3.2. Results

3.2.1. Prism Adaptation—Prior to adaptation, no significant difference was found in subjective straight-ahead between the left- and right-shifting prism groups ($t(37) = .19$). A repeated-measures factorial ANOVA was conducted on the reports of subjective straight-ahead, with Prisms (between-Running Head: PRISM ADAPTATION 21 subjects variable: left-shifting vs. right-shifting) and Session (within-subjects variable: pre-adaptation vs. post-adaptation) factors (Fig. 5). A significant interaction was found between Prisms and Session ($F(1,37) = 24.25, p < .001$), and paired-samples t -tests confirmed significant adaptation to the prisms. Specifically, for the left-shifting prism group, subjective straight-ahead was significantly shifted to the right ($t(19) = 4.42, p < .001$) from pre-adaptation to post-adaptation, while for the right-shifting prism group it was shifted to the left ($t(18) = -2.88, p = .01$).

3.2.2. Simultaneous-tilt Susceptibility—The magnitudes of illusion susceptibility in the different experimental conditions are reported in Table 1. Prior to prism adaptation, initial tests across all participants confirmed that the outer array was capable of inducing a perceived tilt of the inner array, with the inner array perceived as being tilted in a direction opposite that of the outer array by $.94^\circ$ ($SD = .53^\circ$; $t(38) = 11.10, p < .001$). In addition, no significant difference in simultaneous-tilt susceptibility was found between the left- and right-shifting prism groups prior to adaptation ($t(37) = .81$).

A 2×2 repeated-measures factorial ANOVA was conducted for Prisms (between-subjects variable: left-shifting vs. right-shifting) and Session (within-subjects variable: pre- vs. post-adaptation), with simultaneous-tilt susceptibility as the dependent variable. No significant main effects were found for Prisms or Session. Importantly, a significant interaction was found between Prisms and Session ($F(1,37) = 4.71, p < .05$). Paired-samples t -tests were used to compare simultaneous-tilt susceptibility pre- to post-adaptation for both left- and right-shifting adaptation groups. A significant increase in susceptibility was found from pre-adaptation to post-adaptation for the left-shifting adaptation group ($t(19) = 2.23, p < .05$). No significant change in susceptibility was found for the right-shifting group ($t(18) = -.73$) from pre-adaptation to post-adaptation. In addition, the magnitude of the change in susceptibility was significantly different across groups ($t(37) = 2.17, p < .05$; Fig. 6), with the left-shifting prism group showing a larger increase in susceptibility from pre- to post-adaptation ($M = .20^\circ, SD = .39^\circ$) compared to the right-shifting prism group ($M = -.06^\circ, SD = .32^\circ$).

3.3. Discussion

The purpose of Experiment 2 was to test whether leftward prism adaptation in healthy individuals can simulate the local processing bias observed in neglect patients by comparing

susceptibility to the simultaneous-tilt illusion, an illusion driven solely by local orientation contrast effects, before and after adaptation. Results from Experiment 2 provide further support that adaptation to left-shifting prisms significantly enhances local processing, with that enhancement reflected in the current results as an increase in simultaneous-tilt susceptibility. As expected, no change in susceptibility was observed in the right-shifting prism group from pre- to post-adaptation.

4. Experiment 3

While the results of Experiments 1 and 2 indicate that leftward prism adaptation increases sensitivity to local cues, it is still possible that leftward adaptation additionally modulates global processing. In Experiment 1, we used a large frame version of the rod-and-frame illusion as a way of isolating possible adaptation effects on global processing, since it is known that the large frame version of the illusion is most strongly driven by global effects. However, previous authors have suggested that even large frames can induce small local contrast effects (Goodenough et al., 1979). It may be, therefore, that adaptation-related changes to the magnitude of the local effects obscured more subtle effects on global processing, with an enhancement of the local effects (as demonstrated in the small frame version of the task) overwhelming a reduction of global effects, resulting in the small increase in large frame susceptibility seen in Experiment 1. Experiment 3 was therefore conducted to more specifically examine whether leftward adaptation modulates global processing independent of local processing, using a behavioral measure that more cleanly isolates the global effects from any possible conflicting influence of local effects.

Unlike the local effects of the rod-and-frame illusion, the global, visuovestibular effects brought about by a tilted frame should exist whether or not a rod is contained within the stimulus. Thus, it should be possible to eliminate the rod from the typical rod-and-frame stimulus and specifically assess the visuovestibular effects of the tilted frame, avoiding any confounding local contrast effects that might otherwise accompany the usual rod-and-frame illusion. In Experiment 3, the tilted frame was accompanied by a fixation point and a large centered circle – since the circle was uniformly round, it would provide no directional information that would distort the visuovestibular effects of the frame (Fig. 7). Participants were asked to make saccadic eye movements to the topmost point of the circle, with the expectation that these movements will be biased in the direction of the frame's rotation, reflecting the distortion of perceived vertical brought about by the frame. Susceptibility to this effect in the *saccade-to-vertical task* was assessed before and after prism adaptation – if leftward adaptation decreases sensitivity to global contextual cues, saccades to the top of the circle should be more accurate after adaptation.

4.1. Methods

4.1.1. Participants—Forty-seven participants (17 males, 29 females) were recruited from the University of Oregon Human Subjects Pool for participation in Experiment 3, and all received course credit or monetary compensation for their participation. All participants had normal or corrected-to-normal vision and no known neurological deficits. The mean age of the sample was 21.4 years ($SD = 5.8$). All participants provided informed consent in accordance with the guidelines of the University of Oregon Institutional Review Board.

4.1.2. Saccade-to-vertical Procedure—The equipment used to display the stimuli was the same as that used in Experiments 1 and 2. In addition, an eye tracker (Eyelink 2000, SR Research, Kanata, ON, CAN) was used to monitor fixation and eye movements. Before testing each participant, the eye tracker was calibrated using a grid of 13 visual targets. After calibration, if the average error in fixation was greater than 1° across the 13 targets, the calibration procedure was repeated.

At the beginning of each trial, a fixation point (0.5° of visual angle), response circle (13.7° in diameter, with a stroke width of 0.1°) and a tilted frame (8.6 or 35.9° on a side, with a stroke width of 1°, and tilted either –15 or 15° from vertical) would appear on screen (Fig. 7). Participants fixated on the central fixation point and used the left thumb to press a button on a game-pad controller to initiate subsequent events. After 500 ms, the fixation point disappeared and a tone sounded to cue participants to make a saccade to the topmost point of the response circle. A button press (the same button used to initiate the trial) then triggered the recording of the location of the eye and terminated the trial. Participants completed 44 trials total (11 trials for each combination of frame size and tilt), and trials were aborted and rerun later in the experiment if participants looked away from the fixation point before initiating the trial. In order to gain familiarity with the task, participants first completed 8 practice trials consisting of only the fixation point and outer circle (no frame present).

Performance on each trial in the saccade-to-vertical task was operationalized by calculating the angle of rotation of a vector plotted from the fixation point to the final eye position. Mean rotational errors were calculated (after normalizing for the direction of the frame tilt) to derive a measure of global sensitivity, with greater values indicating larger errors in perceived vertical and, thus, greater susceptibility to the frame.

4.1.3. Prism Adaptation—The apparatus and procedure for prism adaptation were the same as those used in Experiments 1 and 2, with 24 participants adapted to left-shifting prisms and 23 participants to right-shifting prisms. The apparatus and procedures for assessing subjective straight-ahead were identical to those of Experiment 2.

4.1.4. General Procedure—Participants completed the experimental tasks in the following order: 1) pre-adaptation saccade-to-vertical task, 2) pre-adaptation assessment of subjective straight-ahead, 3) prism adaptation, 4) post-adaptation assessment of subjective straight-ahead, and 5) post-adaptation saccade-to-vertical task. The entire session lasted approximately 1 hr. Data from two participants (one from each prism group) were excluded from the analyses due to extreme errors in their reports of subjective straight-ahead (15.32 and 22.32°) in the pre-adaptation session; however, including their data in the analysis of the saccade-to-vertical task had no effect on the general pattern of findings reported below.

4.2. Results

4.2.1. Prism Adaptation—Prior to prism adaptation, no significant difference was found in subjective straight-ahead between the left- and right-shifting prism groups ($t(43) = 1.82$). A repeated-measures factorial ANOVA was conducted on the reports of subjective straight-ahead, with Prisms (between-subjects variable: left-shifting vs. right-shifting) and Session (within-subjects variable: pre-adaptation vs. post-adaptation) factors (Fig. 8). A significant

interaction was found between Prisms and Session ($F(1,43) = 60.06, p < .001$), and paired-samples t -tests confirmed significant adaptation to the prisms. Specifically, for the left-shifting prism group, subjective straight-ahead was significantly shifted to the right ($t(22) = 3.45, p < .01$) from pre-adaptation to post-adaptation, while for the right-shifting prism group it was shifted to the left ($t(21) = -6.99, p < .001$).

4.2.2. Saccade-to-vertical Performance—The magnitudes of distortion of perceived vertical in the different experimental conditions are reported in Table 1. Prior to prism adaptation, initial tests across all participants confirmed that the small and large frames were capable of inducing a distortion of perceived vertical, with reports of the topmost point of the response circle biased in the direction of frame tilt by 1.14° ($SD = 1.12^\circ; t(44) = 6.85, p < .001$) and 1.20° ($SD = 1.47^\circ; t(44) = 5.49, p < .001$), respectively. In addition, prior to adaptation, the left-shifting and right-shifting prism groups did not significantly differ in the magnitude of the distortion of perceived vertical for either small ($t(43) = 1.45$) or large frames ($t(43) = -1.54$).

A $2 \times 2 \times 2$ repeated-measures factorial ANOVA was conducted for Prisms (between-subjects variable: left-shifting vs. right-shifting), Frame Size (within-subjects variable: small vs. large) and Session (within-subjects variable: pre- vs. post-adaptation), with saccade-to-vertical performance (mean error in angular degrees) as the dependent variable. No significant interaction was found between Prisms and Session ($F(1,43) = .95$), and no other main effects or interactions were found to be significant. To confirm the null effects, paired-samples t -tests were used to compare the mean error (in angular degrees) in perceived vertical from pre- to post-adaptation for each prism group. For small frames, no significant change in perceived vertical was found in either left-shifting ($t(22) = .76$) or right-shifting ($t(21) = .60$) adaptation groups from pre- to post-adaptation (Fig. 9a). For large frames, a trend was found for the left-shifting adaptation group in that errors in perceived vertical decreased from pre- to post-adaptation, suggesting a decreased susceptibility to the large frame, but this trend failed to reach significance ($t(22) = -1.85, p = .078$; Fig. 9b). No significant change in perceived vertical was found for the right-shifting adaptation group for large frames ($t(21) = -.36$). In addition, the magnitude of the change in perceived vertical from pre- to post-adaptation did not significantly differ between left-shifting and right-shifting prism groups for small frames ($t(43) = -.032$) or large frames ($t(43) = 1.05$).

4.3. Discussion

The purpose of Experiment 3 was to examine whether prism adaptation modulates global processing mechanisms independent of local processing. The saccade-to-vertical task was devised to isolate the global visuovestibular effects of the rod-and-frame illusion – the elimination of the rod as part of the stimulus, and the change from the typical categorical judgment of perceived rod orientation to a sensorimotor response that directly indicates perceived vertical, ensured that the visuovestibular effect would not be confounded with the local contrast effect also associated with the typical rod-and-frame paradigm. Prior to adaptation, saccadic eye movements to the topmost point of the response circle were significantly biased in the direction of the tilted frame, demonstrating that the saccade-to-

vertical task is capable of providing a sensitive measure of the global visuovestibular effects of the frame.

In spite of the sensitivity of the saccade-to-vertical task, we were unable to detect any significant effects of prism adaptation on the magnitude of the visuovestibular effect of the frame, indicating that neither leftward nor rightward adaptation is capable of modulating the global component of the rod-and-frame illusion. This seems at odds with the findings of Bultitude and Woods (2010), who found that global interference in the Navon task was significantly diminished after leftward adaptation in healthy participants. However, this may be more of an apparent difference, rather than a real one. First, it may be that although our analysis of the saccade-to-vertical data had sufficient power to detect the global visuovestibular effect of the tilted frame, the analysis may have been too underpowered to detect more subtle adaptation-related modulations of the effect. (In relation to this point, it should be noted that leftward adaptation in the current study was associated with a decrease in susceptibility to the effects of the large frame in Experiment 3, but this change was of only marginal significance.) Second, it is possible that these differences in the effects of adaptation on global processing are due to real differences in the types of global mechanisms that underlie the rod-and-frame illusion and interference effects in Navon stimuli. Further research is therefore needed to clarify the modulatory effects of prism adaptation on global processing in both healthy and clinical samples.

5. General Discussion

Adaptation to left-shifting prisms in healthy individuals has been shown to simulate many of the perceptual and sensorimotor symptoms of hemispatial neglect (for a review, see Michel, 2006). Bultitude and Woods (2010) found that leftward adaptation in healthy individuals approximated the local processing bias observed in hemispatial neglect patients, but this was due primarily to a decrease in global processing, with only a nonsignificant trend of an enhancement in local processing. In contrast, the current study provided a clear demonstration that leftward adaptation in healthy individuals can enhance local processing, as reflected in an increase in susceptibility to two illusions (the small frame rod-and-frame illusion and the simultaneous-tilt illusion) known to be driven by local orientation contrast effects associated with the contextual elements within the display (the frame and surrounding array, respectively). In both illusions, susceptibility has been proposed to be driven by lateral inhibition among orientation-selective neurons in primary visual cortex (Blakemore, et al., 1970; Carpenter & Blakemore, 1973; Poom, 2000; Chen, 2005). The current findings indicate that these low-level neural processes are susceptible to an adaptation-related modulation.

One possible mechanism by which prism adaptation could affect low-level processing in primary visual cortex is through feedback from higher-level cortical areas, in the form of attentional effects. Indeed, it has been suggested that prism adaptation can alter the balance in activation across the left and right hemispheres, and more specifically across the left and right parietal lobes, with concomitant changes in attentional processing (e.g., Michel, 2006). For instance, an attentional bias in the visual field contralateral to the predominant hemisphere that is active (Kinsbourne, 1970) may shift back toward ipsilateral space

following adaptation-induced activations. Within neglect patients, adaptation to right-shifting prisms would allow for a correction of the imbalance between the hemispheres brought about by the lesion, shifting activation back to the remaining healthy tissue in the right hemisphere and allowing for a diminishment of the neglect symptoms. In healthy individuals, leftward adaptation would shift the balance away from the right hemisphere and toward the left, bringing about the alterations of attention that simulate neglect. Other experimental paradigms can also cause a similar rebalancing. For example, the use of transcranial magnetic stimulation to disrupt neural processing in left parietal cortex can diminish neglect symptoms in patients with right hemisphere lesions (Brighina, et al., 2003; Oliveri, et al., 2001), while stimulation of left parietal cortex can cause neglect-like effects in healthy individuals (Brighina, et al., 2002; Fierro, et al., 2000; Fierro, Brighina, Piazza, Oliveri, & Bisiach, 2001). Similarly, merely making repeated pointing movements to the right half of space (without prisms) can mimic various effects of neglect (Dupierrix, Alleysson, Ohlmann, & Chokron, 2008; Dupierrix, Gresty, Ohlmann, & Chokron, 2009), including a decrease in global interference in the Navon task (Herlihey, Black, & Ferber, 2013). Given the evidence that the right and left hemispheres are specialized for the processing of global and local information, respectively (Fink et al., 1996; Fink et al., 1997; Delis, et al., 1986; Robertson & Lamb, 1991; Robertson et al., 1988), it would not be surprising that a shift in the balance of activation between the hemispheres would have an impact on the relative proportion of global and local processing in a given task.

Assuming that prism adaptation is capable of modulating attention, are there mechanisms by which attentional effects could, in turn, alter the low-level mechanisms that drive the local contrast effects associated with the simultaneous-tilt and rod-and-frame illusions? Several studies have demonstrated that attention modulates the activation of neurons in primary visual cortex (Gandhi, Heeger, & Boynton, 1999; Serences, Saproo, Scolari, Ho, & Muftuler, 2009). Even more specifically, attention has been shown to modulate the effects of contextual information contained within stimulus elements lying outside of the classical receptive fields of these neurons (Freeman, Sagi, & Driver, 2001; Ito & Gilbert, 1999; Roelfsema, Lamme, & Spekreijse, 1998; Wannig, Stanisior, & Roelfsema, 2011). Similar attentional mechanisms may be involved in the modulation of susceptibility to the local contrast effects that underlie the small frame rod-and-frame and simultaneous-tilt illusions.

In conclusion, the results of the current study demonstrate that leftward adaptation in healthy individuals increases susceptibility to a subset of visual illusions known to be driven by local contextual processing, and that leftward adaptation has only a marginal effect, if any, in reducing global processing. This suggests that leftward adaptation simulates the local processing bias of neglect patients primarily by increasing susceptibility to local cues. Finally, these results confirm that leftward adaptation not only affects lateral shifts of visuospatial attention (Colent et al., 2000; Michel et al., 2003) and locomotor biases (Michel et al., 2008), but also shifts from one level of processing to another.

Acknowledgments

This research was supported by the National Institute of Health (NIH)/Institute of Neuroscience Systems Physiology Training Program Grant (#5 T32 GM007257-33).

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Highlights

- ◆ Assessed local and global processing after prism adaptation in healthy individuals.
- ◆ Leftward adaptation enhances the local effects that drive illusion susceptibility.
- ◆ Leftward adaptation has only a marginal effect on susceptibility to global cues.
- ◆ Adaptation-related enhancement of local processing simulates local bias of neglect.

Figure 1.

The large and small frame versions of the rod-and-frame stimuli in Experiment 1, drawn to scale. Only the counterclockwise frame condition is shown, with a vertically-oriented rod. Typically, the tilted frame causes the rod to appear tilted in the opposite direction.

Figure 2.

Mean errors in subjective straight-ahead (SSA) measured before adaptation (pre-adaption), after adaptation (post-adaptation), and after the completion of the final rod-and-frame assessment (post-task) for the left- and right-shifting prism groups in Experiment 1. Positive values on the y-axis indicate rightward errors; negative values indicate leftward errors. In all figures, error bars indicate ± 1 SEM.

Figure 3.

a. Change in rod-and-frame susceptibility for the small inducing frame from pre to post-adaptation for the left- and right-shifting prism groups in Experiment 1. **b.** Change in susceptibility for the large inducing frame.

Figure 4.

The simultaneous-tilt stimulus used in Experiment 2, drawn to scale. Only the counterclockwise-tilted condition is shown, with a vertically-oriented central array. Typically, the tilted array in the annulus causes the central array to appear tilted in the opposite direction.

Figure 5. Mean errors in subjective straight-ahead (SSA) measured before (preadaption) and after (post-adaptation) prism adaptation for the left- and right-shifting prism groups in Experiment 2.

Figure 6.

The change in simultaneous-tilt susceptibility from pre- to post-adaptation for the left- and right-shifting prism groups in Experiment 2.

Figure 7.

The large and small frame versions of the saccade-to-vertical task of Experiment 3, drawn to scale. Only the counterclockwise-tilted condition is shown. Participants were asked to make saccadic eye movements from the central fixation point to the topmost point of the response circle. Global distortions of the perception of vertical should be reflected as a bias in the reported location of the circle's topmost point.

Figure 8. Mean errors in subjective straight-ahead (SSA) measured before (pre-adaptation) and after (post-adaptation) prism adaptation for the left- and right-shifting prism groups in Experiment 3.

Figure 9.

a. Change in small frame saccade-to-vertical performance (i.e., mean error in angular degrees) from pre- to post-adaptation for the left- and right-shifting prism groups in Experiment 3. **b.** Change in large frame saccade-to-vertical performance.

Table 1

Mean susceptibilities (and standard deviations) to the rod-and-frame illusion (Experiment 1), simultaneous-tilt illusion (Experiment 2), and saccade-to-vertical task (Experiment 3).

Prism Group	Rod-and-Frame		Simultaneous-Tilt		Saccade-to-Vertical	
	Small frame	Large frame	Small frame	Large frame	Small frame	Large frame
Left-shifting						
Pre-adaptation	2.09° (1.24°)	1.49° (0.98°)	1.01° (0.49°)		0.90° (1.03°)	1.53° (1.49°)
Post-adaptation	2.47° (0.91°)	1.63° (0.88°)	1.20° (0.49°)		1.06° (0.92°)	1.01° (1.22°)
Right-shifting						
Pre-adaptation	2.54° (1.84°)	1.44° (1.17°)	0.87° (0.57°)		1.38° (1.03°)	0.86° (1.40°)
Post-adaptation	2.39° (1.43°)	1.31° (1.01°)	0.81° (0.51°)		1.53° (1.07°)	0.76° (1.12°)