Research Article

Prismatic Lenses Shift Time Perception

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ABSTRACT—Previous studies have demonstrated the involvement of spatial codes in the representation of time and numbers. We took advantage of a well-known spatial modulation (prismatic adaptation) to test the hypothesis that the representation of time is spatially oriented from left to right, with smaller time intervals being represented to the left of larger time intervals. Healthy subjects performed a time-reproduction task and a time-bisection task, before and after leftward and rightward prismatic adaptation. Results showed that prismatic adaptation inducing a rightward orientation of spatial attention produced an overestimation of time intervals, whereas prismatic adaptation inducing a leftward shift of spatial attention produced an underestimation of time intervals. These findings not only confirm that temporal intervals are represented as horizontally arranged in space, but also reveal that spatial modulation of time processing most likely occurs via cuing of spatial attention, and that spatial attention can influence the spatial coding of quantity in different dimensions.

The involvement of spatial codes in the representation of ordered material has been supported by the finding that numbers are represented analogically according to their magnitude along a left-to-right mental number line (Dehaene, 2003; Ishihara et al., 2006), as well as by the functional links between spatial attention and time perception (Basso, Nichelli, Frassinetti, & di Pellegrino, 1996; Danckert et al., 2007) and between time perception and numbers (Vicario et al., 2008). However, the cognitive and neural mechanisms underlying such interactions are still obscure. A theory of magnitude (Walsh, 2003) has suggested that common cognitive processing underlies the quantitative coding of space and time. We investigated whether

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spatial attention may functionally link these two dimensions. Neuropsychological studies in patients (Basso et al., 1996; Danckert et al., 2007) and psychophysical studies in healthy subjects (Chen & O'Neill, 2001; Mattes & Ulrich, 1998) have found a link between attention and time perception. However, other studies cast doubts on the role of attention in spatially dependent temporal illusions (Johnston, Arnold, & Nishida, 2006; Morrone, Rossi, & Burr, 2005). We tested whether spatialattention shifts, created through prismatic adaptation (PA), induce relative compression and expansion of experiential time. More specifically, our hypothesis was that PA inducing a rightward orientation of spatial attention would produce an overestimation of time intervals, whereas PA inducing a leftward shift of spatial attention would produce an underestimation of time intervals. Indeed, several studies have found that PA ameliorates visuospatial deficits in neglect (Rossetti et al., 1998), most likely through reorienting of spatial attention (Striemer & Danckert, 2007).

EXPERIMENT 1

Method

Participants and Tasks

Twelve right-handed, healthy subjects (6 men, 6 women; age range: 19–34 years) who were totally naive as to the purpose of the study participated. They had no history of neurological diseases. All subjects gave their informed consent for participation in the study.

Subjects sat facing a Macintosh computer, at a distance of 60 cm, with their right hand on the space bar of the keyboard. The visual stimuli were little squares ($1 \text{ cm} \times 1 \text{ cm}$) presented at the center of the computer screen. A blue square was presented for a variable time interval: 1,600 ms, 1,800 ms, 2,000 ms, 2,200 ms, or 2,400 ms. Next, a red square appeared on the screen and remained visible for as long as subjects pressed the space bar on the keyboard. The task was to reproduce the entire duration of the preceding blue square (time-reproduction task) or half the

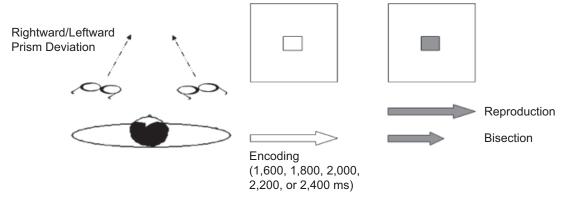


Fig. 1. Experimental procedure. Subjects performed a time-reproduction task and a time-bisection task (represented on the right), before and after leftward and rightward prismatic adaptation (PA; represented on the left). During PA, subjects performed a pointing task while wearing prismatic lenses that induced a shift of the visual field to the right or to the left. The time task was articulated in two steps: In the first step (encoding), subjects were asked to study the duration of a visual stimulus (shown here as a white square), presented for a variable time interval; in the second step, a new stimulus was presented (shown here as a gray square), and subjects were required to reproduce the entire duration (time-reproduction task) or half the duration (time-bisection task) of the previous stimulus.

duration of that square (time-bisection task; see Fig. 1). No accuracy feedback was given. All subjects used their right index finger to respond.

For each task, 50 trials (10 for each time interval) were presented in random order. Subjects performed each task twice in a single session, once before and once after PA. The task order was counterbalanced across subjects. Before starting the experimental session, subjects were allowed to practice (100 trials) both tasks.

PA Procedure

During PA, subjects were seated at a table in front of a box (height = 30 cm, depth = 34 cm at the center and 18 cm at the periphery, width = 72 cm) that was open on the side facing the subjects and on the opposite side, facing the experimenter. The experimenter placed a visual target (a pen) at the distal edge of the top surface of the box, in one of three possible positions (randomly determined on each trial): a central position (0°), 21° to the left of center, and 21° to the right of center. Subjects were asked to keep their right hand at the level of the sternum and to point toward the pen using the index finger of the same hand; the experimenter recorded the end position of the subject's pointing direction. The pointing task was performed in three experimental conditions: preexposure, exposure, and postexposure.

In the *preexposure condition*, subjects performed two types of trials (total of 60 trials). On half of the trials, their pointing was visible to them (as in the exposure condition), and on the other half, they could not see their pointing (as in the postexposure condition). In the *exposure condition*, subjects performed the task while wearing prismatic lenses that induced a 10° shift of the visual field to the right or to the left (90 trials). Subjects could see the last third of the trajectory of their arm (i.e., visible pointing). In the *postexposure condition*, immediately after removal of the prism, subjects were required to make their pointing movements underneath the top surface of the box so that the index finger was not visible at any stage (i.e., invisible pointing; 30 trials).

Results

For each subject, we subtracted the reproduced time intervals before PA from the reproduced time intervals after PA. Thus, this difference was positive when reproduced time was longer after than before PA (underestimation of time duration) and negative when reproduced time was shorter after than before PA (overestimation of time duration). Subjects were divided into two groups depending on the direction of the prism-induced aftereffect (i.e., leftward aftereffect induced by rightward PA, rightward aftereffect induced by leftward PA). A separate analysis of variance (ANOVA) on the difference between pre-PA and post-PA reproduced time was conducted for each task (time bisection and time reproduction), with group as a between-subjects variable and time interval as a within-subjects variable.

A significant effect of prism-induced directional shift was found in the time-bisection task, in which subjects were required to reproduce half the duration of a previously presented visual stimulus. The underestimation of time duration induced by the leftward aftereffect ($M=79\,\mathrm{ms}$) was significantly different from the overestimation of time duration induced by the rightward aftereffect ($M=-59\,\mathrm{ms}$), $F(1,10)=7.11, p_\mathrm{rep}>.93, \,\eta_p^2=.416$ (Fig. 2a). In addition, in the group with the leftward induced aftereffect, underestimation of time duration was greater for medium time intervals (900–1,100 ms) than for shorter (800 ms) and longer (1,200 ms) time intervals ($p_\mathrm{rep}>.88$; see Fig. 2a). This effect likely reflects a range of higher sensitivity to prism-induced shifts, $F(4,40)=3.5,\,p_\mathrm{rep}>.94,\,\eta_p^2=.261.$

The prismatic manipulation of spatial attention also affected performance on the time-reproduction task, in which subjects were required to reproduce the entire duration of a previously presented visual stimulus. The underestimation of time duration induced by the leftward aftereffect ($M=113~{\rm ms}$) was significantly different from the overestimation of time duration

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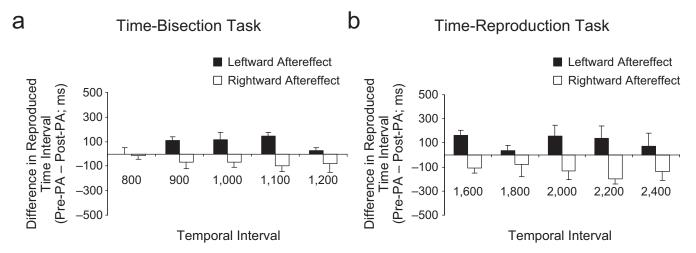


Fig. 2. Effect of prismatic adaptation (PA) on time perception in Experiment 1. The graphs show the mean difference between reproduced time intervals before PA and reproduced time intervals after PA as a function of time interval and direction of the induced aftereffect (right or left). Positive values indicate underestimation of time intervals, and negative values indicate overestimation. Error bars represent standard errors of the means. Results are shown separately for the (a) time-bisection and (b) time-reproduction tasks.

induced by the rightward aftereffect (M = -131 ms), F(1, 10) = 7.96, $p_{\text{rep}} > .93$, $\eta_p^2 = .444$ (Fig. 2b).

We ensured that the pre-PA/post-PA differences in time processing were due to the PA procedure by assessing the presence of both *error reduction* and *aftereffect*. To verify whether subjects showed an error reduction as they adapted to the prisms, we conducted an ANOVA on the mean displacement (expressed as degrees of visual angle) of subjects' visible pointing, with group (leftward aftereffect, rightward aftereffect) as a between-subjects variable and condition (preexposure condition, first three trials of the exposure condition, last three trials of the exposure condition) as a within-subjects variable (more details on this procedure can be found in Frassinetti, Angeli, Meneghello, Avanzi, & Làdavas, 2002). Post hoc com-

parisons were conducted using the Newman-Keuls test. The interaction between group and condition was significant, $F(2, 20) = 11.1, p_{\rm rep} > .99, \, \eta_p^{\ 2} = .526;$ pointing displacement was significantly greater in the first three trials of the exposure condition than in the preexposure condition (leftward aftereffect: $p_{\rm rep} > .88$; rightward aftereffect: $p_{\rm rep} > .98$), but was not significantly different between the last three trials of the exposure condition and the preexposure condition (i.e., subjects exhibited error reduction; leftward aftereffect: $p_{\rm rep} > .32$; rightward aftereffect: $p_{\rm rep} > .36$; Fig. 3a).

To verify the presence of an aftereffect, we compared subjects' displacement during invisible pointing in the preexposure and postexposure conditions. An ANOVA on the mean displacement of invisible pointing responses was carried out with group

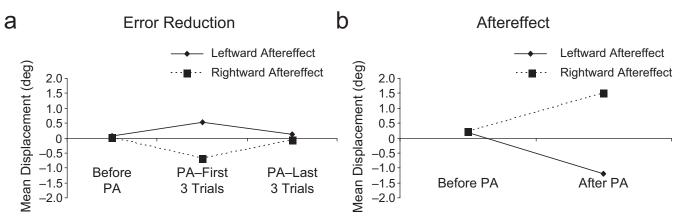


Fig. 3. Mean displacement (in degrees of visual angle) of pointing responses in subjects with a leftward aftereffect and subjects with a rightward aftereffect (induced by rightward and leftward prism adaptation, respectively). Results demonstrating error reduction are shown in (a), which presents mean displacement of subjects' visible pointing before prismatic adaptation (PA) and in the first three and last three trials during PA. Results demonstrating aftereffects of PA are shown in (b), which presents mean displacement of subjects' invisible pointing before and after PA. Negative values indicate a leftward pointing displacement with respect to the target's actual location, and positive values indicate a rightward pointing displacement.

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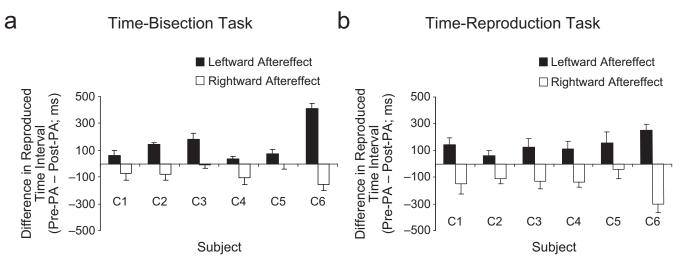


Fig. 4. Effect of prismatic adaptation (PA) on time perception in Experiment 2. The graphs show the mean difference between reproduced time intervals before PA and reproduced time intervals after PA for each subject (C1–C6) after induction of a leftward aftereffect and induction of a rightward aftereffect. Positive values indicate underestimation of time intervals, and negative values indicate overestimation. Error bars represent standard errors of the means. Results are shown separately for the (a) time-bisection and (b) time-reproduction tasks.

(leftward aftereffect, rightward aftereffect) as a between-subjects variable and condition (preexposure, postexposure) as a within-subjects variable. The interaction between group and condition was significant, F(1, 10) = 163.9, $p_{\rm rep} > .99$, $\eta_p^2 = .393$; as expected, the leftward-aftereffect and rightward-aftereffect groups showed significant leftward and rightward deviations, respectively, in the postexposure condition relative to the preexposure condition ($p_{\rm rep}s > .99$; Fig. 3b).

Finally, to assess whether the prism-dependent error reduction or aftereffect influenced time perception, we conducted a separate Pearson correlation analysis for each task. Significant negative correlations were found between error reduction in pointing and the effect of PA on subjects' performance in the time-bisection task ($r = -.67, p_{rep} > .93$) and the time-reproduction task (r = -.76, $p_{rep} > .98$). This means that as the pointing displacement in the last three trials of the exposure condition decreased, the magnitude of the effect of PA on performance in both temporal tasks increased. Similarly, positive correlations were found between aftereffect and the PA effect on subjects' performance in the time-bisection task ($r = .59, p_{rep} >$.89) and the time-reproduction task ($r = .54, p_{rep} > .85$). This means that larger pointing displacements in the postexposure condition (i.e., bigger aftereffect) were accompanied by larger effects of PA on time perception, in both tasks.

EXPERIMENT 2

Method

Six right-handed, healthy subjects (3 men, 3 women; age range: 18–35 years) who did not take part in the previous experiment performed the time-reproduction and time-bisection tasks before and after both rightward and leftward PA. Order of the tasks and order of the direction of prismatic deviation were counterbalanced across subjects. Subjects were examined in two sessions. In the first session, they performed the tasks before PA (baseline), underwent the PA procedure, and then performed the tasks again. After 1 week, in the second session, subjects underwent the same procedure, but with prisms inducing the deviation opposite to that induced in the first session.

Results

For each task, we analyzed the differences in reproduced time (post-PA minus pre-PA) in an ANOVA with direction of aftereffect (left, right) and time interval as within-subjects variables. In the time-bisection task, direction of aftereffect had a significant main effect, F(1, 5) = 9.63, $p_{\rm rep} > .91$, $\eta_p^2 = .659$: leftward aftereffect induced an underestimation (M = 153 ms) of time duration that was significantly different from the overestimation (M = -71 ms) of time duration induced by rightward aftereffect (all subjects showed the effect; see Fig. 4a). In the time-reproduction task, direction of aftereffect also had a significant effect, F(1,5) = 25.5, $p_{\rm rep} > .98$, $\eta_p^2 = .837$: leftward aftereffect induced an underestimation (M = 141 ms) of time duration that was significantly different from the overestimation (M = -144 ms) of time duration induced by rightward aftereffect (all subjects showed the effect; see Fig. 4b). The effect of

¹Error reduction was measured using pointing displacement in the last three trials in the exposure condition, and the aftereffect was calculated from pointing displacement in the postexposure condition. The effect of PA on time perception was measured for each task as the difference between performance after PA and performance before PA; the bigger the difference, the stronger the effect of prism exposure on time perception.

time interval and its interaction with the direction of aftereffect were not significant for either task.

To verify that subjects showed an error reduction, we conducted an ANOVA with direction of aftereffect (left, right) and condition (preexposure condition, first three trials of the exposure condition, last three trials of the exposure condition) as within-subjects variables. This analysis revealed a significant pointing deviation, relative to the preexposure condition, in the first three trials of the exposure condition ($p_{\rm rep} > .89$ for both leftward and rightward aftereffect), but not in the last three trials of the exposure condition ($p_{\rm rep} > .81$ for both leftward and rightward effect), F(2, 10) = 17.92, $p_{\rm rep} > .99$, $\eta_p^2 = .782$. Thus, subjects exhibited error reduction.

To verify the presence of an aftereffect, we conducted an ANOVA on displacement in invisible pointing in the preexposure and postexposure conditions. This analysis showed significant leftward deviation (in the leftward-aftereffect condition) and rightward deviation (in the rightward-aftereffect condition) in the postexposure condition, relative to the preexposure condition ($p_{\rm rep}$ > .99), F(1, 5) = 198.6, $p_{\rm rep}$ > .99, $\eta_p^2 = .975$.

Finally, a positive correlation was found between aftereffect and the effect of PA on subjects' performance in the time-bi-section task ($r = .65, p_{\rm rep} > .98$) and the time-reproduction task ($r = .75, p_{\rm rep} > .99$).²

DISCUSSION

The main finding of this study is that altering spatial attention via PA induces a modification of time processing. Subjects' time processing before PA differed from their time processing after PA, and the directional bias observed after PA depended on the direction of the prismatic deviation. Indeed, leftward and rightward prism deviation induced opposite effects on both time-processing tasks: After rightward optical deviation (inducing a leftward aftereffect), subjects showed a significant underestimation of time duration (relative to before PA), whereas after leftward optical deviation (inducing a rightward aftereffect), they showed a significant overestimation of time duration.

Also supporting the notion of a link between PA and temporal processing are the significant correlations between the effect of PA on subjects' performance on the time-reproduction and time-bisection tasks and the parameters indexing the effectiveness of the PA (error reduction and aftereffect). The effect of PA on time perception correlated negatively with error reduction during PA and positively with aftereffect.

These results were highly consistent across the two experiments, one following a between-subjects experimental design (Experiment 1) and the other using a within-subjects experimental design (Experiment 2). Moreover, the effects of PA were generally the same for all time intervals. These results do not contradict the hypothesis that short durations are represented toward the left and long durations toward the right, but simply indicate that sensitivity to prism-induced (left or right) shifts was similar for all time intervals considered in this study. The consistency of this result further supports the conclusion that attention shifts are linked to changes in the durations of experiential time.

Evidence for a link between spatial attention and time perception comes from studies of both patients and healthy subjects. Recent investigations have demonstrated that patients who exhibit a deficit in orienting attention in space (i.e., neglect patients) may also be impaired in orienting attention in time (Barberovic, Pisella, Morris, & Mattingley, 2004; Basso et al., 1996; Baylis, Simon, Baylis, & Rorden, 2002; Husain, Shapiro, Martin, & Kennard, 1997). For example, Basso et al. (1996) found that visual spatial neglect can cause overestimation of stimulus duration at a neglected location. Also, in healthy participants, a modification of temporal processing is obtained following manipulation of spatial attention (Mattes & Ulrich, 1998). Mattes and Ulrich found that subjects reproduced longer duration in an attended than in an unattended location (see also Chen & O'Neill, 2001; Enns, Brehaut, & Shore, 1999). Vicario, Caltagirone, and Oliveri (2007) reported opposing biases of temporal estimation following rightward and leftward optokinetic stimulation. Here we have shown that time processing can be directly affected by altering spatial-attention processing via PA, thus demonstrating that PA induces a shift of spatial attention that can modify the processing of the time duration of visual stimuli: Shifting spatial attention to the left induces time underestimation, whereas shifting spatial attention to the right induces time overestimation. This finding clearly supports the existence of a functional interaction between spatial attention and temporal processing systems.

A further point deserving discussion concerns the link between PA and spatial attention. Although numerous clinical studies have found that PA induces an amelioration of a visual spatial deficit (i.e., neglect; Farnè, Rossetti, Toniolo, & Làdavas, 2002; Frassinetti et al., 2002), few experiments have explicitly addressed the question of whether adaptation affects the bias in spatial attention that is at the core of neglect (Striemer & Danckert, 2007). Previous investigations have examined the effects of PA on spatial attention in patients, with partially conflicting outcomes. Maravita et al. (2003) showed that visual and tactile extinction were reduced following adaptation to rightward prisms, whereas Morris et al. (2004) found no effect of adaptation on the pathological spatial gradient of visual search times in right-brain-damaged patients. The present results add to this previous evidence, providing convergent support for the notion that PA induces shifts of spatial attention.

In conclusion, these findings show that altering spatial attention via PA induces a modification of time processing;

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²In Experiment 2, we did not calculate correlations between error reduction and the effects of PA on subjects' performance on the time-bisection and time-reproduction tasks because error reduction was almost perfect and values were nearly zero.

whether the effect is temporal expansion or temporal compression depends on the direction of the aftereffect induced by the prismatic deviation. We have demonstrated that spatial attention can be the matrix linking time and space in a "generalized magnitude system." Moreover, our results provide definitive evidence that PA shifts spatial attention in the direction of the aftereffect. Finally, these findings expand the notion that temporal processing has a spatial representation extending from left (short time intervals) to right (long time intervals) by additionally showing how such a spatial code for time can be modulated. Further studies will clarify the anatomical bases of these effects, as well as whether the reported temporal shifts are retinotopic or spatiotopic (Burr, Tozzi, & Morrone, 2007), and whether they affect the judged duration of the standard (encoding) or the motor output (reproduction).

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