Neuropsychologia 53 (2014) 165–170

Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Prism adaptation in the healthy brain: The shift in line bisection judgments is long lasting and fluctuates

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A R T I C L E I N F O

Article history:
Received 23 September 2013
Received in revised form
30 October 2013
Accepted 20 November 2013
Available online 28 November 2013

Keywords:
Line bisection
Prism adaptation
Pseudoneglect
Spatial cognition
Plasticity

A B S T R A C T

Rightward prism adaptation has been shown to ameliorate visuospatial biases in right brain-damaged patients with neglect, and a single session of prism adaptation can lead to improvements that last up to several hours. Leftward prism adaptation in neurologically healthy individuals induces neglect-like biases in visuospatial tasks. The duration of these effects in healthy individuals, typically assumed to be ephemeral, has never been investigated. Here we assessed the time-course of the adaptation-induced modifications in a classical perceptual line bisection task that was repeatedly administered for approximately 40 min after a single session of adaptation to either a leftward or rightward prismatic deviation. Consistent with previous reports, only adaptation to leftward-deviating prisms induced a visuospatial shift on perceptual line bisection judgments. The typical pattern of pseudoneglect was counteracted by a rightward shift in midline judgments, which became significant between 5 and 10 min after adaptation, fluctuated between being significant or not several times in the 40 min following adaptation, and was present as late as 35 min. In contrast, the sensorimotor aftereffect was present immediately after adaptation to both rightward and leftward deviating prisms, decayed initially then remained stable until 40 min. These results demonstrate that both the sensorimotor and visuospatial effects last for at least 35 min, but that the visuospatial shift needs time to fully develop and fluctuates. By showing that the effects of prism adaptation in the undamaged brain are not ephemeral, these findings reveal the presence of another, so-far neglected dimension in the domain of the cognitive effects induced by prism adaptation, namely time. The prolonged duration of the induced visuospatial shift, previously considered to be a feature of prism adaptation unique to brain-damaged subjects, also applies to the normal brain.

1. Introduction

Prism Adaptation (PA) is a classic technique for reversibly modifying sensorimotor correspondences and has been extensively investigated (Hay, Langdon, & Pick, 1971; Hein & Held, 1962; Held & Freedman, 1963; Held & Mikaelian, 1964; Helmholtz, 1867; Stratton, 1896; for review see Redding & Wallace, 2006). Wedge prisms produce a lateral shift of the visual field, and adaptation of hand pointing movements to displaced vision is now considered to be one of the most promising techniques for treating neglect symptoms (Luauté, Halligan, Rode, Jacquin-Courtois, & Boisson, 2006a; Milner & McIntosh, 2005; Newport & Schenk, 2012). Indeed, since the original demonstration of its efficacy in ameliorating performance on standard neuropsychological tests of neglect (copying a drawing, drawing from memory, reading) (Rossetti et al., 1998) PA has been shown to promote the resetting of the oculo-motor system (Serino, Angeli, Frassinetti, & Làdavas, 2006) and to improve performance on a range of tasks that tap into visuospatial cognition like line bisection (Pisella, Rode, Farnè, Boisson, & Rossetti, 2002), global/local processing (Bultitude, Rafal, & List, 2009), haptic exploration (McIntosh, Rossetti, & Milner, 2002), wheel-chair navigation (Jacquin-Courtois, Rode, Pisella, Boisson, & Rossetti, 2008), and visual imagery (Rode, Rossetti, & Boisson, 2001), possibly by acting mainly on the dorsal stream (Fortis, Goedert, & Barrett, 2011; Striemer & Danckert, 2010b). PA also improves performance on non-visual tasks like tactile and auditory extinction (Jacquin-Courtois et al., 2010; Maravita et al., 2003).

In addition to its ability to *reduce* neglect symptoms in patient populations, a remarkable feature of PA is its ability to *induce*

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http://dx.doi.org/10.1016/j.neuropsychologia.2013.11.013

neglect-like behavior in healthy subjects. For example, PA changes behavior on visuospatial tasks like line bisection, greyscales, global/local processing, and haptic exploration (Berberovic & Mattingley, 2003; Bultitude & Woods, 2010; Colent, Pisella, Bernieri, Rode, & Rossetti, 2000; Girardi, McIntosh, Michel, Vallar, & Rossetti, 2004; Jackson & Newport, 2001; Loftus, Vijayakumar, & Nicholls, 2009; Michel et al., 2003). It also alters spatial remapping (Bultitude, Van der Stigchel, & Nijboer, 2013) and the estimated duration of auditory stimuli (Magnani, Pavani, & Frassinetti, 2012). In this respect, PA is similar to some brain-modulation techniques, such as repetitive transcranial magnetic stimulation (rTMS) and transcranial direct current stimulation (tDCS), which can alleviate neglect symptoms in patients (Brighina et al., 2002; Koch et al., 2008; Oliveri et al., 2001; Sparing et al., 2009) and induce neglect-like behavior in healthy participants (Fierro et al., 2000; Giglia et al., 2011; Romei, Driver, Schyns, & Thut, 2011; Sparing et al., 2009).

It is important to note that the direction of the prismatic displacement is pivotal for improving neglect in patients or inducing neglect-like behavior in healthy subjects. Neglect symptoms in patients improve only after adaptation to rightward-deviating prisms (Luauté et al., 2012) and visuospatial performance in healthy subjects is shifted only after adaptation to leftward-deviating prisms (Berberovic & Mattingley, 2003; Colent, Pisella, Bernieri, Rode, & Rossetti, 2000; Michel et al., 2003; Nijboer, Vree, Dijkerman, & Van der Stigchel, 2010). In addition to differing in terms of the direction of the prismatic displacement required to induce visuospatial adaptation effects, neglect patients and healthy subjects also differ with respect to the duration of these effects. For example, a single session of PA in neglect patients can significantly improve neglect symptoms for at least two hours (Rossetti et al., 1998) and in some patients for up to several days (Farnè, Rossetti, Toniolo, & Làdavas, 2002; Pisella et al., 2002). Two-weeks of treatment can produce positive effects for one to six months (Frassinetti, Angeli, Meneghello, Avanzi, & Làdavas, 2002; Serino, Bonifazi, Pierfederici, & Làdavas, 2007), and a single patient treated daily for three months still had improved detection of contralesional visual stimuli two years after the prism treatment (Nijboer, Nys, Van der Smagt, Van der Stigchel, & Dijkerman, 2011). In healthy subjects, perceptual changes are assumed to last only a few minutes, but this idea appears to come from the fact that almost all studies examined visuospatial effects only in the few minutes following adaptation, and not from data showing that these effects disappear at later times.

In this study we examined sensorimotor and visuospatial aftereffects in healthy participants multiple times after prism adaptation. Accuracy in open-loop pointing was used to measure the sensorimotor aftereffects and line bisection judgments measured the visuospatial aftereffect. Young participants typically make midline judgments to the left of the true center (Bowers & Heilman, 1980; Jewell & McCourt, 2000; Toba, Cavanagh, & Bartolomeo, 2011). This left bias is termed pseudoneglect, and there is a large body of evidence showing that adaptation to leftward-deviating prisms causes participants to shift their midline judgments to the right, thus reducing (Loftus et al., 2009; Nijboer et al., 2010), or cancelling (Colent et al., 2000; Berberovic & Mattingley, 2003; Michel et al., 2003) their pseudoneglect. Since we were particularly interested in the time course of visuospatial aftereffects produced by PA we designed a pre/multiple-posts experiment in which we assessed pointing accuracy and midline judgments every 5 min for 40 min after a single session of PA.

2. Methods

2.1. Participants

Forty healthy volunteers participated in the study. First, twenty participants (10 males, mean age=20.8, standard error of the mean (SEM)=0.46) underwent adaptation to leftward-deviating prisms and then another twenty participants (8 males, mean age=20.8 SEM=0.31) were adapted using rightward-deviating prisms. All participants had normal or corrected-to-normal vision and were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). They all gave informed consent and were paid for their participation in the study. The study was approved by the local ethics committee and was conducted in accordance with the ethical standards of the 1964 Declaration of Helsinki (last update: Seoul, 2008).

2.2. Procedure

Throughout the experiment participants were comfortably seated with their head positioned on a chinrest. The experiment consisted of nine blocks (one before and eight after PA). Each experimental block lasted a maximum of five minutes, and included six open-loop pointing movements with the right index finger towards a central target as well as the Landmark (perceptual line bisection) task. The open-loop pointing movements (which took approximately 30 s) were always performed before the Landmark task. Response times during the Landmark task varied across participants (and for a given participant across blocks), resulting in a variable block duration of between 4 and 5 min. The experimenter carefully monitored the timing to ensure that each experimental block started at the same time (i.e. 0, 5, 10, 15, 20, 25, 30, 35, and 40 min after prism adaptation).

The block before adaptation provided baseline measurements of behavior on the open-loop pointing and line bisection tasks. These measures were then compared with those obtained in each of the eight post-adaptation blocks (Fig. 1). In order to reduce the possibility of deadaptation across time participants were instructed to keep their eyes closed and to avoid moving their right hand unless instructed to perform the open-loop pointing movements. An additional series of six open-loop pointing movements was administered after the eighth block to assess whether the sensorimotor aftereffect was still present at the end of the experiment.

2.3. Prism adaptation

Participants were fitted with prismatic goggles that deviated their visual field by 15° either leftward ($n=20$) or rightward ($n=20$). They were seated in front of a white horizontal board on which three target dots (5 mm diameter) were positioned at 0, −10 and +10° from their body midline at a distance of 57 cm from their eyes. They performed a total of 150 verbally instructed pointing movements with their right index finger towards the right (+10°) and left (−10°) targets in a pseudorandom order. Before pointing they placed their right index finger on the starting position, which was just in front of their chest. Participants could not see their hand when it was in the starting position and during the first third of the pointing movement. Participants were instructed to point with the index finger extended, to execute a one-shot movement at a fast but comfortable speed, and to return their hand to the starting position only when instructed by the experimenter.

After 150 pointing movements the prismatic goggles were removed and behavior on the sensorimotor and visuospatial tasks was repeatedly measured using open-loop pointing movements to the central target (0°) and the Landmark task.

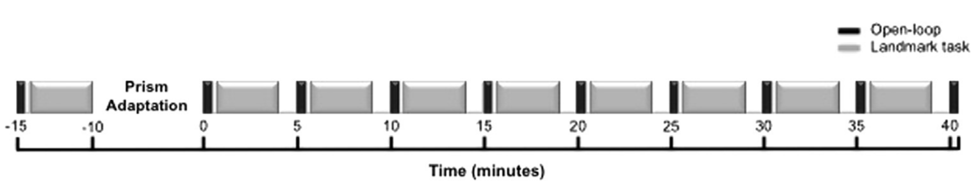

Fig. 1. Experimental design. Time course of the experiment. The experiment consisted of nine experimental blocks (one before and eight after prism adaptation) plus an open loop pointing measure after the eighth block. For each of the nine experiment blocks open loop pointing was always performed before the Landmark task. Because of variation in response times during the Landmark task the end of one block and the beginning of the next were separated by between 0 and 60 s.