NEUROPSYCHOLOGIA

Neuropsychologia 44 (2006) 2766–2773

www.elsevier.com/locate/neuropsychologia

Reaching errors in optic ataxia are linked to eye position rather than head or body position

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Received 17 June 2005; received in revised form 11 October 2005; accepted 25 October 2005
Available online 29 November 2005

Abstract

When reaching towards a visual stimulus, spatial information about the target must be transformed into an appropriate motor command. Visual information is coded initially in retinotopic coordinates, while the reaching movement ultimately requires the specification of the target position in limb-centred coordinates. It is well established that the posterior parietal cortex (PPC) plays an important role in transforming visual target information into motor commands. Lesions in the PPC can result in optic ataxia, a condition in which the visual guidance of goal-directed movements is impaired. Here, we present evidence from two patients with unilateral optic ataxia following right PPC lesions, that the pattern of reaching errors is linked to an eye-centred frame of reference. Both patients made large errors when reaching to visual targets on the left side of space, while facing and fixating straight ahead. By varying the location of fixation and the orientation of the head and body, we were able to establish that these large errors were made specifically to targets to the left of eye-fixation, rather than to the left of head-, body-, or limb-relative space. These data support the idea that visual targets for reaching movements are coded in eye-centred coordinates within the posterior parietal cortex.

Keywords: Visuomotor; Dorsal stream; Posterior parietal cortex; Unilateral

1. Introduction

One of the most important functions of vision is to provide information for the guidance of our actions. When reaching towards a visual target, spatial information about its location must be transformed into an appropriate motor command. However, visual information is coded initially in retinotopic coordinates, while the reaching movement ultimately requires the specification of the target position in limb-centred coordinates. It is well established that the posterior parietal cortex (PPC) plays an important role in transforming visual target information into motor commands (Jeannerod, 1997; Milner & Goodale, 1995). Single cell recordings in the monkey indicate that many neurones in the PPC have visual as well as motor properties (Hyvärinen & Poranen, 1974; Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975). Neurones in different areas of the PPC have been found to be associated with various types of movement, including reaching, grasping and saccades. During the last 30 years, a great deal of research has been devoted towards an understanding of those neurones in the PPC whose activity is associated with visually guided reaching (Burnod et al., 1999; Caminiti, Ferraina, & Johnson, 1996; Johnson, Ferraina, Bianchi, & Caminiti, 1996).

One way to transform an eye-centred coordinate system to a limb-centred coordinate system for guiding reaching movements is by adding extra-retinal signals, such as proprioceptive input about the position of the eyes and head (Andersen, 1995). Signals from the eye muscles about the position of the eyes with respect to the skull can be added to retinal input to create a head-centred coordinate system. Subsequently, a body-centred coordinate system can be achieved by adding head position signals from for example the neck muscles. Indeed, there is some

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doi:10.1016/j.neuropsychologia.2005.10.018

evidence that such transformations occur in the PPC in the monkey (Andersen, 1995; Brotchie, Andersen, Snyder, & Goodman, 1995). However, an alternative method suggests that both target location and hand location can be coded and compared in an eye-centred reference frame (Buneo, Jarvis, Batista, & Andersen, 2002). Indeed, more recent studies suggest that reaching neurones in the PPC code the target in eye-centred reference frames (Batista, Buneo, Snyder, & Andersen, 1999; Cohen & Andersen, 2002). Considering that during natural reaches, the eyes and hand move in a coordinated fashion towards the visual target (Neggers & Bekkering, 2000), it may be particularly efficient to code the target initially in a common eye-centred reference frame.

In humans, lesions to the PPC can result in optic ataxia, a condition in which the visual guidance of goal-directed movements is impaired (Bàlint, 1909; Perenin & Vighetto, 1988). Patients with optic ataxia are impaired in reaching towards visual targets, particularly when these targets appear in their peripheral visual field (Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003; Perenin & Vighetto, 1988). A simple way to test for optic ataxia is to ask patients to fixate one point (for example, the examiner's nose) and reach towards an eccentric stimulus (for instance, a pencil held by the examiner). In patients with optic ataxia following bilateral lesions, reaching errors may be severe for any eccentric target, regardless of the hand used, but more specific patterns of error are observed following unilateral lesions. Several patients with unilateral optic ataxia tend to make large errors only for contralesional targets (field effect). For some patients this 'field effect' is combined with a hand effect, resulting in increased misreaching for the contralesional hand (Revol et al., 2003). However, as patients are usually assessed with their head and eyes aligned with the body-midline, it is not clear whether the field effects observed in unilateral optic ataxia are determined by eye-centred, head-centred or body-centred coordinates. In a previous study, Buxbaum and Coslett (1998) varied whether eye and/or head movements were restricted during reaching movements of their optic ataxic patient DP. They observed that reaching errors were particularly severe when eye movements were fixed, although they also found a small effect of head restriction. In the current study, we tested two patients with unilateral optic ataxia in a reaching experiment in which the head and/or eye *orientation* were varied independently of body orientation, in order to determine which frame of reference has the dominant influence upon the pattern of reaching errors following right posterior parietal damage. The pattern of errors produced suggests that the field effect arises with respect to an eye-centred reference frame.

2. Experiment 1

2.1. Patient

FM, an 85 year-old woman, who had sustained a right parietal haemorrhagic infarct 8 months previously. Computerized tomography (CT) brain imaging, performed 1 day post-onset of symptoms, showed a large right parietal haemorrhagic infarct. A second CT-scan performed 9 months post-stroke, revealed a lesion affecting right parieto-occipital areas (Fig. 1). FM had displayed clinical signs of visual neglect acutely, but these had resolved entirely by the time of testing, since she scored 139 from 146 on the Behavioural Inattention Test (cut-off 129: Wilson, Cockburn, & Halligan, 1987). Her visual fields were found to be intact by confrontation. Her motor functions (maximum tapping rate, maximum grip force) were symmetrical, as was her joint position sense. Her two-point discrimination for touches to the palm of the hand was 1.7 mm on the left and 0.6 mm on

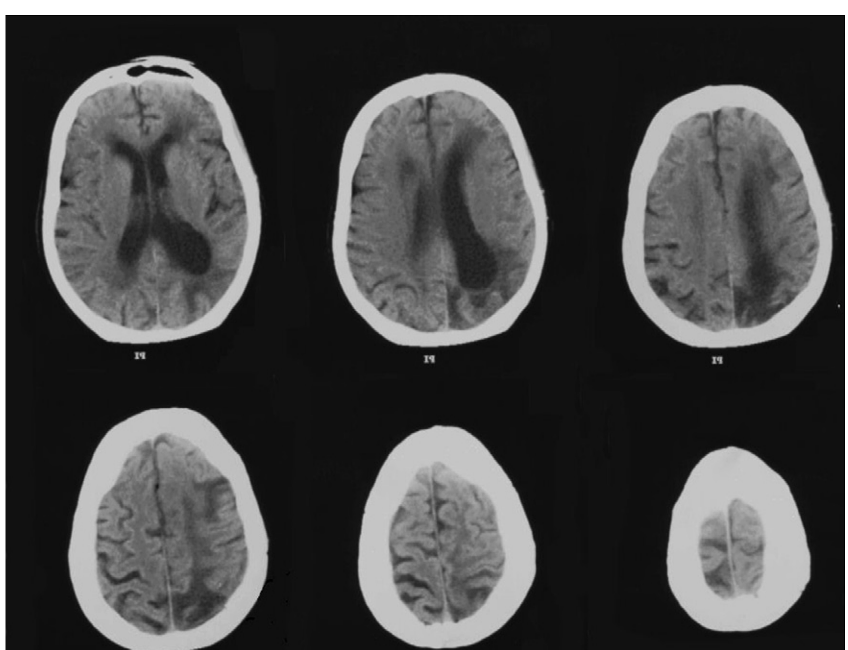

Fig. 1. CT-scan of patient FM made 9 months after stroke onset and 1 month after testing. The right hemisphere is shown on the right in this figure. Note the large right parieto-occipital lesion.

the right side. She showed normal discrimination of complex visual forms, scoring 26 from 32 (cut-off 23) on the Benton test (Benton, Hamsher, Varney, & Spreen, 1983). Additionally, since FM was strongly left-handed, she was also examined for signs of apraxia (copying of unfamiliar gestures; Goldenberg, 1995) and aphasia (very short version of the Minnesota aphasia test; Powell, Bailey, & Clark, 1980), and performed normally on both tests. Examination of her pointing performance indicated that FM made large errors when pointing, with either hand, to eccentric targets on the left side of space, but could point accurately to eccentric targets on the right or to fixated targets at any location. Since FM was left-handed, she was allowed to use her left hand for the experimental pointing task. This study was part of an ongoing research program for which ethical approval had been granted by the Tayside Committee on Medical Research Ethics.

2.2. Experimental set up

FM was required to point, with her left index finger, to one of four horizontally arrayed light emitting diodes (LED) embedded in a large sheet of black perspex, placed flat on a black wooden table. Three fixation positions were used: central, 6 cm to the left of the leftmost target LED, and 6 cm to the right of the rightmost LED (see Fig. 2). The fixation positions were small red dots that were present at all times. The target LEDs were situated 6 and 12 cm to the left and right of the central fixation position (approximately 8.5° and 17° visual angle), and were visible only when illuminated. The starting position was a small red dot placed 15 cm from the table edge nearest to the subject and 25 cm from the central fixation position. The central fixation position and the starting position were aligned with the subject's mid-sagittal axis.

Movements were recorded using the *Minibird* movement recording system (Ascension Technologies Inc.), which sampled the 3D position of an electro-magnetic marker, attached to the tip of the left index finger, at a frequency of 86.1 Hz.

2.3. Procedure

Two different pointing conditions were performed. In the 'aligned' condition, FM fixated the central fixation position with her body and head facing straight ahead (Fig. 2, top). In this condition, eye-, head-, body- and limb-centred frames of references were aligned. In the 'eyes-and-head-turned' condition, FM fixated at the right fixation position for the two rightmost targets and the left fixation position for the two leftmost targets (Fig. 2, centre and bottom). Her nose pointed to the fixation position she was looking at, but her body-midline remained forward-facing, and the hand-starting position remained the same as in the aligned condition. In this condition, targets to the *left* of the body-midline and the hand starting position fell within the *right* visual field and to the *right* of the head-midline. Similarly, targets to the *right* of the body-midline and hand fell within the *left* visual field and to the *left* of the head-midline. 'Aligned' and 'eyes-and-head-turned' (EHT) conditions were presented in an A–EHT–EHT–A schedule. Within each block of 12 trials, each of the four target LEDs was presented three times, resulting in a total of 24 trials for each condition across blocks. Head position and eye-fixation was monitored by an investigator, who sat opposite FM.

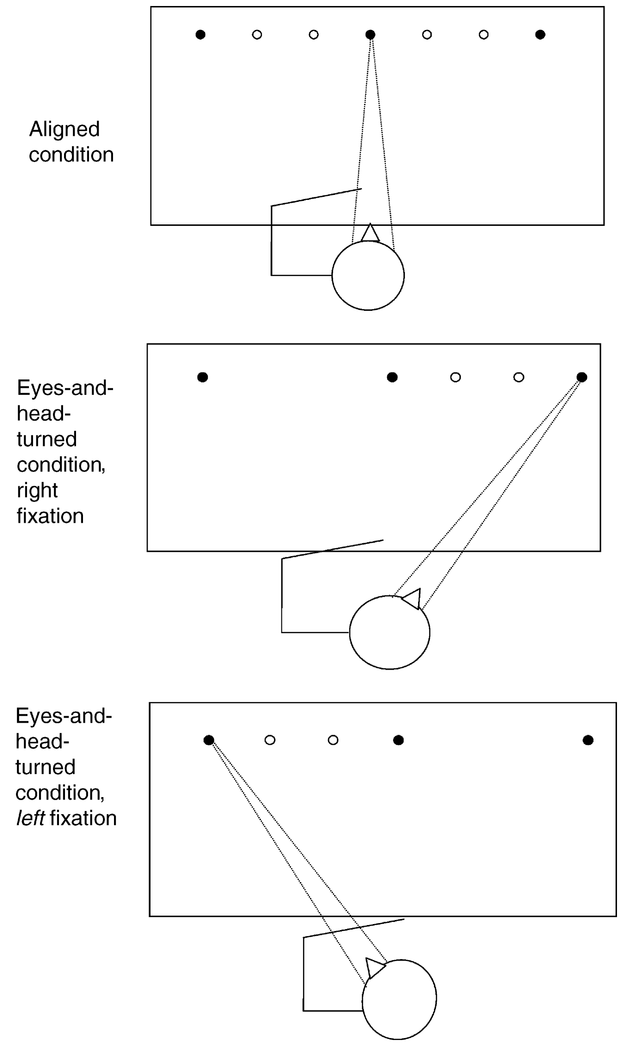

Fig. 2. The set up for Experiment 1. The fixation positions are depicted in black, the targets in white. The top picture shows the set up in the 'aligned' condition in which eye-, head-, body- and limb-centred frames of references were aligned. The central and bottom figures show the 'eyes-and-head-turned' condition. Here, the head and eyes are aligned with the rightmost fixation position for the targets on the right (central figure), and with the leftmost fixation position for targets on the left (bottom figure), while the body remained facing forward.

2.4. Data analysis

End point errors were calculated by comparing the end point position of the index finger in the *xy*-plane with the average *xy*-position in the calibration trial for the same target. For each target, at the end of the experimental session, a calibration trial was recorded in which FM was required to place her left index finger as accurately as possible on the target. She was allowed to foveate the target and take as long as she considered necessary. The position of her finger on the target was subsequently recorded for 1 s and the average position over the 86 samples was used for comparison with end of movement reaching positions.

End of movement was determined by comparing the vertical (z) position of the index finger during the pointing movement with the vertical position of the finger in the corresponding calibration file. The end of the movement was defined as the first frame in which the vertical position of the index finger was equal to, or lower than, the average vertical position of the index finger in the calibration file. In a small number of trials due to differences in the rotation of the hand between calibration and pointing file, vertical position of the index finger in the pointing movement never fell below the vertical finger position in the calibration file. In these files, the lowest vertical finger position was taken as the end of the movement. End point errors in the horizontal (xy) plane were entered as dependent variable in a two-way ANOVA, with condition (‘aligned’ condition versus ‘eyes-and-head-turned’ condition) and target side (left or right of body-midline) as independent variables.

2.5. Results

Fig. 3 shows that FM’s resultant reaching errors in the aligned condition were larger to targets on the left of body-midline. In the ‘eyes-and-head-turned’ condition, errors were larger to targets on the *right* of body-midline, therefore on the left of the head-midline and the fixation position [Fig. 3]. A two-way ANOVA showed no significant main effects of condition ($F(1,44) = 0.04$) or target side ($F(1,44) = 0.24$), but a significant interaction between condition (‘aligned’ condition versus ‘eyes-and-head-turned’ condition) and target side (left or right of body-midline) ($F(1,44) = 17.95$, $p < 0.001$). Subsidiary t-tests showed significant differences between left and right for both aligned ($t(22) = 2.61$, $p < 0.01$) and non-aligned conditions ($t(22) = -3.39$, $p < 0.005$), but in opposite directions.

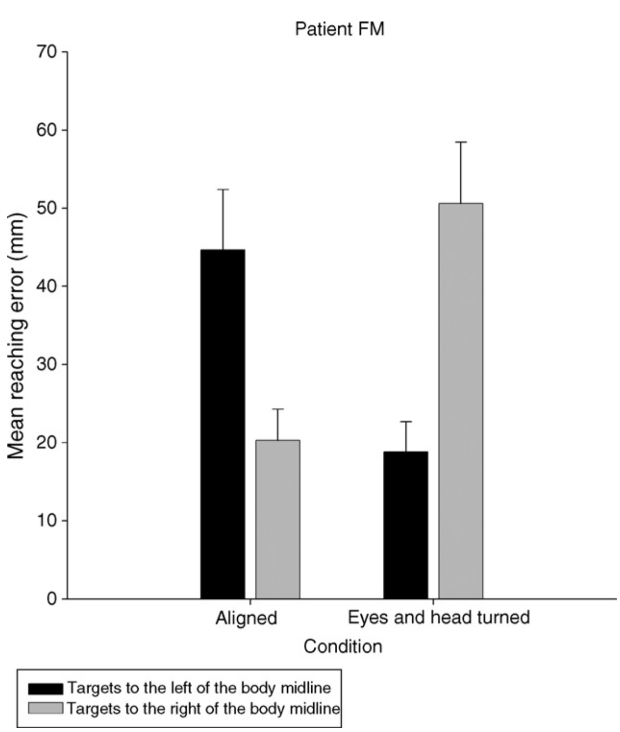

Fig. 3. Mean resultant reaching errors in the horizontal (xy) plane for Experiment 1. The errors for targets on the left of body-midline are depicted in black. For targets on the right, the errors are shown in grey. The error bar depicts the standard error (S.E.).

2.6. Discussion

The findings of Experiment 1 suggest that the lateralized appearance of optic ataxic errors in patient FM was anchored to either a head-centred or eye-centred frame of reference, but was independent of body- and hand-relative coordinates. Unfortunately, FM was unable to comply successfully with instructions to direct the head and the eyes toward different positions simultaneously, which would have allowed us to dissociate eye- and head-centred frames of reference. However, we recently had the opportunity to test another patient, who could comply with these more complex demands, and these investigations are reported as Experiment 2.

3. Experiment 2

3.1. Patient

LS, a 56-year-old, right-handed man, suffered an infarct in the right hemisphere 3 weeks prior to assessment. LS exhibited mild signs of visual neglect on the star cancellation (missed 10 items on the left; Wilson et al., 1987) and Schenkenberg line bisection task (missed five lines on the left, average rightward deviation = 7 mm; Schenkenberg, Bradford, & Ajax, 1980) and other visuospatial deficits as tested with VOSP (abnormal on the cube analysis and position discrimination subtests; Warrington & James, 1991) and Benton Judgement of Line Orientation (a score of 17, 3rd percentile; Benton et al., 1983). Pressure sensitivity (von Frey hairs) and joint position sense were symmetrical and no motor deficits were found for the individual muscle groups, although reduced coordination was noted on the left side. Reflexes were symmetrical and visual fields were found to be full by confrontation. LS also performed normally on the Goldenberg copying of unfamiliar gestures test (Goldenberg, 1995). A T2-FLAIR MRI scan (Fig. 4) revealed a frontal and a superior parietal ischaemic lesion affecting the border zone between the supply territories of the medial cerebral artery and the anterior cerebral artery and the border zone between the supply territories of the medial cerebral artery and the posterior cerebral artery.

Clinical examination of his reaching performance indicated that LS made large errors when reaching, with either hand, to eccentric targets on the left side of space, but could reach accurately to eccentric targets on the right or to fixated targets at any location. LS also used his left hand for the experimental pointing task. The study was part of an ongoing research program for which ethical approval had been granted by the Medical Research Ethics committee of the University Medical Centre, Utrecht.

3.2. Experimental set up

We assessed patient LS on a pointing task that was modified from the set up used with FM. Targets and fixation positions

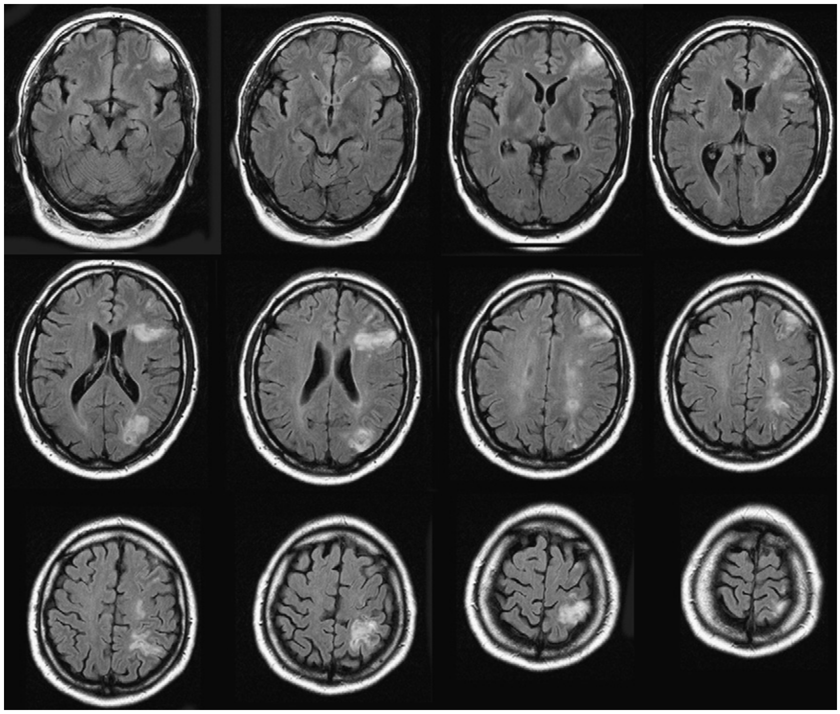

Fig. 4. MRI scan (T2-FLAIR) of the lesions of patient LS. Multiple cortical and subcortical lesions affecting among others frontal, superior parietal and parieto-occipital regions are clearly visible.

consisted of coloured dots printed on white paper. Again, three fixation positions were used: central, 10 cm to the left of the leftmost target, and 10 cm to the right of the rightmost target (see Fig. 5). The targets were situated 10 and 20 cm to the left and right of the central fixation position (approximately 15° and 30° visual angle). The central fixation position and the starting position were aligned with the subject's mid-sagittal axis. The targets were blue, green, black and yellow, while all three fixation positions were red. The distance between the starting position (a small blue dot) and the central fixation position was 30 cm, with the starting position located 5 cm from the table edge.

Movements of the left index finger were recorded using the Minibird (Ascension Technologies Inc.) electromagnetic movement recording device at a sampling rate of 86.1 Hz.

3.3. Procedure

In each trial, LS was required to point to a specified one of the four coloured targets. Each trial started with LS fixating the relevant fixation position and the targets being covered with a white piece of paper (in the centre of the paper a small square was cut to allow viewing of the central fixation position while the targets were covered). Prior to the start of the trial, LS was told which target to point to (e.g. "point to the yellow dot"). As soon as the targets became visible LS was required to point to the target while maintaining fixation. Trials in which LS did not maintain fixation, or pointed clearly to the wrong target were repeated at the end of each block of trials. Head position and eye-fixation was monitored by an investigator who sat opposite LS.

Three different conditions were performed. The 'aligned' condition was identical to that used in Experiment 1 (Fig. 5, top). In the 'eyes-turned' condition LS fixated the left fixation position for the two leftmost targets, and the right fixation position for the two rightmost targets (Fig. 5, centre), while his head and body always faced straight ahead. Thus, in the 'eyes-turned' condition, the targets to the *left* of the body- and head-midline fell in the *right* visual field, while the targets to the *right* of the body- and head-midline fell in the *left* visual field. In the 'head-turned condition', the eyes always fixated the central fixation position and the body faced straight ahead, while the nose pointed towards the left fixation position for the two leftmost targets, and the right fixation position for the two rightmost targets (Fig. 5, bottom). Thus, in the 'head-turned condition', the targets to the *left* of the body-midline and eye-fixation fell to the *right* of the head-midline, while the targets to the *right* of the body-midline and eye-fixation fell to the *left* of the head-midline. 'Aligned' (A), 'eyes-turned' (ET) and 'head-turned' (HT) conditions were presented in an A–ET–HT–HT–ET–A design, with the first and second half of the experiment being performed on consecutive days. Within each block of 12 trials, each target was presented three times, in a pseudo-randomized order.

3.4. Data analysis

End point errors were calculated by comparing the end point position of the index finger in the horizontal (*xy*-) plane with the average *xy* position in the calibration trial for the same target. For each target, at the end of the experimental session, a calibration trial was recorded in which LS was required to place his left index finger as accurately as possible on the target. He

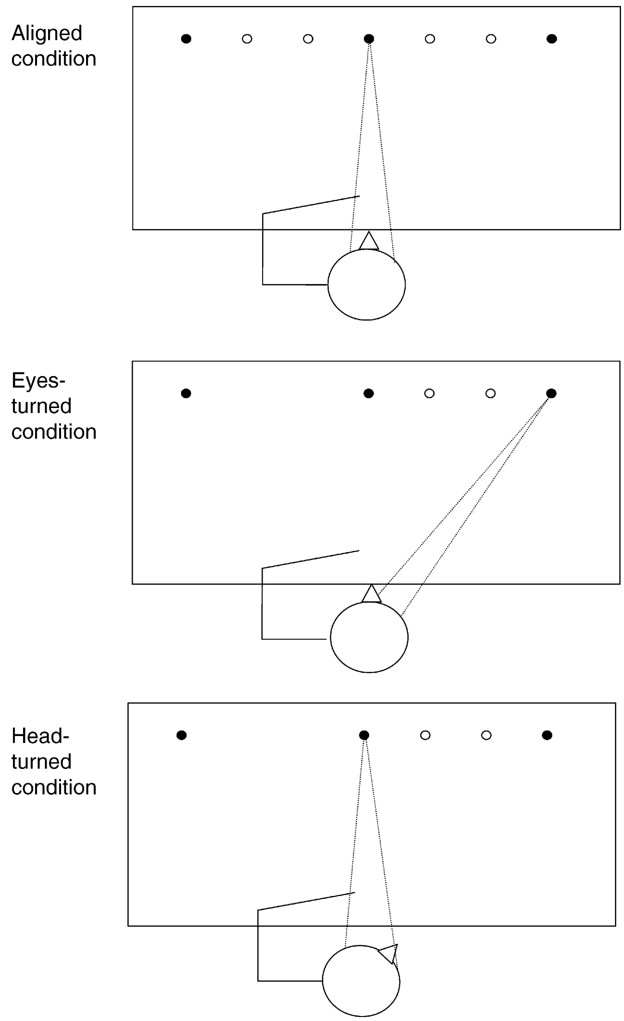

Fig. 5. The set up for Experiment 2. The fixation positions are depicted in black, the targets in white. In the actual set up, the target had different colours (from left to right, blue, green, black and yellow), while fixation positions were all red. The top picture shows the set up in the ‘aligned’ condition in which eye-, head-, body- and limb-centred frames of references were aligned. The centre figure shows the ‘eyes-turned’ condition. Here, the eyes are focused on the leftmost fixation position for the targets on the left, and on the rightmost fixation position for targets on the right. The head remained facing forward. The bottom figure shows the set up in the ‘head-turned’ condition. Here, patient LS was always fixating with his eyes centrally, while his head was facing the rightmost fixation position for the targets on the right. Similarly, for the two targets on the left, his head was turned towards the leftmost fixation position.

was allowed to foveate the target and take as long as he considered necessary. The position of his finger on the target was subsequently recorded for 1 s and the average position over the 86 samples was used for comparison with end of movement reaching positions.

End of movement was determined through a combination of positional and velocity criteria. The positional criterion was defined as the vertical position (z-direction) of the index finger being equal to, or lower than, the average vertical position of the index finger in the calibration file. The velocity criterion was set at 50 mm/s or below. Data analysis was performed on the end point errors in the horizontal (xy-) plane. These errors were entered as dependent variable in a two-way ANOVA, with condition (‘aligned’ condition, ‘head-turned’ and ‘eyes turned’ condition) and target side (left or right of body-midline) as independent variables.

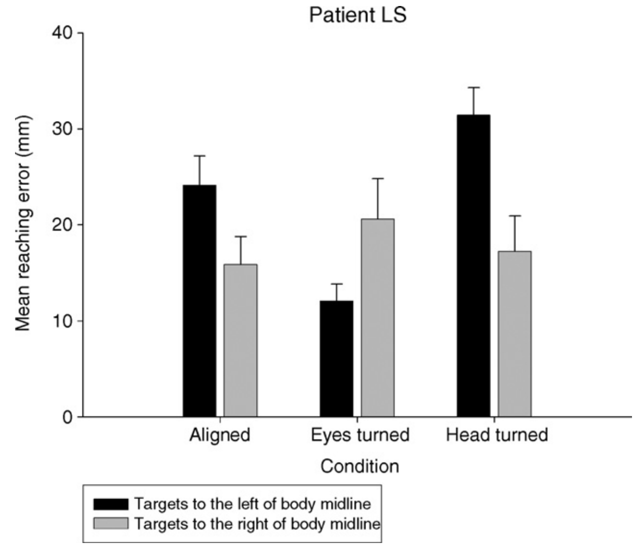

Fig. 6. Mean resultant errors in the horizontal (xy) plane for Experiment 2. The errors for targets on the left of body-midline are depicted in black. For targets on the right of the body-midline, the errors are shown in grey. The error bar depicts the standard error (S.E.).

3.5. Results

In the aligned condition, LS made larger pointing errors to targets on the left than on the right [Fig. 6, left]. In the eyes-turned condition, pointing errors were larger to targets on the *right* of the body- and head-midline, thus in his *left* visual field (Fig. 6, centre). In the head-turned condition, errors were larger to targets on the *left* of the body-midline and eye-fixation, thus to the right of LS’s head-midline (Fig. 6, right). A two-way ANOVA confirmed a significant interaction ($F(2,66) = 6.91$, $p < 0.005$) between condition and side of target with respect to the body. A significant main effect was found for condition ($F(2,66) = 3.18$, $p < 0.05$), but not for hemispace ($F(1,66) = 3.27$). Subsidiary t-tests of hemispace differences for each condition separately revealed a significant effect of hemispace in each case (one-tailed—aligned condition: $t(22) = 1.97$, $p < 0.05$; ‘eyes-turned’ $t(22) = -1.87$, $p < 0.05$; ‘head-turned’ $t(22) = 3.05$, $p < 0.01$).

4. General discussion

The results of Experiment 2 disambiguate those of Experiment 1, in which patient FM was tested with her head and eyes together directed toward extreme lateral fixation positions, causing a reversal in her error pattern. Experiment 2 shows that patient LS exhibited a similar reversal to FM *only* when his eyes were turned towards the lateral location. There was no effect of turning his *head* alone towards a peripheral location. Although conducted in two different patients, the results of these two experiments together suggest that unilateral optic ataxic patients with right hemisphere lesions make larger reaching errors contralesional to the point of fixation and that these errors are not influenced by either head- or body-relative coordinates. This conclusion can be reached firmly in the case of patient LS, though the limitations of Experiment 1 did not allow us to exclude a possible role of head-centred coordinates in patient FM. Moreover, it is possible that different patterns would be obtained in different optic ataxic patients, so that the critical reference frame mediating any field effect would need to be determined on a case-by-case-basis.

The present findings are consistent with the idea of an impairment in eye-centred coding during visually guided reaches. They are also consistent with previous neurophysiological studies showing eye-centred reaching-related activity in the monkey posterior parietal reach region (Batista et al., 1999; Cohen & Andersen, 2002). In humans, neuroimaging studies have confirmed eye-centred coding of target location in the posterior parietal cortex during memory-guided reaches (Medendorp, Goltz, Vilis, & Crawford, 2003). Recent complementary studies suggest that updating of target position in gaze-centred coordinates following a saccade is defective in optic ataxic patients and that target position with respect to point of fixation at the time of reaching rather than at time of stimulus display is the critical determinant of the error pattern (Khan, Pisella, Rossetti, Vighetto, & Crawford, 2005; Khan, Pisella, Vighetto, et al., 2005). In combination with these studies, our findings provide converging evidence for eye-centred coding of reach targets in the posterior parietal cortex.

Of course, the reaching movement must ultimately be specified in limb-centred coordinates. Thus, although eye-centred coding of reaching targets may be particularly efficient in the early stages of visuomotor processing, further transformations are required. There is evidence that premotor areas in the frontal lobe, closer to the motor output, code reach targets in limb-centred coordinates (Graziano, Taylor, & Moore, 2002; van Donkelaar, Lee, & Drew, 2002). Indeed, optic ataxia has been described after frontal lesions as well (Nagaratnam, Grice, & Kalouche, 1998).

The PPC may also be involved in the transformation to a limb-centred coordinate system, as there is neurophysiological evidence for partial coding to head and perhaps even body-centred coordinates in the monkey (Andersen, 1995; Brotchie et al., 1995). However, neuronal activity in the PPC is only *modulated* by such effector variables: it is not determined by them (Andersen, 1995; Brotchie et al., 1995). The current findings therefore suggest that unilateral optic ataxia after right posterior parietal lesions reflects an impairment of coding of visual targets at a fairly early stage in the visuomotor transformation processes, at which targets are coded in eye-centred coordinates. Interestingly, this may not be the case for all cases of optic ataxia. Other patients exhibit a different pattern, with errors being mainly related to the limb used rather than a visual field effect (Jackson, Newport, Mort, & Husain, 2005; Perenin & Vighetto, 1988) or combination of both (Revol et al., 2003). This finding suggests the possibility of coding in intrinsic (muscle, postural) coordinates. Therefore, the different manifestations of optic ataxia may depend upon which visuomotor coordinate system is primarily affected (Buxbaum & Coslett, 1998).

Acknowledgements

This work was supported by research grants from the Leverhulme Trust (grant number F00128C), the Wellcome Trust (grant number 052443) and NWO (Netherlands Organisation for Scientific Research, 452-03-325). We thank Drs. Richard Roberts and Martine van Zandvoort for their help with the patients' scans, and the patients for their co-operation.

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