

Dissociation between intentional and automatic remapping: Different levels of inter-hemispheric transfer

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ARTICLE INFO

Article history:

Received 12 July 2010

Received in revised form 25 January 2011

Available online xxxx

Keywords:

Optic ataxia

Posterior parietal cortex

Visual remapping

Antipointing

Inter-hemispheric transfer

ABSTRACT

In order to efficiently interact with our environment we need to constantly to update the spatial representation of visual targets for movement. This is required not only when we move our eyes but also when we want to reach toward a location different from the actual physical target (for example symmetrical). These two types of remapping are very different in nature, one being automatic, and the other intentional. However, they both have been shown to involve the posterior parietal cortex (PPC). To further investigate the role of this brain region in automatic and intentional remapping processes and the level of inter-hemispheric transfer of visuo-motor information in these two conditions of reaching, we tested two patients with unilateral optic ataxia (OA) in two different tasks: reaching to a memorised visual target after an intervening eye movement (trans-saccadic remapping) and an anti-reaching task. We showed that lesions of the PPC had different implications for these two tasks. In the trans-saccadic remapping task, movements toward the contralesional field were disrupted, even when the visual target was presented in the ipsilesional field. In contrast, in the anti-reaching task, the patients were mostly impaired in conditions where the target was presented in the contralesional field, even if the movement was executed toward the ipsilesional field. We postulate that the transfer of the visuo-motor information between hemispheres occurs before the parietal cortex in trans-saccadic remapping (transfer of visual information), and at the parietal level or after in anti-reaching (transfer of visuo-motor information).

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1. Introduction

The evolution of the capacity for tool-use in primates has resulted in situations where the correspondence between vision and action is not direct. For example, in order to control a cursor using a computer mouse, one must learn the spatial rule that moving the cursor vertically “upward” requires a “forward” horizontal movement. This “non-standard” visuo-motor mapping (Sergio, Gorbet, Tippett, Yan, & Neagu, 2008), considered to be intentional (even though it can become automatic once learned), has mainly been studied using mirror tasks such as anti-saccades or anti-reaching across the horizontal meridian (Connolly, Goodale, Desouza, Menon, & Vilis, 2000; Medendorp, Goltz, & Vilis, 2005). In order to successfully perform these types of tasks, it is thought that an inversion of the vectorial motor plan is calculated, requiring an inter-hemispheric transfer of visuo-motor information (Schlag-Rey, Amador, Sanchez, & Schlag, 1997).

The second type of remapping process, considered to be automatic, occurs every time a self movement changes the position of a target relative to the retina. For example, trans-saccadic remapping allows the brain to keep track of the location of salient objects in the visual scene across exploratory saccades (Colby, Duhamel, & Goldberg, 1995), requiring a constant exchange of information between the cerebellar hemispheres (Bays & Husain, 2007). This type of remapping can be tested using a trans-saccadic reaching paradigm in which subjects view the target in their peripheral vision but make a saccade to a second fixation position located on the opposite side of the target before reaching to it (Henriques, Klier, Smith, Lowy, & Crawford, 1998). The intervening saccade purportedly transfers the internal representation of the target location into the opposite hemisphere (Medendorp, Goltz, Vilis, & Crawford, 2003).

Interestingly, both types of remapping processes have been shown to involve an exchange of information at the level of the posterior parietal cortex (Colby & Goldberg, 1999; Merriam, Genovese, & Colby, 2003; Medendorp et al., 2003, 2005; Van Der Werf, Jensen, Fries, & Medendorp, 2008). Further investigations with monkey electrophysiology and human neuroimaging have shown that trans-saccadic remapping also occurs in earlier

extra-striate regions (Merriam & Colby, 2005; Merriam, Genovese, & Colby, 2007). These observations are consistent with the results of Khan, Pisella, Vighetto, et al. (2005) and Khan, Pisella, Rossetti, Vighetto, and Crawford (2005) who demonstrated preserved trans-saccadic remapping in optic ataxia patients following lesions of the posterior parietal cortex (PPC), sparing the earlier extra-striate visual areas.

Optic ataxia (OA) is characterized by reaching errors that cannot be attributed to purely visual, proprioceptive or motor deficits (Garcin, Rondot, & de Recondo, 1967; Perenin & Vighetto, 1988), but rather to a deficit of direct visuo-manual transformation (Rossetti & Pisella, 2002; Rossetti, Pisella, & Vighetto, 2003) or “standard” visuo-motor mapping (Pisella et al., 2009). Typically, OA is revealed in a *fixation task* in which the patients are required to reach in their contralesional peripheral visual field (field effect) and/or with their contralesional hand (hand effect) (Blangero et al., 2010; Perenin & Vighetto, 1988). In contrast, their reaching is comparable to controls in their ipsilesional field with their ipsilesional hand. In the trans-saccadic reaching paradigm (*saccade task*, Khan, Pisella, Vighetto, et al., 2005), patients were asked to use their ipsilesional hand to reach to targets viewed in one visual field but whose representation was remapped into the other visual field subsequent to a saccade. For example, after the target was flashed in the contralesional field, patients would make an eye movement and then reach to the remembered (extinguished) target now represented within their ipsilesional visual field. When the target was initially presented in the ipsilesional visual field, patients exhibited reaching errors after the target representation was remapped through the saccade into their damaged visual field. Conversely, patients exhibited accurate reaching when the target was initially presented in their contralesional visual field. These results indicate that in the automatic remapping condition, the critical factor for reaching errors is not in which visual field the target is viewed but in which visual field the movement is directed (i.e. the reaching field). This pattern of results therefore demonstrates an inter-hemispheric transfer of the visual target location *before* a visuo-manual transformation by the PPC.

In the present study, we aimed at investigating intentional as well as automatic remapping processes in the same OA patients in order to determine whether they involve inter-hemispheric transfer at the same level of processing. Automatic remapping was tested using the trans-saccadic reaching task and we expected to confirm previous results (Khan, Pisella, Vighetto, et al., 2005) in two new unilateral OA patients. Intentional remapping was tested using an anti-reaching task performed during fixation with the ipsilesional hand. We hypothesize that in this task, the information transferred would not be simply the visual target location (such as has been shown for the trans-saccadic task), but rather the motor plan. Since the PPC is involved in the visuo-manual transformation, we propose that the inter-hemispheric transfer in this case will occur at or after the level of the PPC. A PPC lesion should result in deficient motor plans in the contralesional visual field. Therefore, when the target is initially presented in the contralesional visual field, an inaccurate motor plan should be formed, and subsequently transferred to the ipsilesional side, revealing reaching errors in the ipsilesional visual field. Such intentional remapping should therefore induce the opposite pattern of errors in OA patients when compared with the automatic remapping condition, i.e. the critical factor for the presence of reaching errors should be the field in which the visual target is presented and not the field in which reaching occurs. Measurements of the reaching errors in these two tasks in patients with PPC lesions should thus potentially allow us to distinguish between the two levels of inter-hemispheric transfer and thereby to differentiate automatic (saccadic) vs. intentional (mirror) remapping both anatomically and functionally.

2. Methods

Since the aim of the paper was to compare the effect of PPC lesions on intentional and automatic remapping, we tested two patients with PPC lesions in a trans-saccadic remapping task as well as in an anti-reaching task. A control subject (female, 36 years old) was also tested in the same tasks.

2.1. Patient descriptions

Patient MFL is a left-handed female of 60 years who suffered from haemorrhagic stroke in the right hemisphere, 16 years before testing. The lesion damaged the parieto-occipital junction and the caudal part of the intra-parietal sulcus and of the superior parietal lobule (Fig. 1A). Following this focal lesion, MFL exhibited optic ataxia symptoms isolated to the left visual field using both hands.

Patient PER is a 71 year old, right-handed female who suffered from a haemorrhagic stroke in the right hemisphere one year before testing. Her posterior parietal lesion included the entire superior parietal lobule and intra-parietal sulcus, extending slightly to the junction between the supramarginal and the angular gyri. The occipital lobe and the post-central gyrus were spared (Fig. 1B). At the time of testing, clinical assessment revealed optic ataxia in her left visual field using both hands, and with her left hand in both hemifields.

2.2. Apparatus

Patients sat in complete darkness in front of a custom experimental device. It comprised a high speed CRT monitor (frequency:

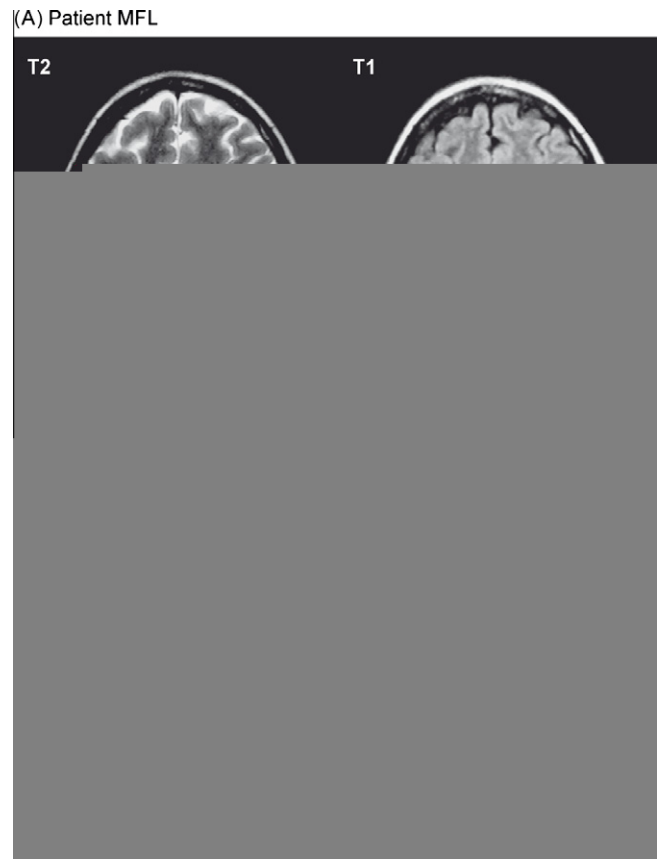


Fig. 1. MRI slices showing lesions of patient MFL (A) and patient PER (B) under T1 (left) and T2 (right) contrasts. For both patients, the lesions include the parieto-occipital junction (PO), the superior parietal lobule (SPL) and the posterior part of the intra-parietal sulcus (IPS).

160 Hz) with a 21-inch touch screen that used surface acoustic wave technology (Intellitouch, ELOTouchSystems) to record fingertip positions, coupled with a stimulus presentation device with high spatial and temporal resolution (Visual Stimulus Generator, ViSaGe, Cambridge Research Systems, Rochester, UK) (160 MHz pixel clock; 200 kHz line scan rate; 200 Hz frame rate). A High Speed Video Eyetracker attached to a head and chin rest (Cambridge Research Systems, Rochester, UK) registered eye movements by means of an infra-red camera (sampling frequency: 250 Hz; resolution: 0.05°). The eyetracker, the stimulus presentation device and the touch screen were synchronised by a custom software interface developed in our laboratory. The subjects' eyes were at a distance of 37 cm from the screen.

2.3. Procedure

2.3.1. Experiment 1: reaching during fixation vs. after a saccade

We used an experimental procedure similar to the one used by Khan, Pisella, Vighetto, et al. (2005) and Khan, Pisella, Rossetti, et al. (2005). Each trial in both the Fixation and Saccade conditions began with the illumination of the hand starting position at the bottom of the tactile screen. When the system detected that the hand was in position, an eccentric eye fixation position (white cross) appeared (Fig. 2A). There were six possible fixation positions relative to the centre of the screen, aligned horizontally (at 30°, 25°, 20° left and 20°, 25°, 30° right). After the system detected that the eyes were at the correct position and remained there for 500 ms, a reaching target (closed white circle) was illuminated for 800 ms at the centre of the screen. Patients were asked to maintain gaze on the fixation position during the presentation of the peripheral reaching target. The target was then extinguished. In the Fixation condition, after a 500 ms delay, the patients heard an auditory tone which indicated that they were to reach to the remembered target position while maintaining fixation (Fig. 2A –

left panel). In the Saccade condition, a second fixation position appeared on the other side of the centre of the screen – with the same eccentricity (Fig. 2A – right panel). The patients were asked to saccade to the new fixation position. After the system detected that the eyes were at the correct position and remained there for 500 ms, the auditory tone sounded indicating that they were to reach toward the remembered target position while maintaining fixation on the new fixation position. There were five repetitions per target position. The target locations were randomly presented across the six possible locations. All trials for each condition (Fixation and Saccade tasks) were done in separate blocks. The Fixation condition was performed first.

2.3.2. Experiment 2: pro vs. anti-reaching

Each trial began with a fixation cross presented in the centre of the screen (Fig. 2B). Patients were asked to fixate the cross and to place their finger on the cross. After the system detected that both effectors were at the correct position and remained there for 500 ms, a peripheral reaching target was presented for 800 ms. There were 6 possible target positions arranged horizontally (40°, 30°, 20° left, 20°, 30°, 40° right). The target was then extinguished. After a delay of 500 ms, an auditory tone instructed the patients to reach. In the Pro-reaching condition, patients were asked to reach to the remembered target position (Fig. 2B – left panel). In the Anti-reaching condition, patients were asked to reach to the mirror target position relative to the central fixation (Fig. 2B – right panel). There were five repetitions per target position. The two conditions (Anti and Pro-reaching) were blocked.

3. Results

In the Saccade and Anti-reaching conditions, the visual target position is different from the reaching target position. In these remapping conditions, the target location encoded in one

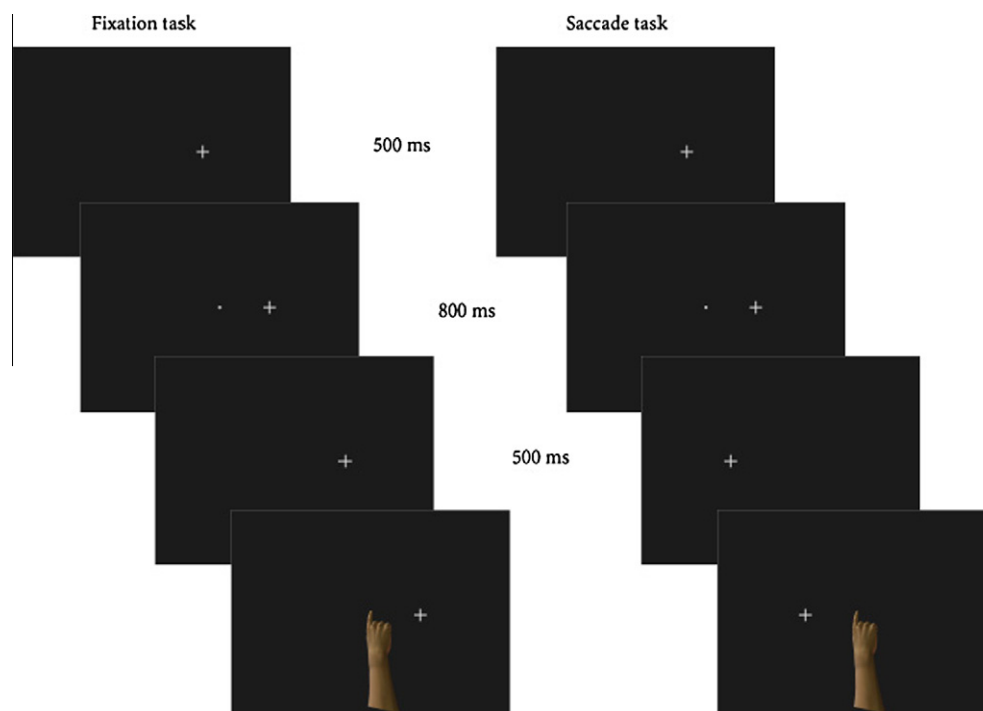


Fig. 2A. Illustration of the conditions in Experiment 1. The left panel depicts the Fixation task. Patients were asked to fixate a cross presented on the screen for 500 ms. Next a target appeared in the centre of the screen for 800 ms followed by a delay period of 500 ms. An auditory tone then prompted the patients to reach toward the memorised position of the target. The right panel depicts the Saccade task. The only difference from Fixation task is that after the target presentation, the fixation cross was displaced and the patients were asked to make a saccade to its new position.

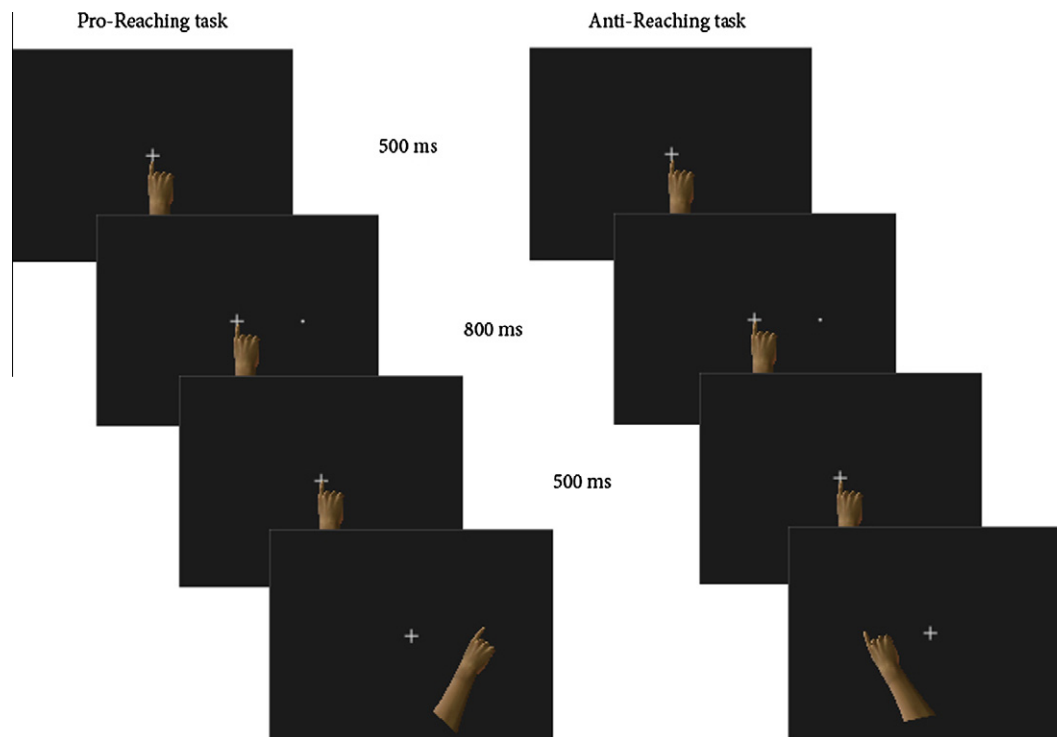


Fig. 2B. Illustration of the conditions in Experiment 2. The left panel depicts the Pro-reaching task. Patients were asked to maintain both their gaze and right index finger on a central fixation cross for 500 ms. Next a target appeared in the periphery for 800 ms followed by a delay period of 500 ms. An auditory tone then sounded, indicating that they should reach toward the remembered position of the target. The right panel depicts the Anti-reaching task. The trial was identical to the Pro-reaching task except that patients were instructed to reach toward the mirror position of the memorised target location.

hemisphere is to be transferred to the other hemisphere and the reaching movement is directed toward the opposite visual field from which the visual target was viewed. The main aim of this article is to investigate which factor induces reaching inaccuracy for each of these two conditions, the visual field where the target was initially presented or the reaching field.

3.1. Experiment 1: fixation vs. saccade

We conducted a three-way analysis of variances (ANOVA) on the absolute reaching errors with the patients, the visual target position and the task (fixation vs. saccade) as factors. There was no difference between the two patients ($F(1, 77) = 1.98$; $p > 0.05$) nor were there any significant interactions with the other two factors ($p > 0.05$). The two patients behaved in the same manner and showed similar reaching errors. There was a main effect of the visual target position ($F(5, 77) = 13.79$; $p < 0.001$) as well as a main effect of the task ($F(1, 77) = 13.03$; $p < 0.001$). Additionally, a significant interaction between the task and the visual target position ($F(5, 77) = 21.98$; $p < 0.001$) indicated that the patients did not exhibit the same pattern of behaviour in the two tasks. As can be seen in Fig. 3, whereas the largest reaching errors in the fixation task occurred when the visual target was presented in the patients' left visual field (consistent with their lesions in the right hemisphere), the largest reaching errors in the remapped condition were when the target was originally presented in their right (ipsilesional) visual field (Fig. 3C). For both Fixation and Saccade conditions, linear contrast analyses grouping leftward vs. rightward targets revealed significant differences between the visual fields (Fixation condition – $t(21) = -7.2$, $p < 0.001$, Saccade condition – $t(24) = 9.6$, $p < 0.001$).

Taken together, these results replicate the findings of Khan, Pisella, Vighetto, et al. (2005) showing that the reaching errors of patients with unilateral optic ataxia do not depend on the visual

field in which the target is originally presented but rather on which hemifield the movement will be directed to.

3.2. Experiment 2: pro vs. anti-reaching

The same analyses were conducted for this experiment. A three-way ANOVA evaluated the differences between the patients, the tasks and the visual target positions on the absolute reaching errors of the patients. Patients behaved comparably with no difference in the magnitude of errors ($F(1, 91) = 0.88$; $p > 0.05$). There was a main effect of the task ($F(1, 91) = 15.09$; $p < 0.001$) – the patients were more inaccurate in the anti-reaching condition – as well as a significant effect of the visual target position ($F(5, 91) = 18.75$; $p < 0.001$). However, there was no interaction in this experiment, indicating that the errors in both tasks followed the same pattern as can be seen in Fig. 4. We can observe that both in the Pro- and Anti-reaching conditions, the errors were greater when the visual target was presented in the left (contralesional) visual field (Fig. 4C). For both Pro- and Anti-reaching conditions, linear contrast analyses grouping leftward vs. rightward targets revealed significant differences between the visual fields (Pro condition – $t(24) = 2.5$, $p < 0.05$, Anti condition – $t(24) = 4.8$, $p < 0.001$).

3.3. Combined results

The mean and standard deviation of the patients' reach reaction times in both conditions and both experiments are presented in Table 1.

If we pool the data from the two patients and group them into the two visual fields, (contra or ipsilesional) for both experiments, we can clearly observe that the critical factor differs between the two experiments. For the automatic remapping experiment, the errors for the Fixation and Saccade task depend on the visual field

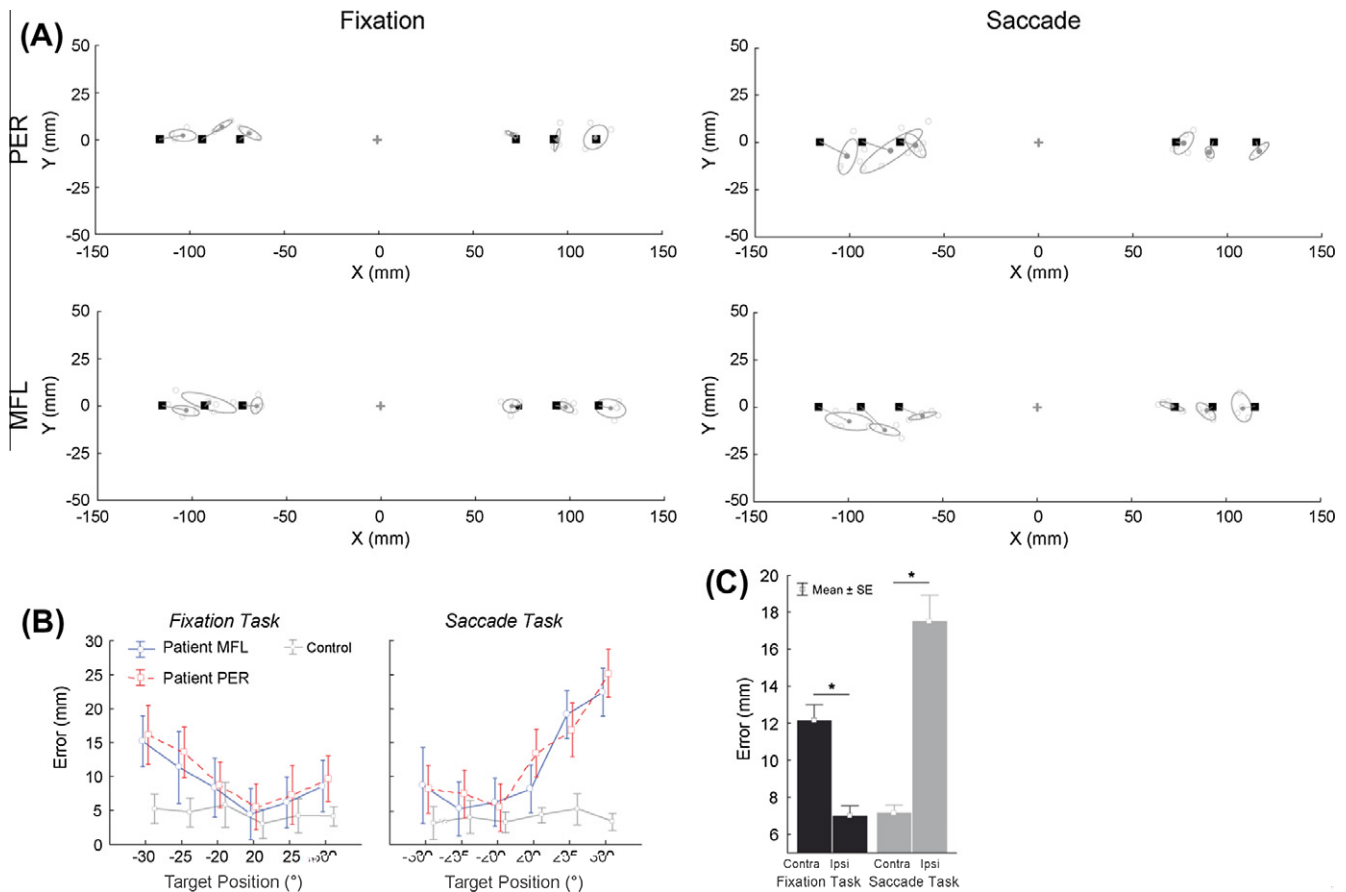


Fig. 3. (A) 2D illustration of the reaching endpoints in the Fixation and Saccade conditions of Experiment 1 for both patients relative to the position of the gaze (symbolised by the cross) at the time of the execution of the movement. Each movement endpoints (empty circles), the mean endpoints (filled circle) and the confidence ellipses (95%) are represented for each target position. (B) Mean and confidence intervals (95%) for absolute reaching errors (in mm) for the two patients and a control subject (Patient MFL in blue, Patient PER in red, control in grey) in the Fixation (left panel) and the Saccade (right panel) conditions plotted as a function of the visual target location relative to fixation at the time of the presentation of the visual target. (C) Mean and standard errors of both patients' combined reaching errors (in mm) as a function of the location of the visual target collapsed into the contralesional vs. ipsilesional visual fields for Experiment 1. Asterisks illustrate significant differences based on linear contrast analysis comparing targets in the left vs. right visual fields.

toward which the movement is directed and not on the visual field in which the visual target was presented, as can be seen clearly in Fig. 3C. In contrast, in the intentional remapping experiment the errors depend on the visual field in which the visual target was presented (Fig. 4C).

4. Discussion

The aim of this study was to test the hypothesis that intentional remapping, which takes place during an Anti-reaching task (Experiment 1) involves a different level of inter-hemispheric transfer compared to the automatic remapping that occurs in a trans-saccadic remapping task (Experiment 2). The present neuropsychological study provides pieces of evidence in favour of this hypothesis.

First, the baseline conditions of each experiment (Pro and Fixation) confirmed the well-known pattern of errors of unilateral optic ataxia when the ipsilesional hand is used: errors appeared to vary as a function of gaze, i.e. in eye-centred (Dijkerman et al., 2006; Khan, Pisella, Rossetti, et al., 2005; Khan, Pisella, Vighetto, et al., 2005) and increase with visual target eccentricity (Blangero et al., 2010). This appeared to be the main factor influencing reach errors, however due to the differences in task requirements, it is possible that other factors might be involved. Specifically the two experiments differed in a number of factors such as absolute eye

and target locations in body/space coordinates as well as the reach movement start position. Although there is much evidence that the brain represents hand and target position in eye-centred reference frames (Batista, Buneo, Snyder, & Andersen, 1999; Caminiti et al., 1999; Khan et al., 2007), it could be that other reference frames might also be used simultaneously (e.g. Beurze, Van Pelt, & Medendorp, 2006; Buneo, Jarvis, Batista, & Andersen, 2002; Chang, Papadimitriou, & Snyder, 2009; McGuire & Sabes, 2009) and could be involved in the different experiments to different degrees due to task differences. However, as mentioned above, the results clearly show that the biggest influence on reach errors was the target location as a function of gaze, depending either on where it was encoded or remapped.

The automatic remapping, induced in the trans-saccadic task, seems to occur before the information reaches the PPC since in that task our two patients with PPC lesion (1) were impaired when reaching toward their contralesional field, even if the target was originally presented in their "healthy" visual field and (2) transferred visual information acquired in the contralesional field to the spared cortical hemisphere, as revealed by accurate movements in their ipsilesional visual field. This suggests that the transfer mechanisms are not impaired in our patients and therefore do not take place at the level of the (damaged) PPC. Although parietal, frontal and occipital extra-striate cortices, as well as the superior colliculus, have been shown to remap visual stimulus representations in conjunction with eye movements (Duhamel, Colby, &

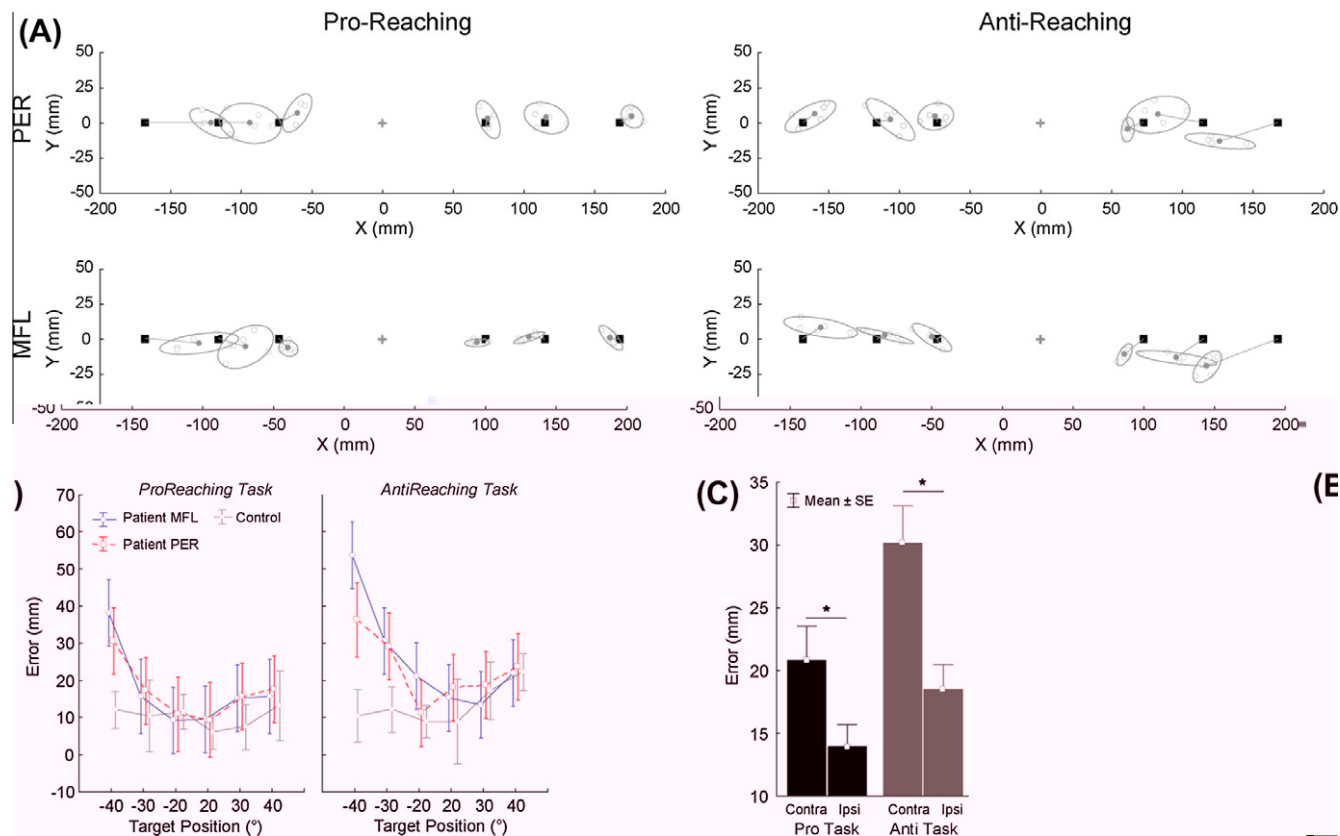


Fig. 4. (A) 2D illustration of the reaching endpoints in the Pro-reaching and Anti-reaching conditions for both patients relative to the position of the gaze (symbolised by the cross) at the time of the execution of the movement. Each movement endpoints (empty circles), the mean endpoints (filled circle) and the confidence ellipses (95%) are represented for each target position. (B) Mean and confidence intervals (95%) for absolute reaching errors for the two patients and a control subject (Patient MFL in blue, Patient PER in red, control in grey) in the Pro-reaching (left panel) and Anti-reaching (right panel) conditions plotted as a function of the visual target location relative to fixation at the time of the presentation of the visual target. (C) Mean and standard errors of both patients' combined reaching errors (in mm) as a function of the location of the visual target collapsed into the contralesional vs. ipsilesional visual fields for Experiment 2. Asterisks illustrate significant differences based on linear contrast analysis comparing targets in the left vs. right visual fields.

Table 1
Mean and standard deviation of reach reaction times (in ms) for all conditions and experiments.

	Fixation		Saccade	
	Left	Right	Left	Right
PER	543.31 ± 101.47	576.65 ± 132.28	602.82 ± 114.67	639.36 ± 121.37
MFL	630.23 ± 86.64	613.87 ± 88.67	634.20 ± 148.42	665.12 ± 114.18
	Pro-reaching		Anti-reaching	
	Left	Right	Left	Right
PER	570.05 ± 129.19	566.05 ± 98.79	699.11 ± 73.82	626.83 ± 107.35
MFL	613.60 ± 104.43	546.15 ± 81.14	667.80 ± 133.36	651.00 ± 102.21

Goldberg, 1992; Nakamura & Colby, 2002; Umeno & Goldberg, 1997), the crucial site of inter-hemispheric transfer in trans-saccadic remapping was proposed to be the PPC (Duhamel et al., 1992; Heide, Blankenburg, & Kömpf, 1995; Medendorp et al., 2003; Merriam et al., 2003). The results of the present paper confirm that, within the PPC, the region whose lesion leads to OA is not crucial for trans-saccadic remapping to occur. In their study of trans-saccadic remapping in patients with bilateral OA, Khan, Pisella, Rossetti, et al. (2005) showed that one patient (AT), with extensive damage to both parietal lobes as well as visual areas, could not correctly transfer the visual information of target position across hemispheres, while a second patient (IG), with more focal damage involving the superior parietal lobule and the

parieto-occipital and intra-parietal sulci, could correctly transfer information. Nakamura and Colby (2002) showed that more than half of the neurons recorded in monkey area V3A exhibit remapped activity. This proportion decreases in earlier visual areas. Similar findings have been shown in neurologically intact human subjects using functional neuroimaging (Merriam et al., 2007). In contrast to the dorsal PPC, the temporo-parietal junction, spared in OA but not in parietal neglect and constructional apraxia, might be crucially involved in automatic remapping, leading to specific symptoms such as spatial disorganisation during drawing or visual search (Pisella & Mattingley, 2004; Pisella et al., 2011; Russell et al., 2010).

The intentional remapping involved in the anti-reaching task led to different patterns of reaching errors in our two OA patients compared to the trans-saccadic remapping task. Indeed, in this task, the crucial factor leading to reaching inaccuracies was the visual field in which the target was originally presented and not the visual field in which the movement was executed. These results imply that it is not the same type of information that is transferred in this task as in the trans-saccadic remapping task. Very few studies have used the anti-reaching paradigm and of these, most were mainly behavioural studies (Carey, Hargreaves, & Goodale, 1996; Chua, Carson, Goodman, & Elliott, 1992; Heath, Maraj, Gradkowski, & Binsted, 2009; Maraj & Heath, 2010). Furthermore, most of them were restricted to the analysis of the movement kinematics (Carey et al., 1996; Chua et al., 1992) and the direction of the reaching errors (Heath et al., 2009; Maraj & Heath, 2010). The main finding from these studies was an increase in reaction time resembling

results from similar paradigm which has been extensively employed: the anti-saccade paradigm. Because the only difference between anti-saccade and anti-reaching is the effector used to execute the movement, it might be possible that the same visuo-motor mechanisms are involved in these two paradigms. In the anti-saccade literature, it has been suggested that the planning of anti-saccades is based on the inversion of the motor vector of the pro-saccade (Schlag-Rey et al., 1997). Alternatively, the visual switching hypothesis has been proposed for anti-saccades, which states that it is the target position that is remapped rather than the visuomotor vector. A strong argument in favour of this hypothesis comes from Zhang and Barash (2000) and the “paradoxical activity” they found in visual neurons of the lateral intra-parietal sulcus (LIP), which corresponds to a visual response to the stimulus in the remapped receptive field. However, the same authors (Zhang & Barash, 2004) also showed that some LIP neurons that have persistent activity in the memory interval show an “inversion” in their activity from the visual direction to the motor direction during anti-saccade trials. Therefore, depending on the type of LIP neurons (persistent or visual), both hypotheses (motor vector inversion or visual target inversion) have neurophysiological support. It could be that both mechanisms are involved, but at different time scales. Neuroimaging studies have also shown a switching of activity in

the posterior parietal cortex (Medendorp et al., 2005; Moon et al., 2007; Van Der Werf et al., 2008) with the first activity due to the sensory stimulation, followed by the motor plan activity. The present results with OA patients clearly argue in favour of the motor plan inversion (Schlag-Rey et al., 1997) for anti-reaching. Lesions of the posterior parietal areas largely disrupted the visuo-manual transformation of the target when it was presented in the patients’ contralesional visual field and this erroneous motor plan was transferred into the spared hemisphere (for motor execution in the ipsilesional visual field). Conversely, when the target was presented in the ipsilesional visual field, an accurate motor plan was transferred into the damaged hemisphere (for motor execution in the contralesional visual field). The inter-hemispheric transfer might therefore occur at the level of the frontal cortex. Indeed, different neuroimaging studies in humans have shown the importance of frontal areas (FEF, SEF, DLPFC, pre-SMA) in the preparation of anti-saccades (Connolly et al., 2002; Curtis & D’Esposito, 2003; Ford, Goltz, Brown, & Everling, 2005).

Despite the fact that intentional and automatic remapping can be both observed in the same region of the posterior parietal cortex (see Medendorp et al. (2003) for trans-saccadic remapping and Medendorp et al. (2005) for anti-saccades), the present study provides clear evidence that these two mechanisms differently implicate the posterior parietal cortex. We suggest that the two remapping mechanisms (automatic and intentional) involve hemispheric transfer of sensorimotor information at different levels (Fig. 5). Concerning the location of the hemispheric transfer, the present results from the saccadic remapping task as well as previous one (Khan, Pisella, Vighetto, et al., 2005) are in favour of a posterior location, prior to the lesion site, probably in extrastriate areas (Nakamura & Colby, 2002) or in the temporo-parietal junction (Pisella et al., 2011). On the other hand, the intentional remapping transfer revealed in the anti-reaching task would occur at the level of the PPC itself or more anterior (e.g. in the pre-frontal cortex). It is not possible, in regards to the present study, to clearly state on the location of these inter-hemispheric transfers.

5. Conclusions

By comparing the performance of two patients with PPC lesions in two different tasks involving different types of remapping processes, we were able to demonstrate that the automatic and the intentional transfer of sensorimotor information occurs at different levels within the stream for visuo-manual transformations.

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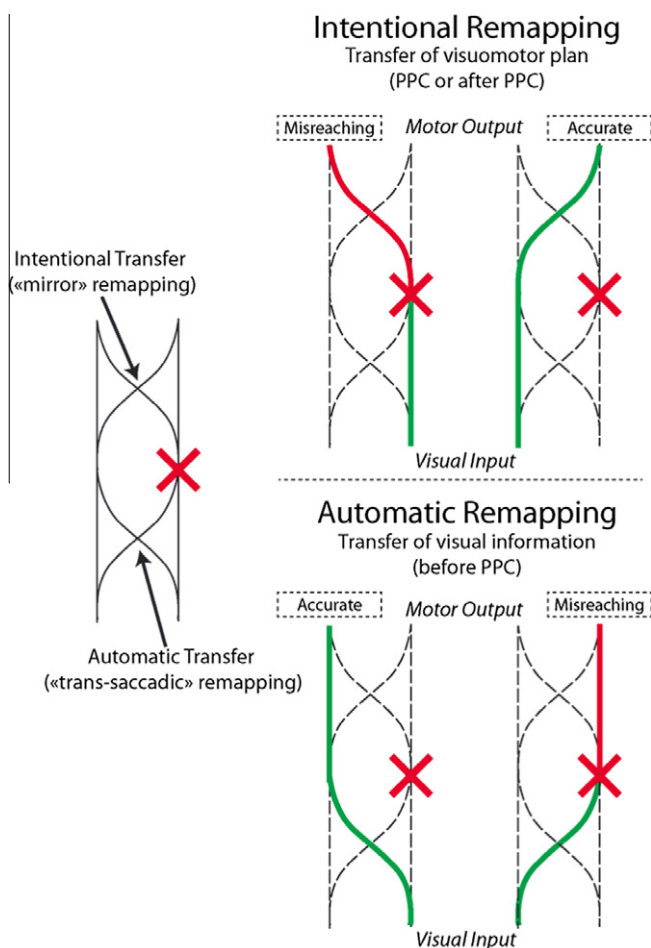


Fig. 5. Schematic of the proposed level of inter-hemispheric transfer of visuo-motor information involved in the two different types of remapping, intentional and automatic. In the case of intentional remapping, the transfer would occur at the level of the PPC or after, inducing, for patients with unilateral optic ataxia, reaching errors for targets originally presented in the contralesional visual field. For automatic remapping, the transfer would occur before the PPC, inducing reaching errors for patients with unilateral optic ataxia for movements directed toward the contralesional field.

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