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Research report

Causal evidence for posterior parietal cortex involvement in visual-to-motor transformations of reach targets

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ABSTRACT

It has been posited that the posterior parietal cortex (PPC) is involved in the visual-to-motor transformation for reach planning. Such a transformation is required because in general the retinal information and the arm motor command do not align, for example in the case of non-zero eye/head orientations. Here, we present behavioral data from a patient with unilateral optic ataxia consecutive to damage to the superior parietal lobule including the intraparietal sulcus in the right hemisphere, who we asked to reach to visual targets under different head roll angles. An accurate visual-to-motor transformation has to integrate head roll to compensate for the rotated retinal location of the target, resulting in a head roll-independent pattern of reach endpoints. If however, head roll is not compensated for, reach endpoints should vary across different head rolls, reflecting a reach plan based on the rotated retinal target location. Remarkably, the patient compensated for head roll when reaching to targets presented within his intact right visual field (VF) (not different from controls) but not for reaches to targets in the contralesional left VF. The amount of compensation was the same irrespective of whether the initial hand position was located in the left or right VF, showing that this transformation concerns only the target location and not the hand-target motor vector. We interpret these findings as causal evidence for the involvement of the PPC in integrating head roll signals in the visual-to-motor transformation of the reach target.

1. Introduction

Movement planning requires a sensory-to-motor transformation (Crawford et al., 2004; Snyder, 2000; Soechting and Flanders, 1992). In the case of the visual-to-motor transformation for reaching, visual information enters the brain in retinal coordinates, whereas the arm motor plan needs to be specified in a coordinate system relative to the shoulder, the insertion point of the arm (Flash and Sejnowski, 2001). Therefore, retinal inputs have to be transformed into shoulder-centered coordinates by means of a reference frame transformation that takes the relative misalignment of the

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eyes, head and body into account (Blohm and Crawford, 2007; Crawford et al., 2004).

Current views state that this transformation occurs in a distributed parietal–frontal network of areas; correlates of the visual-to-motor conversion for reaching have been shown in the posterior parietal cortex (PPC) (Battaglia-Mayer et al., 2003; Batista et al., 1999; Buneo et al., 2002; Cohen and Andersen, 2002) as well as the dorsal part of the pre-motor cortex (Battaglia-Mayer et al., 2003; Batista et al., 2007; Pesaran et al., 2006). The PPC has long been known as a sensory association area (Hyvarinen, 1982); it receives visual information from striate and extra-striate areas (Robinson et al., 1978) and carries information about eye and head position from proprioception (Brotchie et al., 1995), inner ear organs (Andersen et al., 1999) and efference copies of the motor commands (Mountcastle et al., 1975). In addition, neurophysiological recordings in the PPC have shown gain modulation of visual receptive fields by eye and head position signals (Andersen et al., 1985; Brotchie et al., 1995), which is believed to be the signature of reference frame transformations (Blohm and Crawford, 2009). Previous reaching studies on optic ataxia patients with PPC damage (Perenin and Vighetto, 1988) have shown that early internal representations of target location are accurate (Khan et al., 2005b) suggesting that the PPC is involved in reference frame transformations which result in reaching deficits to visual targets. However the causal role of the PPC for a retinal-to-shoulder transformation has never been explicitly tested.

With chronic lesions, a consistent deficit argues strongly for a causal role of an area for a certain process, since plasticity mechanisms have been unable to eliminate the functional deficit even after many years (Rafal, 2006). We asked a patient with chronic left optic ataxia resulting from damage to the superior parietal lobule (SPL) and the intraparietal sulcus (IPS) in the right hemisphere and a group of neurologically intact controls to reach to targets from different initial hand positions (IHPs) while the head was straight or rolled to either shoulder.

We used head roll as a tool to dissociate retinal and shoulder-centered reference frames, allowing us to directly address the role of the PPC in the visual-to-shoulder reference frame transformation for reaching. The advantage of head roll is that it rotates the retinal stimuli around the fovea without compromising their visual quality. Under different head roll orientations, the visual input is rotated around the line of sight, creating a misalignment of visual and shoulder reference frames. This requires a head roll-dependent reference frame transformation to compensate for this misalignment. We evaluated the subjects' ability to compensate for head roll in the visuomotor transformation against our predictions; if head roll was not accounted for at all, we would expect a rotation of reach endpoints that is equal to the rotation of the visual image on the retina, resulting in large head-roll dependent changes in reach endpoints. This is shown in Fig. 1, where the leftward reach target (relative to the shoulder – Fig. 1A) is rotated relative to the retinal axes when the head is rolled to the left (Fig. 1B). Our tilted reaching setup is depicted in Fig. 1C, which results in targets being projected in a specific manner onto the reaching surface. Thus, if the head is straight, the reach target is projected directly to the left of the fixation (open solid circle in Fig. 1B). However, if the head is rolled to the left and head roll is not compensated for, the reach would be shifted to the target's retinal position (open dotted circle) which is projected further in depth on the reaching surface, i.e., the subject would reach to the target's retinal position as if the head was upright. In contrast, when

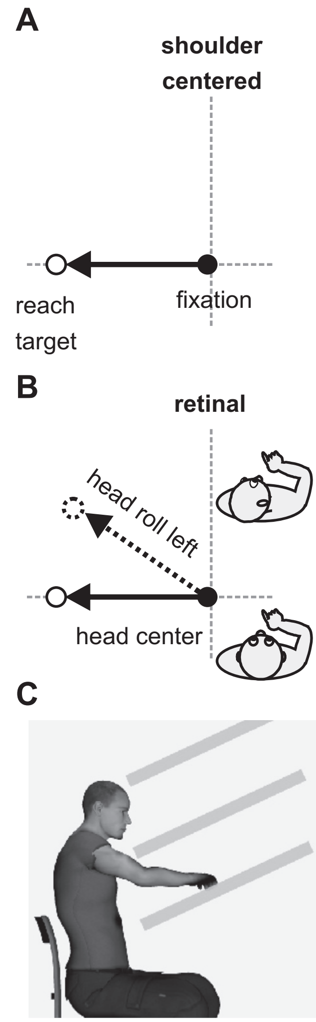

Fig. 1 – Schematic of hypothesis. A. In a shoulder-centered reference frame, the leftward reach target (open circle) is directly left of the fixation (black filled circle) regardless of head roll as shown by the arrow. The dotted lines represent the cardinal axes relative to the shoulder. B. However, in a retinal reference frame, the location of the reach target changes depending on head roll. If the head is at center, the reach target direction matches that of the shoulder-centered reference frame (solid arrow). However, when the head is rolled toward the left shoulder (as in the upper icon), the direction of the reach target relative to the cardinal axes changes (dotted arrow). C. Depiction of the tilted reaching setup. Subjects viewed targets projected from the top surface, through a half-reflecting mirror (middle surface) onto a tilted reaching surface. All surfaces were tilted 30°. Through this setup, subjects reached to targets without visual feedback of their hand.