BRAIN RESEARCH 1358 (2010) 160–171

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BRAIN RESEARCH

Research Report

Interruption of visually perceived forward motion in depth evokes a cortical activation shift from spatial to intentional motor regions

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ARTICLE INFO

Article history:
Accepted 17 August 2010
Available online 24 August 2010

Keywords:
Optic flow
fMRI
Freezing of gait
Premotor cortex
Pre-SMA

ABSTRACT

Forward locomotion generates a radially expanding flow of visual motion which supports goal-directed walking. In stationary mode, wide-field visual presentation of optic flow stimuli evokes the illusion of forward self-motion. These effects illustrate an intimate relation between visual and motor processing. In the present fMRI study, we applied optic flow to identify distinct interfaces between circuitries implicated in vision and movement. The dorsal premotor cortex (PMd) was expected to contribute to wide-field forward motion flow (FFw), reflecting a pathway for externally triggered motor control. Medial prefrontal activation was expected to follow interrupted optic flow urging internally generated action. Data of 15 healthy subjects were analyzed with Statistical Parametric Mapping and confirmed this hypothesis. Right PMd activation was seen in FFw, together with activations of posterior parietal cortex, ventral V5, and the right fusiform gyrus. Conjunction analysis of the transition from wide to narrow forward flow and reversed wide-field flow revealed selective dorsal medial prefrontal activation. These findings point at equivalent visuomotor transformations in locomotion and goal-directed hand movement, in which parietal–premotor circuitry is crucially implicated. Possible implications of an activation shift from spatial to intentional motor regions for understanding freezing of gait in Parkinson's disease are discussed: impaired medial prefrontal function in Parkinson's disease may reflect an insufficient internal motor drive when visual support from optic flow is reduced at the entrance of a narrow corridor.
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1. Introduction

Forward locomotion generates a characteristic streaming motion of environmental features through the visual field. This 'optic flow' implies a radial expansion from the central point on the horizon ahead, provided that the observer does not fixate a specific object (Gibson, 1954; Wurtz et al., 1993). Distant objects are located near the center of the visual field and move slowly from it, while nearby objects are in the peripheral field and move further in eccentric direction with

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doi:10.1016/j.brainres.2010.08.050

increasing speed. In stationary condition, a similar sensation of forward self-motion can be evoked by presenting a pattern of expanding radial optic flow in the lower part of the visual field (Kovács et al., 2008). This visual effect is in line with the finding that humans make use of optic flow to walk to a goal (Warren et al, 2001). The latter suggests visuomotor coordination equivalent to the support of visual information to accomplish adequate reaching movements (Johnson et al., 1996; Sakata et al., 1997).

In Parkinson's disease (PD), which is predominantly characterised by motor symptoms such as rigidity and bradykinesia, support of sensory cues on walking is illustrated by gait improvement that has been demonstrated by the presentation of parallel traverse lines on the walking surface (Azulay et al., 1999; Suteerawattananon et al., 2004). Suppression of this gait improvement by stroboscopic light further demonstrated that perceived motion of the stripes, induced by the patient's walking, was an essential aspect of gait support and favoured the involvement of visuomotor circuitry responsive to rapidly moving targets (Azulay et al., 1999). In contrast to the supportive effects of sensory cues, incompatible stimuli may obstruct intended movements in PD and may even result in deviant movement patterns aligned to these external cues (Freeman et al., 1993; De Jong et al., 1999). With regard to gait, such motor blocking occurs at the transition to narrow spaces (Giladi et al., 1992; Okuma, 2006). Given the impact of optic flow on gait, both in normal conditions and in PD, we employed functional magnetic resonance imaging (fMRI) to gain further insight in the interconnection between pathways involved in processing optic flow and circuitry implicated in motor control.

Functional imaging of the human brain has demonstrated that visual motion processing strongly involved activation of extrastriate visual area V5 (Watson et al., 1993; Tootell et al., 1995), while the specific perception of forward motion in depth was related with activations distributed over extrastriate visual regions ventral to V5 (the fusiform gyrus), dorsal V3, and the dorsolateral precuneus of the superior parietal lobe (De Jong et al., 1994; Morrone et al., 2000; Kovács et al., 2008). Particularly, the parietal involvement was proposed to reflect the ability to play a central role in visuomotor coordination, i.e., control of locomotion, integrated with temporal cortex processing associated with the perception of the environmental scene. Widely described functional interconnection between posterosuperior parietal areas and dorsolateral premotor regions in visuomotor coordination underscores that external stimuli indeed efficiently influence motor control (Wise et al., 1997; Clavagnier et al., 2007). Prefrontal cortical regions, on the other hand, may exert an inhibitory effect on such external triggers, complementing the internal generation of movements (De Jong and Paans, 2007; Koechlin and Hyafil, 2007). With regard to internal movement generation, particularly medial frontal regions such as (pre-) supplementary motor area (SMA) and medial prefrontal cortex have been reported to play a prominent role (Lau et al., 2004; Rushworth, 2008; Brass and Haggard, 2008). These frontal regions are major output targets of the basal ganglia, reached via the thalamus (Middleton and Strick, 2000). Dysfunction of such projections in PD leads to a disturbed balance between external and internal impacts on the cerebral organization of movement, with increased vulnerability to external cues (Praamstra and Plat, 2001; Hallett, 2008) that may either enhance or obstruct intended movements.

In the present study, on healthy subjects, we aimed to explore how visual stimulation might influence cerebral circuitry implicated in gait control. To that end, we presented wide-field radially expanding optic flow, mimicking the perception of forward motion in depth, followed by a transition to a narrow flow field. We hypothesized to find activations evoked by wide-field forward flow in the parietal and dorsal premotor cortex (PMd), while such activations were expected to stop at the transition to the narrow flow field. At this transition, medial prefrontal activation was expected to occur, reflecting a functional shift between circuitries implicated in respectively externally enhanced and internally generated motor control. Given the fact that motor-related cortical circuitry maintains a level of intrinsic activation in resting state without a specific motor task (Xiong et al., 1999), we assumed it plausible that specific visual stimulus conditions might indeed interact with such functional circuitry. To deal with the bias related to the size of the visual field, a condition with reversed wide-field flow was included. Compared to forward flow, less biological significance with regard to locomotion has been attributed to such reversed flow (Ptito et al., 2001; Wunderlich et al., 2002).

2. Results

2.1. *The illusion of self-motion*

The control static stimulus display (Cstat) did not evoke any sensation of self-motion and was rated 0 ± 0.1 (mean ± SD). The scores for wide forward flow (FFw), wide reversed flow (RFw), and narrow-field forward flow were 6.8 (±2.4), 6.3 (±2.7) and 3.0 (±1.9), respectively. Ratings for these visual motion conditions were significantly different from the score attributed to Cstat ($P < 0.001$). The illusion of self-motion evoked by each of the two wide-field optic flow conditions was significantly stronger than the sensation evoked by the narrow flow field ($P < 0.001$). No significant difference was found between ratings for this illusion in FFw and RFw. One might consider that although FFw mimics the most natural circumstance of perceived forward self-motion, reversed flow is a visual experience which became particularly familiar in modern life, e.g., during travelling in a train seated backwards.

2.2. *Forward wide flow*

Cerebral activations related to the perception of forward self-motion were identified by contrasting FFw to Cstat (condition 1>7). Significant increases were distributed around the posterior part of calcarine sulcus, including the fovea representation in the primary visual cortex (V1) and over the lateral extrastriate visual cortex (with putative area V3) extending into the visual motion area V5 (Fig. 1). Particularly, on the right side, the cluster that included V5 spread ventrally. In dorsal direction, significant increases were bilaterally found at the junction of the occipital and parietal cortex around the

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