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Processing of visual gravitational motion in the peri-sylvian cortex: Evidence from brain-damaged patients

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ABSTRACT

Rich behavioral evidence indicates that the brain estimates the visual direction and acceleration of gravity quite accurately, and the underlying mechanisms have begun to be unraveled. While the neuroanatomical substrates of gravity direction processing have been studied extensively in brain-damaged patients, to our knowledge no such study exists for the processing of visual gravitational motion. Here we asked 31 stroke patients to intercept a virtual ball moving along the vertical under either natural gravity or artificial reversed gravity. Twenty-seven of them also aligned a luminous bar to the vertical direction (subjective visual vertical, SVV). Using voxel-based lesion-symptom mapping as well as lesion subtraction analysis, we found that lesions mainly centered on the posterior insula are associated with greater deviations of SVV, consistent with several previous studies. Instead, lesions mainly centered on the parietal operculum decrease the ability to discriminate natural from unnatural gravitational acceleration with a timed motor response in the interception task. Both the posterior insula and the parietal operculum belong to the vestibular cortex, and presumably receive multisensory information about the gravity vector. We speculate that an internal model estimating the effects of gravity on visual objects is constructed by transforming the vestibular estimates of mechanical gravity, which are computed in the brainstem and cerebellum, into internalized estimates of virtual gravity, which are stored in the cortical vestibular network. The present lesion data suggest a specific role for the parietal operculum in detecting the mismatch between predictive signals from the internal model and the online visual signals.

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1. Introduction

Reference to gravity is critical to keep balance and orientation in space, and to interact with objects (Howard, 1982). More generally, gravity reference helps estimating the current state of our environment, i.e. the spatial orientation of our body and surrounding objects, and it also helps predicting future states, i.e. whether or not we (or an object) are about to topple, or when a falling object will land. There is now ample behavioral evidence that under normal conditions the brain estimates gravity direction and acceleration quite accurately (see Lacquaniti et al., 2015). Perceptual estimates of the direction of gravity are typically assessed in a dark environment by asking participants to align a luminous bar to the Earth-vertical (subjective visual vertical, SVV (Dichgans, Held, Young, & Brandt, 1972; Mittelstaedt, 1983; Tarnutzer, Bockisch, Straumann, & Olasagasti, 2009; Udo de Haes & Schöne, 1970; Vingerhoets, De Vrijer, Van Gisbergen, & Medendorp, 2009)). As for the estimates of gravity effects on visual motion, these are assessed by asking participants to intercept a target falling along the vertical direction (Lacquaniti & Maioli, 1989; McIntyre, Zago, Berthoz, & Lacquaniti, 2001; Vishton, Reardon, & Stevens, 2010; Zago et al., 2004) or to judge the duration of fall (Moscatelli & Lacquaniti, 2011).

Our ability to estimate gravity direction and acceleration is striking if one considers that information about the gravity vector provided by each single sensory channel is ambiguous and noisy. Thus, the vestibular otoliths signal the net gravito-inertial acceleration, and cannot distinguish between gravitational and inertial components (Fernández & Goldberg, 1976). Moreover, the neural estimates of head tilt relative to gravity are noisy (De Vrijer, Medendorp, & Van Gisbergen, 2008; MacNeilage, Banks, Berger, & Bülthoff, 2007), and the visual estimates of target accelerations are generally poor (Brouwer, Brenner, & Smeets, 2002; Werkhoven, Snippe, & Toet, 1992). However, weighted combinations of multisensory cues with prior assumptions about the environment can yield very accurate estimates (Angelaki, Klier, & Snyder, 2009). For SVV estimates, visual, vestibular, somatosensory and visceral cues are integrated with a prior assuming that the head and body are most likely oriented near the vertical (De Vrijer et al., 2008; MacNeilage et al., 2007). For the estimates of gravitational acceleration when intercepting descending targets, visual and vestibular cues are integrated with a prior assuming that the target is most likely accelerated by Earth's gravity (Lacquaniti et al., 2015).

Critically, new sensory evidence, if sufficiently robust, can overrule prior expectations and yield responses more appropriate to the current context (Angelaki et al., 2009). For instance, the prior expectation of Earth gravity for a descending target can be overridden by strong sensory evidence that gravity effects are lacking (Bosco, Carrozzo, & Lacquaniti, 2008; Indovina et al., 2005; McIntyre et al., 2001; Miller et al., 2008; Zago et al., 2004). Indeed, both the prior expectation of gravity effects on an object motion as well as the ability to detect artificial violations of these effects are present at an early age. Thus, 11-months old infants expect that an unsupported object falls, that an object moving down an inclined plane accelerates and an upwardly moving object decelerates, and they are surprised to see violations of these expectations (Kim & Spelke, 1992; Stahl & Feigenson, 2015).

The ability of human adults to discriminate between target motion compatible with natural gravity and motion incompatible with natural gravity was tested in a series of studies in which participants pressed a button to intercept a virtual ball moving along the vertical under either natural gravity (1g) or artificial reversed gravity (−1g), while their brain responses were measured with functional magnetic resonance imaging (Indovina et al., 2005; Maffei, Macaluso, Indovina, Orban, & Lacquaniti, 2010; Miller et al., 2008). It was found that 1g trials were associated with significantly greater activity than −1g trials in regions located within and around the Sylvian fissure, including the posterior insular cortex, retro-insula, parietal operculum, supramarginal gyrus, and superior temporal gyrus (see also Fautrelle, Pichat, Ricolfi, Peyrin, & Bonnetblanc, 2011). Indovina et al. (2005) further showed that these brain sites, responding to the contrast of 1g versus −1g visual stimuli, co-localize with regions independently activated by vestibular caloric stimuli. They then suggested that the cortical regions responding to visual gravitational motion belong to the multi-modal vestibular network. In particular, the posterior insula, retroinsular cortex, and parietal operculum represent the putative human functional equivalent (Brandt & Dieterich, 1999; Lopez & Blanke, 2011; Lopez, Blanke, & Mast, 2012; Zu Eulenburg, Caspers, Roski, & Eickhoff, 2012) of the parieto-insular vestibular cortex of the monkey, the core region of vestibular cortex described by Guldin and Grüsser (1998).

While fMRI studies show which regions are involved in a task, brain lesion studies allow deducing which regions are necessary (Chatterjee, 2005; Müller & Knight, 2006; Rorden & Karnath, 2004). Thus, the neuroanatomical substrates for processing the direction of gravity in the SVV task have been extensively studied in neurological patients (Baier, Suchan, Karnath, & Dieterich, 2012; Baier, Thömke, et al., 2012; Baier, Zu Eulenburg, et al., 2013; Barra et al., 2010; Brandt, Dieterich, & Danek, 1994; Dieterich & Brandt, 1993; Hegemann, Fitzek, Fitzek, & Fetter, 2004; D. Pérennou et al., 2014; D. A. Pérennou et al., 2008; Rousseaux, Braem, Honoré, & Saj, 2015; Rousseaux, Honoré, Vuilleumier, & Saj, 2013; Tarnutzer, Wichmann, Straumann, & Bockisch, 2015). Although a pathologic tilt of the SVV has been observed after lesions at several different brain sites, the involvement of the posterior insular and retroinsular cortex has been a relatively consistent finding across several such studies (Baier, Zu Eulenburg, et al., 2013; Barra et al., 2010; Brandt et al., 1994; Rousseaux et al., 2013; but see Baier, Conrad, et al., 2013). In particular, using quantitative voxel-based lesion-behavior mapping, Baier, Suchan, Karnath, & Dieterich (2012) found a significant association between tilt of SVV and lesion of the insular cortex and inferior frontal gyrus in acute unilateral stroke patients.

By contrast, no study to our knowledge investigated the neuroanatomical correlates of altered timing estimates for targets moving along the vertical in brain-damaged patients. In fact, compared with the extensive literature dealing with SVV estimation, relatively few studies have explored how