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Simulated self-motion in a visual gravity field: Sensitivity to vertical and horizontal heading in the human brain

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ABSTRACT

Multiple visual signals are relevant to perception of heading direction. While the role of optic flow and depth cues has been studied extensively, little is known about the visual effects of gravity on heading perception. We used fMRI to investigate the contribution of gravity-related visual cues on the processing of vertical versus horizontal apparent self-motion. Participants experienced virtual roller-coaster rides in different scenarios, at constant speed or 1g-acceleration/deceleration. Imaging results showed that vertical self-motion coherent with gravity engaged the posterior insula and other brain regions that have been previously associated with vertical object motion under gravity. This selective pattern of activation was also found in a second experiment that included rectilinear motion in tunnels, whose direction was cued by the preceding open-air curves only. We argue that the posterior insula might perform high-order computations on visual motion patterns, combining different sensory cues and prior information about the effects of gravity. Medial–temporal regions including parahippocampus and hippocampus were more activated by horizontal motion, preferably at constant speed, consistent with a role in inertial navigation. Overall, the results suggest partially distinct neural representations of the cardinal axes of self-motion (horizontal and vertical).

Introduction

Brain mechanisms for visual perception of heading direction during self-motion have drawn considerable attention (Britten, 2008; Orban, 2001; Warren, 2006). Multiple visual signals are relevant, including optic flow, monocular or stereo depth, and path. Sensitivity to these signals has been revealed in different brain regions of the monkey, such as the dorsal medial superior temporal area (MSTd, Duffy and Wurtz, 1991; Froehler and Duffy, 2002; Gu et al., 2006; Lagae et al., 1994), ventral intra-parietal area (VIP, Chen et al., 2011), parieto-occipital V6 area (Galletti et al., 2001), and in their putative human homologues (Bremmer et al., 2001; Cardin and Smith, 2010; Kovács et al., 2008; Morrone et al., 2000; Orban and Jastorff, in press; Peuskens et al., 2001; Wall and Smith, 2008).

Although less studied, also the visual effects of gravity may contribute to heading perception. Thus, the cardinal directions, horizontal and vertical, are cued by the orientation of several features of a realistic scene (e.g., the horizon, trees, buildings, people). Moreover, visual kinematics can differ between vertical and horizontal motion. In the absence of friction, downward free-fall and upward motion under gravity are associated with a constant acceleration and deceleration respectively, whereas horizontal motion unfolds at constant speed once ceased the effects of applied impulsive forces.

Mechanisms for dealing with object motion under gravity have been studied extensively (Zago et al., 2009). It has been shown that visual estimates of this type of motion depend on a prior of gravity effects (McIntyre et al., 2001; Moscatelli and Lacquaniti, 2011), are affected by vestibular inputs (Senot et al., 2012), and are encoded in a visual–vestibular network whose core region is represented by the posterior insula (Indovina et al., 2005). Indeed, this network responds to both vertical target motions coherent with gravity and vestibular caloric stimulation in human fMRI studies (Indovina et al., 2005).

Here we consider the possibility that the horizontal and vertical directions of self-motion are represented in partially distinct neural circuits. In particular, the previously described visual–vestibular network might process vertical self-motion direction by taking into account the visual effects of gravity as in the case of object motion. In a previous fMRI study, horizontal and vertical small-field optokinetic stimulation (colored objects on a rotating drum) activated the same multiple visual, oculomotor and vestibular cortical and subcortical

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regions (Dieterich et al., 1998). However this study did not address the issue of the visual effects of gravity during apparent self-motion. To address this issue, we measured the fMRI brain signals associated with simulated roller-coaster rides within diverse realistic visual landscapes (Baumgartner et al., 2008). The roller-coaster car traveled along tracks consisting of separate vertical and horizontal rectilinear sections, connected by curves. In both vertical and horizontal sections, the car accelerated, decelerated, or moved at constant speed. Car acceleration/deceleration was coherent with gravity for vertical motion, while the same acceleration/deceleration was artificial for horizontal motion. In a first experiment the roller-coaster car traveled in mountain landscapes (Outdoors) while it traveled within dark tunnels in a second experiment (Indoors). In the latter case the direction of movement was cued by the preceding open air curves only. We introduced the Outdoors/Indoors manipulation in order to control for possible visual unbalance between conditions in the Outdoors experiment.

Consistent with our hypotheses, we found that vertical visual motion compatible with self-motion under gravity engaged the posterior insula and other brain regions previously associated with vertical object motion under gravity, whereas horizontal motion at constant speed engaged the hippocampus. In a control behavioral experiment, we asked participants to rate the sensation of self-motion associated with each rectilinear section of the Outdoors protocol, and we found that this sensation did not differ significantly between vertical and horizontal sections.

Methods

Participants

Thirty-nine right-handed subjects with normal or corrected-to-normal vision gave written informed consent to participate in accordance with the procedures established by the Ethics Committee of the Santa Lucia Foundation. Thirteen subjects (7 males and 6 females, 19–32 years old) participated in the Outdoors fMRI protocol, thirteen subjects (6 males and 7 females, 18–32 years old) participated in the Indoors fMRI protocol, and thirteen subjects (6 males and 7 females, 26–42 years old) participated in the control behavioral protocol with rating of self-motion perception ("self-motion intensity perception" experiment).

Visual stimuli

Rides on a roller-coaster were simulated by displaying first-person perspective views of animated visual scenes compatible with forward self-motion (Fig. 1). Custom roller-coasters were constructed using several different modules of commercial software (www.nolimitscoaster.com, Mad Data, Joerg Henseler, Erkrath, Germany). Each ride consisted of ups, downs, horizontal tracks, and curves in pseudo-three-dimensional space, as well as different acceleration profiles and brake passages (see below). AVI videos were displayed by means of Presentation 14.1 (Neurobehavioral Systems Inc., Albany, Canada), at 1024×768 pixels, 60 frames per second, 24°×19° visual angle. The participant's view was that of a passenger sitting in the front-car and looking straight ahead. Separate vertical ("V") and horizontal ("H") rectilinear sections were connected by curved sections. A red fixation cross (0.5°) was displayed at the center of the scene, corresponding to the focus of expansion during rectilinear motion.

In the Outdoors protocol, the car traveled all the time in the open air, across several different mountain landscapes (Figs. 1A, C). In the realistic scenarios of the roller-coaster, low-level visual features (i.e. luminance, color, contrast, texture, optic flow) and figural elements (e.g., grass, trees, lakes, sky) could not be matched between vertical and horizontal sections.

To eliminate these confounds in the rectilinear sections (conditions of interest in the present study), the car traveled in the open air only in the curved sections of the Indoors protocol (Fig. 1C), whereas it traveled within tunnels in the rectilinear sections (Fig. 1B). In the tunnels, only the track was illuminated, resulting in identical visual patterns for the vertical and horizontal sections. In this manner, the current direction of rectilinear motion (V or H) was solely indicated by the visual context of the immediately preceding curve (i.e., whether the curve turned left, right, up, or down).

Design

Along rectilinear sections, the car moved at constant speed, constant acceleration (9.8 m s^{-2}), or constant deceleration (-9.8 m s^{-2}), depending on the section. Acceleration or deceleration was consistent with gravity (and negligible friction) for vertical motion, so that downward motion was accelerated (as in free-fall) while upward motion was decelerated. Instead, the same acceleration or deceleration was consistent with powered propulsion for horizontal motion. The vertical condition simulated purely vertical displacements along the terrestrial vertical in absence of friction and horizontal perturbation forces that could cause the car to lose adherence with the binaries.

In the following, acceleration and deceleration are cumulatively denoted as "a", while constant speed motion is denoted as "c". Overall we used a 2×2×2 factorial design (Fig. 2A), crossing motion direction (V/H), motion law (a/c), and visual context (Outdoors/Indoors). Thus, in the ensuing analyses, vertical sections with acceleration and deceleration were lumped together and the same was done for horizontal sections.

Epochs of continuous motion (46 blocks, 34–95 s duration range, 67 s average duration, Fig. 2B) were inter-leaved with static epochs (46 blocks, 15 s duration). In the latter epochs, the car stopped at the current location along the path (resulting in static V or static H conditions). Each motion direction and each motion law were pseudo-randomly assorted across the rectilinear sections of each block. In each experiment, we used 8 different roller-coasters (consisting of different combinations of track elements), each one associated with 2 different background scenarios (consisting of different landscapes). Thus, there were a total of 16 different scenarios.

Trials

There were a total of 60 trials for condition Va (vertical accelerated motion) and 60 trials for condition Ha (horizontal accelerated motion). In half of these trials, the car accelerated and in the other half it decelerated (1.6–6 s duration range, 3.4 s average duration in both cases). There were a total of 28 trials for condition Vc (vertical constant speed motion), half upwards (2.4–8.2 s duration range, 5.6 s average duration) and half downwards (4.2–8.6 s duration range, 6 s average duration). Condition Hc included 25 trials (range of 2.7–10.5 s, average 7 s). For both H and V, the speed values of the constant speed trials matched the average speeds of the accelerated trials.

Tasks

Participants were instructed to fixate the central cross while paying attention to the current direction of car motion. At a random time, the color of the fixation cross changed from red to green for 0.5 s, at an average time interval of 40 s ($\pm$15 s SD, 6–134 s range) relative to the previous color change. Participants pressed one of two buttons as soon as possible after the color change to indicate whether they judged that the current direction of motion was vertical or horizontal. Because of the impoverished visual cues, the direction of motion could be difficult to discriminate during the Indoors protocol. Thus, two days before the scanning session, participants in this protocol underwent a training session which was identical to the experimental