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Alessandro Moscatelli and Francesco Lacquaniti

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Processing of Targets in Smooth or Apparent Motion Along the Vertical in the Human Brain: An fMRI Study

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Maffei V, Macaluso E, Indovina I, Orban G, Lacquaniti F. Processing of targets in smooth or apparent motion along the vertical in the human brain: an fMRI study. *J Neurophysiol* 103: 360–370, 2010. First published November 4, 2009; doi:10.1152/jn.00892.2009. Neural substrates for processing constant speed visual motion have been extensively studied. Less is known about the brain activity patterns when the target speed changes continuously, for instance under the influence of gravity. Using functional MRI (fMRI), here we compared brain responses to accelerating/decelerating targets with the responses to constant speed targets. The target could move along the vertical under gravity (1g), under reversed gravity (−1g), or at constant speed (0g). In the first experiment, subjects observed targets moving in smooth motion and responded to a GO signal delivered at a random time after target arrival. As expected, we found that the timing of the motor responses did not depend significantly on the specific motion law. Therefore brain activity in the contrast between different motion laws was not related to motor timing responses. Average BOLD signals were significantly greater for 1g targets than either 0g or −1g targets in a distributed network including bilateral insulae, left lingual gyrus, and brain stem. Moreover, in these regions, the mean activity decreased monotonically from 1g to 0g and to −1g. In the second experiment, subjects intercepted 1g, 0g, and −1g targets either in smooth motion (RM) or in long-range apparent motion (LAM). We found that the sites in the right insula and left lingual gyrus, which were selectively engaged by 1g targets in the first experiment, were also significantly more active during 1g trials than during −1g trials both in RM and LAM. The activity in 0g trials was again intermediate between that in 1g trials and that in −1g trials. Therefore in these regions the global activity modulation with the law of vertical motion appears to hold for both RM and LAM. Instead, a region in the inferior parietal lobule showed a preference for visual gravitational motion only in LAM but not RM.

INTRODUCTION

Many animal species depend on visual motion perception for survival. Thus interception or avoidance of a moving target requires the estimate of its spatial-temporal trajectory. The neural underpinnings of visual motion processing for constant speed targets have been studied extensively both in the monkey and man (for reviews, see Born and Bradley 2005; Orban et al. 2003). Less is known about the brain substrates of kinematic estimates when the target speed changes continuously (Lisberger and Movshon 1999; Price et al. 2005; Schlack et al. 2007). In particular, target objects are frequently accelerated by Earth gravity ($1g = 9.81 \text{ m/s}^2$), as in free-fall or projectile motion. Visual information about gravitational acceleration

seems to contribute to perception of causality and naturalness of inanimate motion (Kim and Spelke 1992; Twardy and Bingham 2002), perception of distance and size of falling objects (Watson et al. 1992), perception of biological motion (Troje and Westhoff 2006; Vallortigara and Regolin 2006), perception of human body postures (Lopez et al. 2009), judgments of time intervals (Grealy et al. 2004; Huber and Krist 2004), and manual interception of falling targets (Lacquaniti and Maioli 1989a,b; McIntyre et al. 2001; Zago et al. 2004). However, the brain substrates for processing visual gravitational motion are still incompletely understood.

Two previous functional MRI (fMRI) studies from our laboratory (Indovina et al. 2005; Miller et al. 2008) compared the brain activity associated with button-press interception of targets moving under normal gravity (1g) with the activity associated with interception of targets moving under an artificial reversed gravity (−1g). Normal gravity targets decelerated while ascending and accelerated while descending. Vice versa, −1g targets accelerated while ascending and decelerated while descending. It was found that 1g trials were associated with significantly more activity than −1g trials in a network encompassing peri-sylvian regions [insula and temporo-parietal junction (TPJ)], premotor and cingulate cortices, lingual gyrus, and subcortical regions (thalamus, putamen, cerebellum, and brain stem). These studies suggested that neural populations might gate the flow of visual motion information within the brain according to the coherence with the effects of gravity on target motion. However, the issue of selectivity with respect to the law of motion has remained open. The network appears to discriminate natural gravity (1g) from an artificial reversed gravity (−1g), but does it also discriminate 1g from 0g (i.e., constant speed motion) along the vertical? This is the first question we wanted to address in this study.

To our knowledge, accelerating/decelerating stimuli have not been previously compared with constant speed stimuli in fMRI studies. On the other hand, time-to-contact estimates of horizontal constant speed motion engage a frontal-parietal network but not the network activated by 1g targets (Field and Wann 2005). Nor is the 1g network engaged by illusory self-motion in-depth generated by an expanding optic-flow stimulus (Field et al. 2007; Kovács et al. 2008; Wall et al. 2008) or by random dots translating at constant speed in arbitrary directions (Culham et al. 1998; Orban et al. 2003; Sunaert et al. 1999). Constant speed optic flow stimuli simulating self-rotation deactivate most regions of the visual gravitational motion network (Brandt et al. 1998; Dieterich et al. 2003b; Kleinschmidt et al. 2002).

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The demonstration of a neural preference for a specific acceleration pattern such as that of 1g targets relative to constant speed targets would not be a trivial finding. Indeed, several psychophysical studies showed that the threshold of discrimination between an arbitrary accelerating (or decelerating) target and a constant speed target is generally high (for a review, see Zago et al. 2009). Consistent with this poor perceptual sensitivity, the motor system does not seem to take into account unpredictable accelerations of a target in timing manual interceptions; instead, the latter are geared to target direction and speed (Engel and Soechting 2000; Port et al. 1997; Senot et al. 2003). Also, electrophysiological studies in the monkey showed that most neurons in a key visual-motion area, the middle temporal (MT) area, are tuned to direction and speed but not to acceleration, although an acceleration signal can be reconstructed from their population response (Lisberger and Movshon 1999; Price et al. 2005; Schlack et al. 2007). Neural responses to acceleration or deceleration in MT may be explained by speed-dependent adaptation rather than by an explicit code for acceleration/deceleration (Schlack et al. 2007). Based on these observations, one might speculate that a selective tuning of 1g relative to 0g and to $-1g$ might result from appropriate “read out” mechanisms of these motion signals.

In the first experiment, we studied brain responses associated with targets in smooth motion [also called real motion (RM)]. In different blocks of trials, the target moved under gravity (1g), under reversed gravity ($-1g$), or at constant speed (0g). Initial speed was randomized from trial to trial to make arrival time unpredictable. At a random time after target arrival at destination, a GO signal instructed the subject to press the button as fast as possible. In this manner, motor response timing was effectively decoupled from the law of target motion. Therefore brain activity in the contrast between different laws of target motion could not be related to motor timing errors, which should not differ across conditions.

The second question we wanted to address is whether the preference for visual gravitational motion holds irrespective of the specific spatio-temporal properties of the visual stimuli. Thus in the second experiment, we tested the hypothesis that some of the brain regions identified in the first experiment as being relatively selective for 1g motion are activated both when subjects intercept 1g targets in smooth motion (RM) and when they intercept 1g targets in long-range apparent motion (LAM) (Anstis 1980; Braddick 1980; Larsen et al. 1983). For both RM and LAM, the target moved up and down at 1g, 0g, or $-1g$ and randomized initial speeds as in the first experiment. LAM was generated by flashing the stationary target in sequence at different locations along the vertical path, with a wide spatial and temporal separation. To our knowledge, this is the first study of accelerating/decelerating LAM. The interception of targets moving at constant speed along a circle in RM or LAM has previously been studied in the monkey (Merchant et al. 2004a,b, 2005). These studies showed that different neural mechanisms in motor cortex and posterior parietal cortex (area 7a) are involved in the interception of these two types of moving stimuli. Stimulus-related activity prevailed in area 7a and hand-related activity prevailed in the motor cortex. Moreover, neural activity was selectively associated with the stimulus angle during RM, whereas it was tightly correlated to the time-to-contact in the LAM condition, particularly in the

motor cortex (for a review, see Merchant and Georgopoulos 2006).

In humans, fMRI studies have shown that LAM activates low-level visual motion regions, also responsive to RM, such as V1 and hMT/V5+ (Goebel et al. 1998; Muckli et al. 2002, 2005; Sterzer et al. 2003, 2006), but LAM also activates selectively a region of the inferior parietal lobule (IPL), which has been described as a substrate for high-level, salient feature-tracking motion processes (Claeys et al. 2003). All these studies used LAM with constant speed; hence we tested whether the IPL region was also modulated by our accelerating/decelerating LAM stimuli.

METHODS

Subjects

A total of 31 healthy adults participated in two experiments after giving written informed consent in accordance with the procedures established by the Ethics Committee of the Santa Lucia Foundation. Twelve subjects (4 females and 8 males; age range, 22–28 yr) participated in *experiment 1*, and 19 subjects (11 females and 8 males; age range, 20–32 yr) participated in *experiment 2*. All subjects had normal (or corrected to normal) vision, right-handed dominance, and no history of neurological disorders. Predominant use of the right hand was indicated both verbally and according to a short version of the Edinburgh handedness inventory (Oldfield 1971). All subjects were naïve to the stimuli, task, and purpose of the experiments. Both *experiment 1* and *experiment 2* involved a training session outside the scanner performed ~ 3 days before the scanning session.

Visual stimuli and general procedures

Subjects underwent fMRI in the supine position while viewing visual stimuli and responding by means of a button-press. Color images (768×768 pixels, 32 bit) were generated by means of custom software (compiled C++ with external libraries) and projected with a digital projector (NEC LT158, 60-Hz refresh rate) through an inverted telephoto lens onto a semiopaque Plexiglas screen mounted vertically inside the scanner bore behind the subject head. The back-projected image was viewed via a mirror mounted on the head coil. The total eye-to-screen distance was 57 cm, and the size of the projected image was 19×19 cm, corresponding to $19^\circ \times 19^\circ$ of visual angle. Subject responses were acquired with an MR-compatible fiber optic-based button response system (FORP, Current Designs), sampled at 1 kHz. We presented a picture of a human figure (4.7°) standing in front of a building (16°) to provide subjects with a spatial reference frame to estimate vertical direction and apparent distance in scene coordinates. The picture was shown as a background in all trials of all experiments, irrespective of the presence or absence of moving stimuli and irrespective of the specific task. In the following, we denote as *motion* conditions those in which a moving stimulus was superimposed on the background, and as *static* conditions, those in which the background was projected in the absence of a moving stimulus. In all trials, subjects were asked to maintain fixation on a red dot (0.3°) placed inside a box held by the hand of the human figure in the picture. In trials requiring a motor response, subjects were asked to press the button with the right thumb. No feedback of response performance (either on-line or off-line) was provided in any of these trials. Each block was preceded by a written text that lasted 3 s and indicated either a *motion* condition or a *static* condition, whereas no cue was given about the specific law (1g, 0g, or $-1g$) or type of motion (RM or LAM).

MOTION STIMULI. A textured sphere (0.49°) moved vertically relative to the scene in a constant force field, first ascending from the box,

elastically bouncing (coefficient of restitution = 1) on the building cornice, and then descending into the box. The overall trajectory of the sphere subtended 11.2° . In $1g$ trials, the acceleration was consistent with natural gravity, that is, the sphere decelerated while moving up and accelerated while moving down. In $-1g$ trials, instead, the acceleration was reversed relative to natural gravity: the sphere accelerated while moving up and decelerated while moving down. The absolute value of acceleration was 9.81 m/s^2 in scene coordinates for both $1g$ and $-1g$ trials (corresponding to $27.5^\circ/\text{s}^2$). In $0g$ trials, instead, the sphere moved at constant speed. The flight duration (FD) of the sphere was varied by changing the value of initial speed. For each motion condition ($1g$, $0g$, $-1g$), FD could take one of five possible values equally spaced between 1.40 and 1.78 s. Mean visual speed ranged between 12.6 and $16^\circ/\text{s}$ in all motion conditions ($1g$, $0g$, $-1g$).

RM TRIALS. The moving sphere was displayed every ~ 16.7 ms (60-Hz refresh rate). Although these stimuli were discrete, the successive targets overlapped even at the fastest speed (the distance that the sphere moved every 16.7 ms was always less than the sphere diameter). This resulted in a smooth motion, which was indistinguishable from a continuously moving target (Gregory and Harris 1984).

LAM TRIALS (EXPERIMENT 2 ONLY). The stationary sphere was flashed at 5 fixed, equispaced ($\Delta x = 2.26^\circ$) locations for 50-ms (3 consecutive frames) duration. The highest location corresponded to the trajectory apex (just below the building cornice), and the lowest location was 2.26° above the arrival point (inside the box). Δt between consecutive flashes was constant for $0g$ trials (between 140 and 178 ms, depending on flight duration), whereas it was variable for $1g$ and $-1g$ trials (between 92 and 390 ms). These Δx and Δt values fall within the interval previously identified as pertaining to long-range apparent motion (Anstis 1980; Braddick 1980; Larsen et al. 1983).

Tasks

EXPERIMENT 1. The aim of the first experiment was to assess the neural preference for visual gravitational motion. To this end, we used four different conditions: a *static* condition, plus three *motion* conditions ($1g$, $0g$, and $-1g$) displayed as RM. In the *motion* trials, subjects were instructed to maintain fixation, observe the sphere motion, and wait for a GO signal before pressing the button. The GO signal was delivered after a random delay ranging between 200 and 500 ms (in steps of 33.4 ms) from the end of sphere motion. This signal consisted in the sudden expansion of the red dot located on the box from 0.3 to 0.5° ; the dot returned to the original size after 200 ms. Subjects were asked to respond as soon as possible after the dot expansion. Thus by design, the motor response timing was uncoupled from visual motion processing. In the *static* trials, instead, there were neither moving stimuli nor motor responses: subjects were instructed to simply maintain fixation on the picture. *Motion* trials [stimulus onset asynchrony (SOA): 2.2/2.9 s, mean: 2.55 s] were grouped in blocks of 15 trials with a pseudorandom order of FD and interleaved with 20 s of static trials. Each run (continuous fMRI acquisition) consisted of 4 blocks of $1g$, $0g$, $-1g$ *motion* trials and *static* trials (a total of 16 blocks in each run). Four runs of ~ 10 min each were presented to each subject during the fMRI acquisition. Runs were separated by a brief rest period.

EXPERIMENT 2. The aim of the second experiment was to study whether some of the regions selectively activated by $1g$ stimuli in the first experiment are also activated when subjects intercept $1g$ targets in RM or LAM (see above). To this end, we presented the three different motion laws ($1g$, $0g$, or $-1g$) either in RM or LAM and asked subjects to intercept the sphere at the expected time of arrival at destination by means of the button press. There were eight different conditions: six *motion* conditions (3 motion laws for both RM and LAM) plus two *static* conditions (1 for RM and 1 for LAM), presented in separate blocks. In the motion interception blocks, we presented the

12 trials (SOA: 2.2/2.6 s), all with the same motion law ($1g$, $0g$, or $-1g$) and motion type (RM or LAM). The *static* blocks included eight control trials (SOA: 2.2/2.6 s). Within each block, the five different trial durations were presented in a pseudorandom order. Each block type ($1g$, $0g$, $-1g$ *motion* and *static* baseline) was presented five times during an fMRI run. The presentation order of motion laws (and baseline) was counterbalanced within runs, whereas blocks of RM and LAM stimuli were presented in separate, alternating runs.

In both RM and LAM *static* trials, there was no moving target in the visual scene, and subjects had to press the button when the fixation dot expanded (from 0.3 to 0.5°) for 200 ms. In LAM *static* trials, in addition to the fixation dot, there was a textured sphere (0.49°) flickering at 12 Hz at one location randomly selected from those used during the LAM interception condition. We used flickering as a control for LAM in agreement with several previous studies (Claeys et al. 2003; Goebel et al. 1998; Liu et al. 2004; Muckli et al. 2005; Zhuo et al. 2003).

Eye movements recording

Eye movements were recorded at 500 Hz with a head-mounted infrared system (Eyelink II, SR Research, Mississauga, Ontario, Canada) during the prescanning session for both experiments and with an ASL 504 eye-tracking system (Bedford, MA) at an acquisition rate of 60 Hz during fMRI in *experiment 1* only.

fMRI data acquisitions

Imaging was performed with a Siemens Magnetom Allegra 3-T head-only scanning system (Siemens Medical Systems, Erlangen, Germany), equipped with a quadrature volume RF head coil. Subjects were provided with noise suppression apparatus (ear plugs and headphones) and lay supine with the head firmly immobilized with foam cushioning. Whole brain BOLD echoplanar imaging (EPI) functional data were acquired with a 3 T-optimized gradient echo pulse-sequence (TR = 2.47 s, TE = 30 ms, flip angle = 70° , FOV = 192 mm, fat suppression). Blocks of 38 image slices were acquired in ascending order (64×64 voxels, $3 \times 3 \times 2.5$ mm, distance factor: 50%). For each participant, a total of 988 (*experiment 1*) or 1016 volumes (*experiment 2*) of functional data were acquired in four consecutive runs. At the end of each run, subjects were given a brief pause to relax.

Behavioral data analysis

For reaction trials (*motion* trials in *experiment 1* and *static* trials in *experiment 2*), response timing was calculated as the difference between the recorded button-press time and the onset time of the fixation dot expansion. We discarded 6.4% of the total number of trials collected in *experiment 1* because the reaction time was < 100 ms (*anticipated* trials), which is shorter than the known visuomotor reaction times (Welford 1988).

For interception trials (*motion* trials in *experiment 2*), response timing was calculated as the unsigned difference (absolute response errors) between the button-press time and the arrival time of the sphere at the fixation point. Absolute errors provide an estimate of the temporal accuracy, regardless of whether the target arrival time is over- or underestimated.

Repeated-measures within-subject ANOVA was performed on the mean values of response timing for $1g$, $0g$, and $-1g$ trials, with type of motion (RM or LAM) and/or law of motion ($1g$, $0g$, or $-1g$) as factors, followed by a post hoc *t*-test with Bonferroni correction. With regard to eye movements inside the scanner, we computed the total numbers of trials in which a saccade was detected (amplitude $> 1^\circ$, duration > 80 ms). ANOVA and post hoc analyses were performed using the Statistica analysis software (Statsoft, Oklahoma), whereas all other data analyses were performed using in-house software written in MATLAB (The MathWorks, Natick, MA).

fMRI data analysis

GENERAL PROCEDURES. Data preprocessing and statistical analyses were performed using the SPM2 software (Wellcome Department of Cognitive Neurology, University College London; implemented in MATLAB 6.5). The first four volumes of data from each of the four runs were discarded to allow for stabilization of longitudinal magnetization. The remaining volumes were submitted to the following preprocessing steps: realignment of all images to the first retained volume to compensate for head motion; normalization to Montreal Neurological Institute (MNI) standard space using the default SPM2 EPI image template and the mean of the functional volumes to allow group analysis; three-dimensional (3D) image smoothing with a 6-mm full-width half-maximum (FWHM) isotropic Gaussian kernel to increase signal-to-noise ratio. Voxel size of the final smoothed images was $2 \times 2 \times 2$ mm.

Statistical analysis was carried out in two stages (Penny et al. 2003). For each subject, BOLD responses for each condition were first estimated with a fixed effects general linear model (GLM) analysis using the smoothed images time series. Voxel time series were processed to remove autocorrelations using a first-order autoregressive model and high-pass filtering (128-s cut-off). Each conditions of interest of *experiment 1* (1g, 0g, -1g *motion* and *static* RM conditions) or *experiment 2* (1g, 0g, -1g RM *motion* conditions; 1g, 0g, -1g LAM *motion* conditions; *static* RM conditions and *static* LAM conditions) was modeled as a short boxcar function (time-locked to the onset of stimuli and with a variable duration corresponding to the trial duration) convolved with SPM2 canonical hemodynamic response function. In *experiment 1*, *anticipated* trials were modeled separately as confound. Parameters of head movements were included as covariates of no interest. Single-subject parameter-estimate images underwent a second step, involving a within-subject ANOVA that modeled the effect of the four conditions of interest in *experiment 1* or the eight conditions of interest in *experiment 2*, plus the main effect of subject. Linear compounds were used to compare the condition effects using between-subject variance. Correction for non-sphericity (Friston et al. 2002) was used to account for possible differences in error variance across conditions and any nonindependent error terms for the repeated measures.

EXPERIMENT 1. Regions selective for visual gravitational motion were assessed using the contrast [1g minus -1g] of *motion* trials. Except where otherwise noted, we used a probability criterion of $P\text{-corr} < 0.05$, that is, corrected for multiple comparisons at cluster level (with cluster size estimated at $P < 0.01$, voxel level), considering the whole brain as the volume of interest (Friston et al. 1994). We considered cubical regions of interest (ROIs; size of $8 \times 8 \times 8$ mm, based on final estimated image smoothness) centered on the activity peak of each activated cluster of the main contrast [1g minus -1g]. Within these ROIs we tested for the contrast [1g minus 0g] using the MarsBaR ROI toolbox for SPM2 (Brett et al. 2002). We also assessed the effect of visual gravitational motion in hMT+/V5. We localized hMT+/V5 by contrasting all *motion* trials versus *static* trials: i.e., [(1g plus 0g plus -1g) minus *static*] ($P\text{-corr} < 0.05$). In each hemisphere, we centered the ROIs for hMT+/V5 at the voxel of peak activity nearest to the junction of the ascending limb of the inferior temporal sulcus and lateral occipital sulcus (cf. Culham 2001; Orban et al. 2003).

EXPERIMENT 2. In this experiment, we first tested for a main effect of visual gravitational motion across RM and LAM: i.e., RM[1g minus -1g] + LAM[1g minus -1g]. In addition, we tested for the interactions between law of motion and type of motion: LAM[1g minus -1g] - RM[1g minus -1g] and the reverse RM[1g minus -1g] - LAM[1g minus -1g]. For both the main effect and the interactions, we considered as regions of interest the four ROIs identified in *experiment 1*. In addition, we also considered hMT+/V5 (using the coordinates from *experiment 1*) and a high-order motion region previously identified in inferior parietal lobule (HM-IPL, using the coordinates from Claeys et al. 2003).

For both experiments, we performed additional regression analyses in each ROI to assess whether different motion laws modulated monotonically the activity. The regression model included one predictor of interest (with the values = 3, 2, or 1, corresponding to the three conditions of interest: 1g, 0g, and -1g) plus the main effect of subject as covariate of no interest.

RESULTS

Experiment 1

In the *motion* trials, subjects viewed a sphere first ascending and then descending in smooth motion (RM) toward the fixation point at 1g, 0g, or -1g. Initial speed was randomized from trial to trial to make arrival time unpredictable. At a random time after the sphere arrival at destination, the fixation dot expanded, instructing the subject to press the button as fast as possible. In this manner, the motor response timing was effectively decoupled from the law of target motion.

Behavior

As expected, the timing of button-press responses did not depend significantly on the specific motion law, i.e., whether the sphere moved at 1g, 0g, or -1g (Fig. 1), as shown by ANOVA ($P = 0.13$ in the scanning session and $P = 0.25$ in the training session outside the scanner).

Subjects maintained adequate fixation under all conditions. ANOVA showed that the percentage of trials with saccades did not depend significantly on the motion law ($P = 0.16$). This percentage was 5 ± 2 , 7 ± 3 , and $5 \pm 2\%$ (SE) for 1g, 0g, and -1g trials, respectively.

Brain activations preferentially associated with visual gravitational motion

Figure 2 shows the regions with greater activation during 1g trials than during -1g trials. These regions included the brain stem (Z-score = 4.05), left lingual gyrus (Z-score = 3.80), left insula (Z-score = 3.23), and right insula (Z-score = 3.87; see Fig. 3 for coordinates). The contrast was significant at $P\text{-corr} < 0.05$ (corrected for multiple comparison at cluster level) in all these regions, except the right insula, where it was

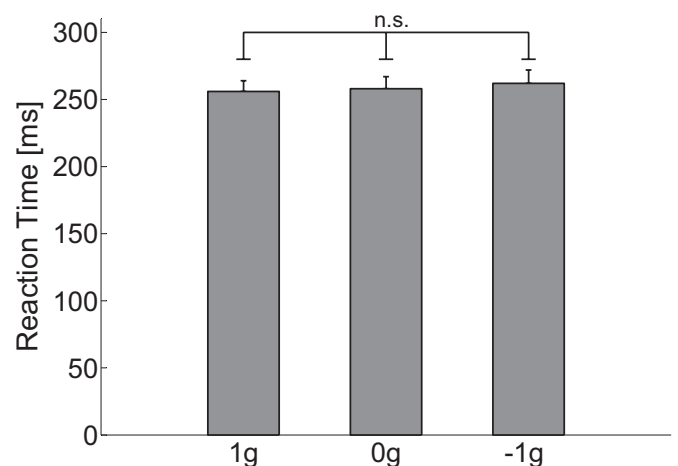


FIG. 1. Effects of motion law (1g, 0g, or -1g) on response time (RT) during the motion task in *experiment 1* (mean \pm SE). The data were collected during functional MRI (fMRI) scanning.

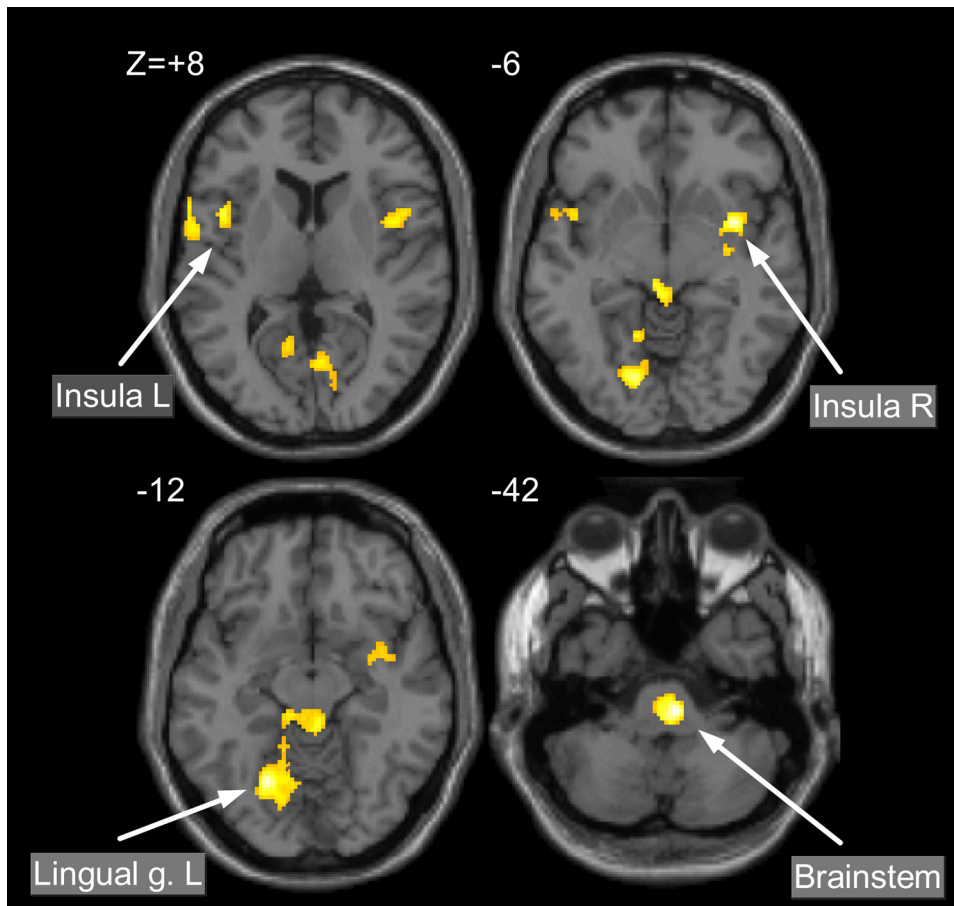


FIG. 2. Effect of visual gravitational motion in *experiment 1*. Statistical maps for the comparison “1g minus $-1g$ ” trials. Transverse sections are taken through the maxima of each cluster. Data are presented in normalized stereotactic space, overlaid on a high-resolution anatomical MR image [CH2, Montreal Neurological Institute (MNI)] with the left side shown on the *left* (numerical labels correspond to the z -coordinate of each axial slice).

marginally significant (P -corr = 0.08). To assess the relative selectivity for 1g motion, we also tested the contrast [1g minus 0g] in these four regions (ROI analyses, see METHODS). All four ROIs were significantly more activated in 1g trials than in 0g trials (all $P < 0.03$). The signal plots show that activity decreased monotonically from 1g to 0g to $-1g$ (Fig. 3). This trend was confirmed by a regression analysis with 1g, 0g, and $-1g$ as an explanatory variable, showing that the activity was linearly modulated by the motion law in all four ROIs (all $P < 0.008$).

Activity in hMT+/V5

We also tested for possible effects of the motion law (1g, 0g, and $-1g$) in the motion-sensitive area hMT+/V5. This area was first localized bilaterally using the contrast between all *motion* trials pooled together and all *static* trials (left hemisphere: $x, y, z = -48, -74, 4$; Z-score = 6.29; right hemisphere: $x, y, z = 48, -70, 2$; Z-score = 6.77). Within these regions, the contrast [1g minus $-1g$], the contrast [1g minus 0g], and the regression with 1g, 0g, and $-1g$ as an explanatory variable did not show any significant effect (all $P > 0.1$, in both hemispheres), indicating that the laws of motion used in our study did not affect differentially the average activity in hMT+/V5 (Fig. 4).

Experiment 2

This experiment was aimed at testing whether some of the brain regions identified in the first experiment as being relatively selec-

tive for 1g motion are activated *both* when subjects intercept 1g targets in smooth motion (RM) *and* when they intercept 1g targets in long-range apparent motion (LAM). For both RM and LAM, the target sphere shifted at 1g, 0g, or $-1g$ with a randomized initial speed, as in the first experiment. LAM was generated by flashing the stationary target in sequence at different locations along the vertical path, with a wide spatial and temporal separation. Notice that, because the target was never flashed at the arrival point in LAM, subjects had to extrapolate the stimulus traversing the vacant space to intercept the target.

Behavior

Subjects maintained adequate fixation under all conditions. The mean percentage of trials with saccadic movements was $7 \pm 2\%$, with no significant effect of the task (interception of 1g, 0g, $-1g$ targets or *static* task), type of motion (RM, LAM), or interaction (ANOVA, $P > 0.2$ for task, motion type, and interaction).

Figure 5 shows the absolute timing errors in intercepting the different targets. ANOVA showed that these errors were significantly affected by the motion law (1g, 0g, or $-1g$) and motion type (RM, LAM) ($P < 0.005$ for motion law, type, and interaction both during training and scanning sessions), but the motion law affected the performance to a greater extent than the motion type. Thus presenting the different visual stimuli as LAM produced a pattern of absolute errors similar to that observed for RM. Bonferroni post hoc tests showed a significant difference ($P < 0.001$) between the responses to $-1g$ targets, on the one hand, and the responses to 1g and 0g targets,

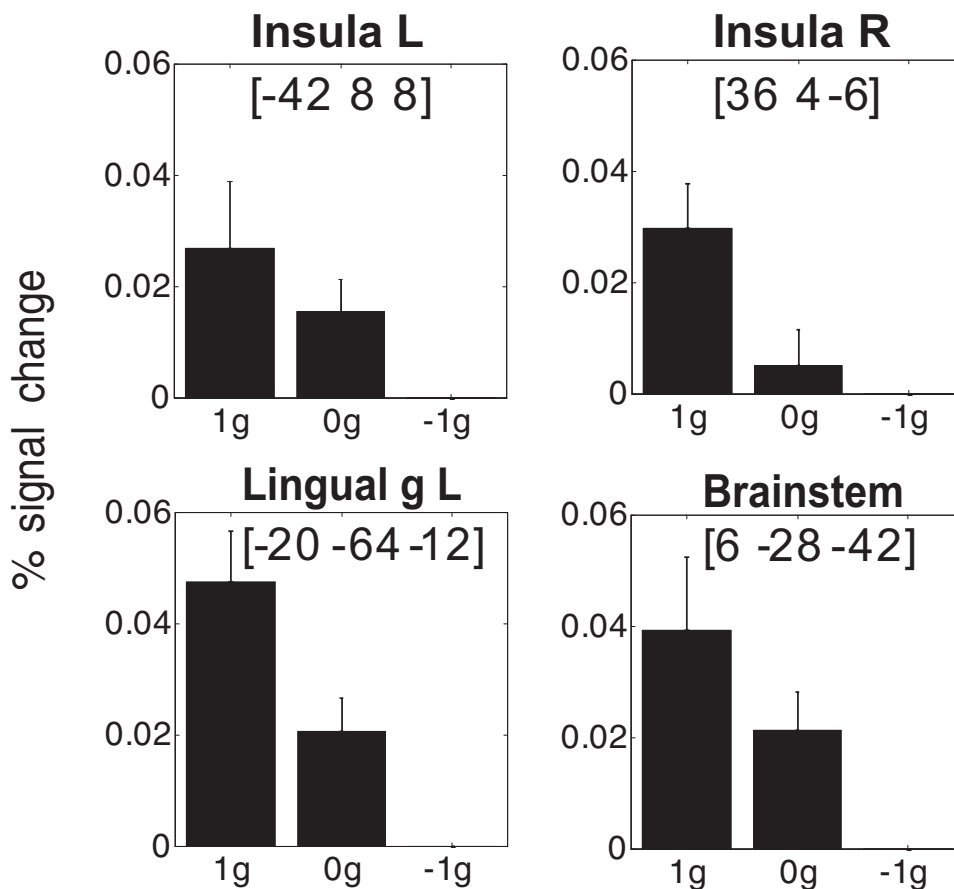


FIG. 3. Mean activity profiles (\pm SE) for regions activated by visual gravitational motion (1g minus -1g) in *experiment 1*. Signal changes are plotted as a function of the stimulus conditions and are expressed as percent signal change compared with -1g trials.

on the other hand, and also between the responses to -1g LAM and those to -1g RM. There were no significant differences ($P > 0.05$) between the responses to 0g targets and those to 1g targets for both RM and LAM. In none of the conditions did timing errors change significantly with task repetition, consistent with the lack of feedback about performance.

Main effect of visual gravitational motion in brain activity

We considered the four ROIs that had been shown to be relatively selective for 1g motion in *experiment 1* (see Fig. 2). First, we tested for the main effect of motion law by pooling across RM and LAM. We found a significant main effect of

visual gravitational motion [1g minus -1g] in the right insula ($P < 0.05$) and in the left lingual gyrus ($P < 0.001$). Figure 6 shows the percent signal changes in these two regions. As in *experiment 1*, also in *experiment 2*, the activity in these two regions decreased monotonically from 1g to 0g and -1g trials and now for both RM and LAM conditions.

The regression analysis with 1g, 0g, and -1g as an explanatory variable confirmed that activity was linearly modulated by the motion law in the left lingual gyrus both for LAM and RM (both $P < 0.01$). In the right insula, these additional tests reached statistical significance only during LAM ($P < 0.05$).

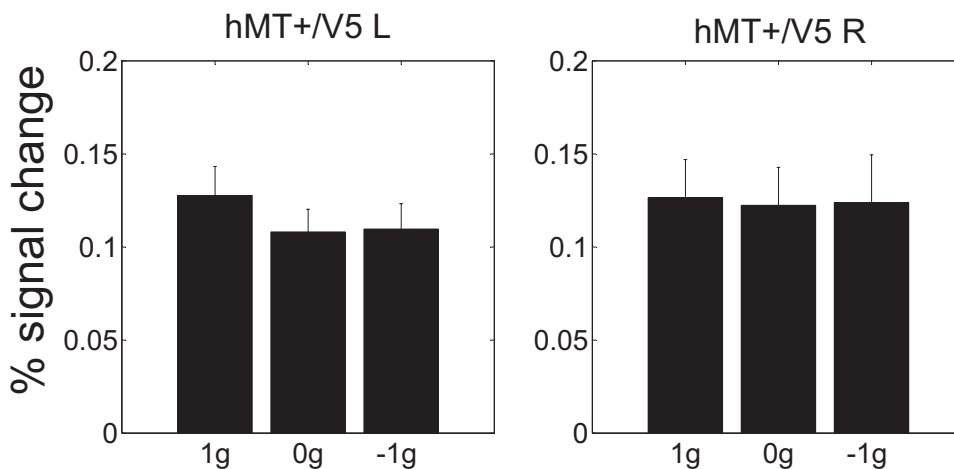


FIG. 4. hMT+/V5: mean activity profiles (\pm SE) for left and right hMT+/V5 in *experiment 1*. To localize hMT+/V5, we contrasted all *motion* conditions (1g, 0g, and -1g) vs. *static*. Signal changes are plotted as a function of the stimulus conditions and are expressed as percent signal change compared with the static task.

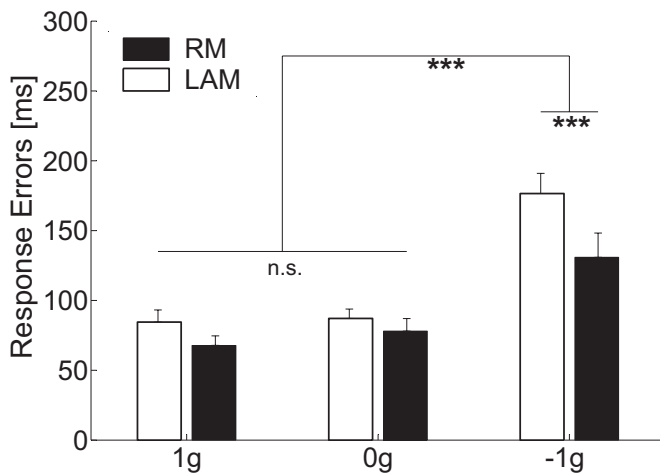


FIG. 5. Effects of the motion law (1g, 0g, or -1g) and motion type (RM, LAM) on interception performance in *experiment 2*. The plot shows the mean absolute errors (\pm SE) in timing the button-press responses. The data were collected during fMRI scanning. Black and white bars correspond to RM and LAM, respectively.

Interactions between motion law and motion type

The interaction (LAM [1g minus -1g] minus RM [1g minus -1g]) and the reverse interaction (RM > LAM) were not significant ($P > 0.1$) in any of the four ROIs that had been shown to be selective for 1g motion in *experiment 1*. In addition to these ROIs, we also tested these interactions in a high-order motion region previously identified in the inferior parietal lobule (HM-IPL) (Claeys et al. 2003). This region has been shown to respond to LAM but not to RM (Claeys et al. 2003), especially under conditions of full visibility (Clavagnier et al. 2007). With the interaction, we tested the hypothesis that HM-IPL should be selectively engaged in LAM but not in RM by 1g targets. We found that the interaction between motion type and motion law (LAM [1g minus -1g] minus RM [1g minus -1g]) indeed yielded a significant activation in the left HM-IPL ($P < 0.01$). The activation site is shown in Fig. 7A, and the percent signal changes are shown in Fig. 7B. In this region, the regression analysis showed a significant linear decrease of activity from 1g to 0g to -1g trials ($P < 0.005$) during LAM but not during RM ($P = 0.9$).

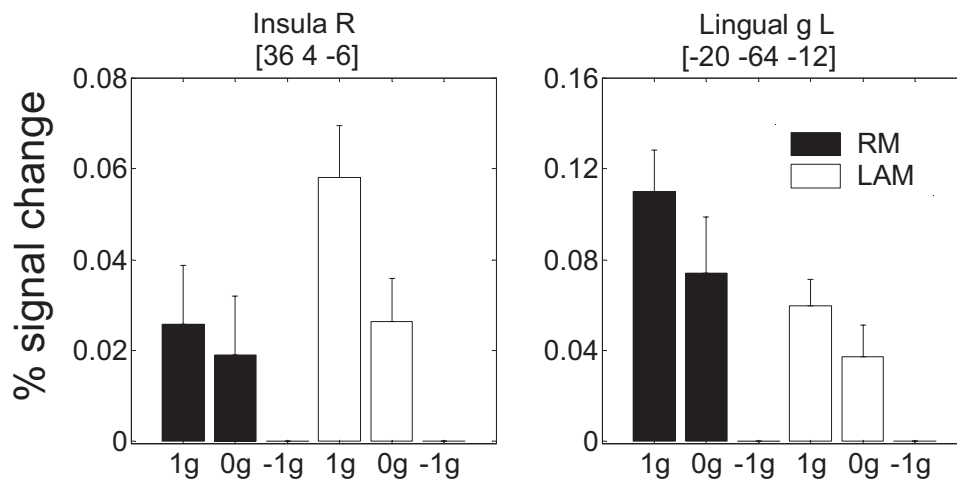


FIG. 6. Mean activity profiles (\pm SE) for insula (left) and lingual gyrus (right) that showed a significant effect of gravitational motion in *experiment 2*. Activity for RM trials is shown in black, whereas for LAM trials is shown in white. Signal changes are plotted as a function of the stimulus conditions and are expressed as percent change compared with -1g trials.

Activity in hMT+/V5

Finally, we assessed the effect of motion law and motion type in hMT+/V5, using the ROIs identified in *experiment 1*. First, for each ROI, we sought to confirm the overall effect of motion in *experiment 2*. The contrast ([RM+LAM] [1g plus 0g plus -1g]) minus *static*) showed significant activation within hMT+/V5, both in the left (-46, -72, 8; Z-score = 6) and the right (48, -70, 12; Z-score = 4.15) hemisphere. Next, we considered the differential effects of the law of motion. We found no significant difference either for the contrast [1g minus -1g] or for [1g minus 0g] (both $P > 0.1$; Fig. 8), indicating that these laws of motion did not affect differentially the average activity in hMT+/V5 (consistent with *experiment 1*). The interaction between law of motion and type of motion (LAM[1g minus -1g] minus RM[1g minus -1g]) showed a significant effect in the left hMT+/V5 ($P < 0.03$) but not in the right hMT+/V5 ($P > 0.22$).

DISCUSSION

Comparison with previous studies

The preferential activation of the insula and lingual gyrus with 1g targets that we found here is consistent with the results obtained in two previous fMRI studies (Indovina et al. 2005; Miller et al. 2008). Brain signals related to the interception of target motion were mainly studied in these previous studies. In this study, instead, we extracted the ROIs from the first experiment based on signals related to passive viewing of target motion followed by a reaction time response temporally uncoupled from the target motion. Thus our results suggest that the insula and lingual gyrus process visual gravitational motion per se, independently of the emission of a timed motor action.

Several previous fMRI studies showed that the lingual gyrus is involved in visual motion processing and may specifically contribute to direction and speed discrimination (Orban et al. 1998; Sunaert et al. 1999, 2000). Moreover, another previous fMRI study showed that both the insula and the lingual gyrus are selectively engaged by 1g targets in RM, irrespective of whether the targets are embedded in a pictorial context (including familiar size cues) or they are embedded in a blank scene (devoid of perspective cues), whereas the brain stem and posterior cerebellar vermis are

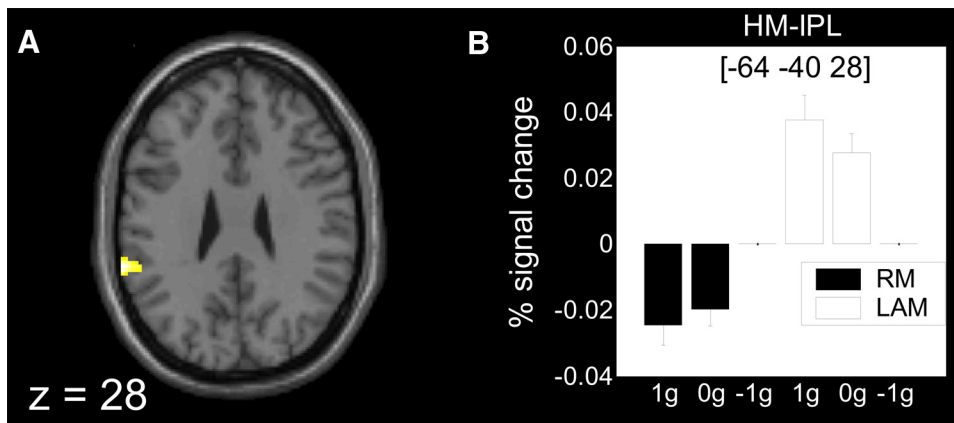


FIG. 7. The effect of gravitational motion specific to LAM in *experiment 2*. *A*: statistical parametric map overlaid on the MNI anatomical template. *B*: mean activity profiles (\pm SE) in high-order motion region identified in the inferior parietal lobe (HM-IPL). MR signals are plotted as a function of the stimulus conditions and are expressed as percent change compared with $-1g$ trials.

specifically activated in the pictorial condition (Miller et al. 2008). Here we confirmed the preference for visual gravitational motion in the insula, lingual gyrus, and brain stem in a pictorial RM, and we found that the insula and lingual gyrus but not the brain stem maintained this preference also in a pictorial LAM.

There is still a debate as to whether LAM represents a high-level motion process distinct from low-level RM or whether both RM and LAM result from the activation of spatio-temporal correlators by appropriate spatial and temporal combinations of stimuli (see for instance, Adelson and Bergen 1985; Cavanagh 1992; Lu and Sperling 2001; Watson and Ahumada 1985). Irrespective of the specific mechanism involved, the spatio-temporal properties of LAM used here differed hugely from those of RM. The finding that the insula and lingual gyrus prefer visual gravitational motion in both RM and LAM suggests that these regions can extract and process this property across a wide range of spatial and temporal frequencies.

Previous imaging studies indicated that LAM activates, in addition to low level motion regions such as V1 and hMT/V5+ (see Introduction), a higher-order motion region located in the inferior parietal lobule close to TPJ (so called HM-IPL region) (Claeys et al. 2003). HM-IPL was described as a substrate for high-level motion processing based on salience, being engaged by color-salient, isoluminant gratings and by quartet-display LAM at 7 Hz (Claeys et al. 2003). Moreover, the activity level in HM-IPL has been shown to correlate with the level of LAM perceptual visibility, as assessed psychophysically (Clavagnier

et al. 2007). These imaging findings fit with patients' studies indicating that IPL lesions may impair LAM perception (Battelli et al. 2001). Here we tested whether HM-IPL at TPJ was modulated by our accelerating/decelerating stimuli, and we found that it showed a preference for visual gravitational motion in LAM but not RM.

Modulation of neural activity with the law of motion

Activity in the insula, lingual gyrus, and IPL/TPJ decreased monotonically from $1g$ to $0g$ and to $-1g$, suggesting the existence of a global modulation of neural activity with the law of motion. The nature of the modulation can be extrapolated only grossly from these data, because only three types of target acceleration were compared. In particular, the demonstration of a neural code narrowly tuned to $1g$ motion would require the comparison of the brain responses to a much finer grain of changes in acceleration. Nevertheless, these findings are not trivial, in so far as very different results could have been predicted based on a number of plausible assumptions. Thus one possibility is that the activity in these regions reflects a cognitive expectancy of gravity effects on target motion. A critical prediction of this hypothesis is that these regions should be activated not only by visual motion that is coherent with natural gravity but also by nongravitational motion, which is mistaken for a gravitational one based on cognitive cues. Several behavioral studies showed that unusual constant speed ($0g$) motion along the vertical can be mistaken for the

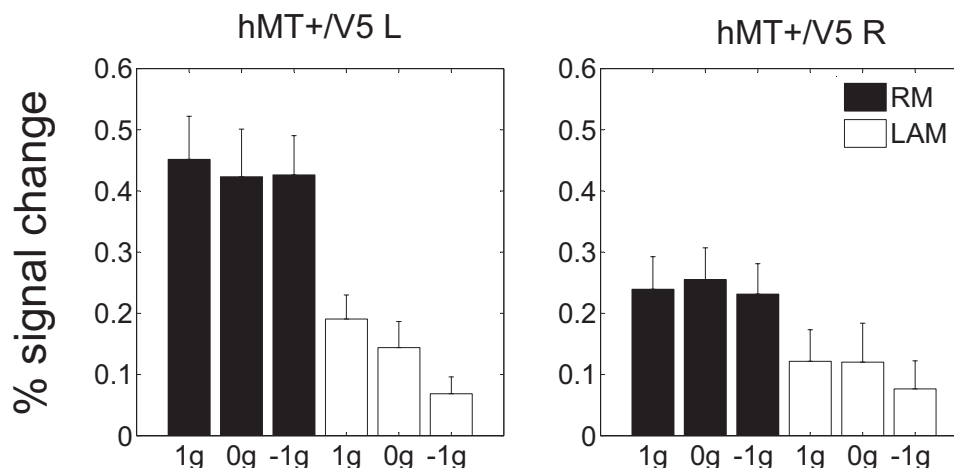


FIG. 8. Mean activity profiles (\pm SE) for left and right hMT+/V5 in *experiment 2*. Activations are plotted as a function of the stimulus conditions and are expressed as percent change compared with the static task.

more usual 1g motion when intercepting a descending target (McIntyre et al. 2001; Zago and Lacquaniti 2005; Zago et al. 2004). Accordingly, one could expect a comparable brain activation in response to 1g and 0g targets (both of which should engage a cognitive expectation of gravity effects), greater than the activation with $-1g$ targets (which may or may not engage gravity expectation, Senot et al. 2005). Here we found that the activity with 1g and 0g targets was indeed greater than the activity with $-1g$ targets, but the activity with 1g targets was also greater than that with 0g targets. Therefore it is unlikely that the activity in these regions reflects a cognitive expectancy of gravity.

Putative mechanisms of modulation

Differential brain responses to stimuli associated with different accelerations may depend on changes of neural speed-tuning induced by the acceleration context. Neural populations in the monkey MT area do exhibit acceleration-dependent speed-tuning (Lisberger and Movshon 1999; Price et al. 2005; Schlack et al. 2007). In particular, Schlack et al. (2007) showed that the preferred speed of single neurons tends to be lower and the tuning width narrower in a constant acceleration condition compared with a constant deceleration condition; the preferred speed in the constant speed condition is intermediate between that of the accelerating and that of decelerating condition. In our experiments, 1g targets consisted of a decelerating phase followed immediately by an accelerating phase in the opposite direction; $-1g$ targets, instead, consisted of the accelerating phase followed by the decelerating phase in the opposite direction. Therefore if we try to extrapolate the results obtained in the monkey MT to the present conditions, we could expect that the time-varying population response in MT should consist of two different tuned functions adjoined at a saddle point (coincident in time with the arrival of the target at the apex of the ball's trajectory). The time-varying response for 1g could be different from that for $-1g$, but their mean value over the whole motion duration (corresponding to the BOLD integrated signal) should be the same. fMRI cannot resolve responses in individual cells, but it is reassuring that the BOLD integrated signal in area hMT+/V5 was not significantly different across 1g, 0g, and $-1g$ targets in RM.

On the other hand, a monotonic modulation of activity in response to 1g, 0g, and $-1g$ motion—as observed in the insula, lingual gyrus, and IPL/TPJ—might reflect a gain-control mechanism operating on acceleration signals such as those recorded in the monkey MT area. According to this hypothesis, the gain of responses to stimuli that are coherent with the effects of gravity on target motion could be boosted relative to the gain with stimuli incoherent with gravity. This could imply a “read out” mechanism of motion signals, matching the stimuli with a reference gravity template. Thus Bayesian combination of an a priori of gravity with a likelihood function related to the visually measured kinematics would predict an a posteriori probability of 1g motion, which decreases monotonically from 1g to 0g and to $-1g$, consistent with the activity profiles reported here. In addition, our results suggest that the gain-control mechanism operates at early visual cortical levels such as the activated region in the lingual gyrus and at later levels such as the insula and IPL/TPJ. The specific involvement of HM-IPL at TPJ for LAM suggests that motion is

recomputed at this level, as first proposed by Claeys et al. (2003).

Gating of visual motion information within the brain according to the coherence with the effects of gravity has also been suggested by a previous study (Bosco et al. 2008). Transcranial magnetic stimulation (TMS) transiently disrupted the activity of hMT/V5+ or of IPL regions close to TPJ during the interception of targets accelerated by gravity or decelerated by reversed gravity in the vertical or horizontal direction. It was found that TMS of hMT/V5+ significantly affected the interception of all tested motion types, regardless of the acceleration (gravity or antigravity) and the direction of motion (vertical or horizontal). Instead, TMS of TPJ significantly affected only the interception of vertical gravity motion.

Sources of gravity information

It has previously been suggested that an internal model calculating the effects of gravity on seen objects is derived from graviceptive information, is stored in vestibular cortex, and is activated by visual motion that seems to be coherent with natural gravity (Indovina et al. 2005; Zago et al. 2004). Consistent with this hypothesis, a previous fMRI study showed that a network of regions including the insula and TPJ, which were selectively activated during the interception of 1g targets, co-localized with the regions which were independently activated by vestibular caloric stimulation (Indovina et al. 2005). In humans, the insula and TPJ in the cortical vestibular system integrate multimodal (visual, vestibular, somatosensory) information (Bense et al. 2001; Bottini et al. 2001; de Waele et al. 2001; Dieterich et al. 2003a,b). These regions receive disynaptic input from the vestibular nuclei complex via the thalamus (de Waele et al. 2001; Guldin and Grüsser 1998). Their lesion may lead to a tilt of the perceived visual vertical and rotational vertigo (Brandt and Dieterich 1999). Focal electrical stimulation elicits sensations of altered gravity or body tilt (Blanke et al. 2002). In the monkey, in addition to the vestibular cortex (Guldin and Grüsser 1998), early visual areas (V2 and V3/V3a), which may correspond to our activated site in the lingual gyrus, show combined effects of visual and otolith information (Sauvan and Peterhans 1999).

The integration of visual gravity with visual motion is likely to take place at multiple levels in the cortex and to involve recurrent connections between early visual areas engaged in the analysis of spatio-temporal features of the visual stimuli and higher visual areas in temporo-parietal-insular regions involved in multisensory integration. Here we focused on the role of lingual gyrus, hMT/V5+, inferior parietal lobule, and insula, but many other areas may be part of the gravity network (Indovina et al. 2005; Miller et al. 2008).

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