Visual gravity cues in the interpretation of biological movements: neural correlates in humans

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ABSTRACT

Our visual system takes into account the effects of Earth gravity to interpret biological motion (BM), but the neural substrates of this process remain unclear. Here we measured functional magnetic resonance (fMRI) signals while participants viewed intact or scrambled stick-figure animations of walking, running, hopping, and skipping recorded at normal or reduced gravity. We found that regions sensitive to BM configuration in the occipito-temporal cortex (OTC) were more active for reduced than normal gravity but with intact stimuli only. Effective connectivity analysis suggests that predictive coding of gravity effects underlies BM interpretation. This process might be implemented by a family of snapshot neurons involved in action monitoring.

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Introduction

Subtle features of biological motion (BM) are perceived from impoverished visual stimuli, such as point-light or stick-figure animations (Johansson, 1973). The interpretation of these stimuli presumably depends on local motion cues from the limbs, as well as on configural cues about changing body shape (Bertenthal and Pinto, 1994; see Blake and Shiffrar, 2007). These configural and motion cues, processed respectively in ventral and dorsal cortical pathways, probably are integrated in OTC (Giese and Poggio, 2003; Jastorff and Orban, 2009; Peelen et al., 2006).

BM interpretation may also depend on cues about the underlying forces. Most movements are governed by Earth gravity, in addition to muscle and inertial forces, and there is behavioral evidence that the effects of gravity relative to the visual scene are taken into account in BM interpretation (Runeson and Frykholm, 1981). For instance, the recognition of BM is strongly impaired when these stimuli are presented upside down (the inversion effect) (Sumi, 1984). This effect is mainly due to a reversal of the normal gravitational cues (Shipley, 2003; Westhoff and Troje, 2007). Moreover, gravitational cues allow to retrieve the size of moving animals (Jokisch and Troje, 2003).

Both the motion and configural parameters of BM rely on gravity. Indeed the time-course of elevation angles, hence the changes of BM shape over time, as well as the foot swing and stance phases are affected by the gravity level. This was shown by changing the effective gravity acting on the lower limbs during locomotion (Ivanenko et al., 2011; Sylos-Labini et al., 2013). Several findings show that the gravitational signals embedded in BM are critical for the analysis of local kinematics (Chang and Troje, 2009; Troje and Westhoff, 2006), and that configural information may modulate this process (Bardi et al., 2014; Hirai et al., 2011). However, to date, it has not been investigated whether gravitational information contributes also to the analysis of BM configural cues.

Here we considered the possibility that gravity may guide the interpretation of BM configural cues. To address this issue, we measured the fMRI brain signals associated with different human gaits (walking, running, hopping, skipping) in which the body oscillates like a pendulum or moves ballistically under gravity (Cavagna et al., 1976). These gaits were first recorded at two different effective gravity levels, that is, at normal Earth's gravity (1g) or at simulated reduced gravity (16% of Earth's gravity, or 0.16g, similar to the Moon gravity). These gaits were then rendered as intact or scrambled stick-figures and presented to naïve observers. The rationale for using several different types of gait was that of increasing the chances of recording brain activity related to features shared across gaits, and of enhancing the BM activation signals (Jastorff and Orban, 2009). A crucial feature in our experimental approach was

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that the overall changes in gait characteristics resulting from simulated hypogravity are unique to this condition, and cannot be produced by modifying muscle or inertial forces in normogravity (Donelan and Kram, 1997; Ivanenko et al., 2002b, 2011; Sylos-Labini et al., 2013). At the same time, however, locomotion in hypogravity complies with the general kinematic constraints of natural BM, i.e., the two-thirds power law relating limb velocity to path curvature and the planar covariance among the changes in segment angles (Ivanenko et al., 2002a,2002b).

We tested whether gravity modulated the activity in the brain sites sensitive to the BM configuration, by examining conditions differing in gravity. These sites were identified by comparing intact vs. scrambled stimuli (Jastorff and Orban, 2009; Peelen et al., 2006). Further, by using dynamic causal modeling (Friston et al., 2003), we explored the mechanisms underlying the influence of gravity on BM configural processing. It has been previously shown that the effect of gravity on object- and ego-motion reveals a distributed network of cortical and subcortical areas, whose primary sites are in TPJ (temporo-parietal junction) and insula (Bosco et al., 2008; Indovina et al., 2005, 2013; Maffei et al., 2010; Miller et al., 2008). Thus, we investigated whether an inter-regional connectivity between cortical areas sensitive to BM configuration (Jastorff and Orban, 2009; Peelen et al., 2006) and those sensitive to gravity could mediate the interpretation of BM. An alternative possibility is that an automatic and early process detecting gravity cues of BM (Bardi et al., 2014; Troje and Chang, 2013) occurs locally in regions selective to BM.

Materials and methods

Participants

Fifteen healthy subjects (6 females and 9 males, age 20 – 29 years), naïve to the experimental goals, gave written informed consent to participate in the fMRI experiments approved by the Ethics Committee of Santa Lucia Foundation.

Stimuli and procedures

The stimuli were generated by recording 116 trials in 8 subjects (4 females and 4 males, 25–45 years; not involved in the fMRI experiments) walking (22 trials), running (28), hopping (22) or skipping (44) on a treadmill at 3–6 km/h (general procedures as in Ivanenko et al., 2011). In half of the trials, subjects were tilted on the coronal plane by 81° respect to the vertical, with each leg suspended in an independent exoskeleton (see Supplemental Information for more details). The resulting effective gravitational acceleration was 0.16g (similar to Moon gravity). Note that we do not claim of being able to reproduce exactly the locomotion on the Moon (that nobody has recorded so far, except for low quality videos of astronauts moving around in heavy spacesuits), but only of producing a locomotion with an effective gravity on the lower limbs equal to 16% of normal gravity. In the remaining trials, subjects stepped in the vertical position (normal gravity, 1g) at matched speeds. The recorded movements of the thigh, shank and foot were then rendered in lateral view as white stick-figures (7° visual-angle (v.a.) in height) against a black background (Fig. 1a). We used stick-figures because in a pilot psychophysical experiment with point-lights we found that observers often misinterpreted hip and knee joints as head and hands, respectively. Moreover, stick-figures are considered as appropriate as or even more appropriate than point-light displays to isolate the role of intrinsic motion by removing detailed information about body morphology (Troje, 2013). In addition to intact stick-figures, we created spatially-scrambled stimuli by changing the stick starting position (Fig. 1a, see also Supplemental Information). This was done by adding a random shift to the middle point of each stick segment. The amplitude of this shift ranged from 35 pixels to 180 pixels. The final size of scrambled configuration matched that of original (intact) stimuli in terms of height (300 pixels, 7° v.a.) and width (200 pixels, 4.6° v.a.) of

the final area covered by the moving stick. Thus the kinematics of each scrambled segment was identical to that of the corresponding segment from intact stimuli, with the overall movement excursion being also matched.

The stimuli were projected (1024×768 pixels, 60-Hz) on a translucent screen inside the scanner behind the participant's head, viewed via a 45°-tilted mirror fixed on the head coil. In each trial, subjects fixated a red square (0.25° v.a.) at the screen center. The task was a simple two-alternative forced choice discrimination (Beauchamp et al., 2002, 2003), with subjects deciding if the stimulus contained normal or reduced gravity by pressing one of two buttons (fORP, Current Designs). To familiarize participants with the stimuli and task, they were trained two days before fMRI, sitting in a chair and viewing a vertical display.

The experimental design was 2×2 factorial, crossing "configuration" (intact or scrambled) and "gravity" (normal or reduced gravity). Each stimulus condition (1g_intact, 1g_scrambled, 0.16g_intact, 0.16g_scrambled) was presented 116 times, for a total of 464 trials presented in six runs acquired for each participant. Each of the 6 runs included either 19 or 20 repetitions of each of the four conditions. The stimuli (duration 2.0 ± 0.5 s, mean $\pm$ SD) were presented in pseudo-random order in a run, alternating rightward and leftward locomotion across runs (balanced across subjects). Inter-trial intervals were randomized with a long-tailed (geometric) distribution, resulting in a mean onset asynchrony of 5.1 s (range 2.8–11.1 s). During fMRI experiments, eye movements were recorded (60 Hz) with an ASL 504 eye-tracking system (Bedford, MA).

Data acquisitions

MR images were acquired with a Siemens Magnetom Allegra 3 T head-only scanning system (Siemens Medical Systems, Erlangen, Germany), equipped with a quadrature volume RF head coil. Participants were provided with noise suppression equipment (ear plugs and headphones) and lay supine with the head 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). 38 slices of BOLD images (volume) were acquired in ascending order (64×64 voxels, $3 \times 3 \times 2.5$ mm^3, distance factor: 50%; inter-slice gap = 1.25 mm; slice thickness = 2.5 mm), covering the whole brain. For each participant, a total of 1032 volumes of functional data were acquired in six consecutive runs. At the end of each run (lasting 6' 30"), the acquisition was paused briefly.

fMRI data preprocessing

Data and statistical analyses were performed using the SPM8 software (Wellcome Trust Centre for Neuroimaging, London, UK) implemented in MATLAB 7.0 (The MathWorks Inc., Natick, MA) using standard procedures (Lindquist, 2008; Mikl et al., 2008). After discarding the first four volumes of each run, images were corrected for head movements, normalized to the standard SPM8 EPI template in the Montreal Neurological Institute (MNI) space, resampled to $2 \times 2 \times 2$ mm^3 isotropic voxel size, and spatially smoothed with a full-width half-maximum (FWHM) isotropic Gaussian kernel of $8 \times 8 \times 8$ mm^3. Voxel time series were processed to remove autocorrelation using a first-order autoregressive model and high-pass filtered (128-s cut-off, first-order autoregressive model).

fMRI analysis

Statistical analysis was performed in two stages. For every participant, BOLD responses were estimated with a general linear model. The four experimental conditions were modeled with a boxcar function (1.5s duration, corresponding to the average response time) time-locked to the stimuli onset and convolved with SPM8 canonical hemodynamic response function. To control for potential differences in