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Dynamic cortical activity during the perception of three-dimensional object shape from two-dimensional random-dot motion

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Abstract

Recent neuroimaging studies implicate that both the dorsal and ventral visual pathways, as well as the middle temporal (MT) areas which are critical for the perception of visual motion, are involved in the perception of three-dimensional (3D) structure from two-dimensional (2D) motion (3D-SFM). However, the neural dynamics underlying the reconstruction of a 3D object from 2D optic flow is not known. Here we combined magnetoencephalography (MEG) and functional MRI (fMRI) measurements to investigate the spatiotemporal brain dynamics during 3D-SFM. We manipulated parametrically the coherence of randomly moving groups of dots to create different levels of 3D perception and to study the associated changes in brain activity. At different latencies, the posterior infero-temporal (pIT), the parieto-occipital (PO), and the intraparietal (IP) regions showed increased neural activity during highly coherent motion conditions in which subjects perceived a robust 3D object. Causality analysis between these regions indicated significant causal influence from IP to pIT and from pIT to PO only in conditions where subjects perceived a robust 3D object. Current results suggest that the perception of a 3D object from 2D motion includes integration of global motion and 3D mental image processing, as well as object recognition that are accomplished by interactions between the dorsal and ventral visual pathways.

Keywords

MEG-fMRI integration; 3D structure perception from motion (3D SFM); Granger causality; effective connectivity; dorsal visual system; ventral visual system

1. Introduction

During naturally occurring three-dimensional (3D) object perception, shapes are often recognized as they move. This form of 3D perception relies on spatial and temporal integration of the moving two-dimensional (2D) information reflected on the retina and is independent of stereopsis and shading information. The dynamics of neural mechanisms of this type of 3D perception are unknown. Perception of a 3D object shape from visually presented moving dots requires integration of the embedded movement and spatial information. Many psychophysical studies have investigated how the visual system extracts 3D structure of objects from 2D motion of random dots (3D structure-from-motion: 3D-

SFM) (Wallach, 1953; Baunstein, 1962; Rogers & Graham, 1979; Caudek & Proffitt, 1993). Electrophysiological studies of nonhuman primates have suggested the involvement of the middle temporal (MT) and the medial superior temporal (MST) neurons in the perception of 3D structure from the optical flow (Bradley *et al.*, 1998; Sugihara *et al.*, 2000). Recent neuroimaging studies suggest involvement of both the dorsal (i.e., the parieto-occipital (PO) and the intraparietal (IP) regions) and the ventral (i.e., the posterior inferior temporal (IT) region) visual systems, as well as the motion processing area MT, in the perception of 3D object from motion (Orban *et al.*, 1999; Paradis *et al.*, 2000; Beers, 2009; Kanai *et al.* 2010, Kolster *et al.* 2010; Abdollahi *et al.*, 2012; Freeman *et al.*, 2012; Garcia *et al.*, 2012). However, the neural dynamics underlying the reconstruction of a 3D object from 2D optic flow is not known.

In this study, we used both neuromagnetic (magnetoencephalography: MEG) and hemodynamic (functional magnetic resonance imaging: fMRI) measures to visualize the dynamic brain responses to 3D structure perception from random-dot motion in the human brain. Also, we employed causality analysis to infer driving relationships between the neural activities along the two visual pathways.

2. Methods

2.1. Subjects and stimuli

Seven healthy right-handed subjects (age between 22–43, 3 females) volunteered in this study. Written informed consent was obtained prior to the experiment complying with the policies of the internal review board of Massachusetts General Hospital.

Visual stimuli consisted of 1000 randomly placed dots inside a spherical area (10° in visual angle), which started to move 500 ms after the onset of presentation with various motion coherences. Stimulus duration was 1000 ms and the interstimulus interval was 1500 ms. The coherence of the motion across dots varied from 0% to 100% (Fig. 1). A fully (100%) coherent stimulus had all the dots moving as if they belonged to a rotating spherical surface with a radius of 10° visual angle. On the other hand, the 80%, 60%, 40%, 20%, and 0% coherence stimuli contained dots moving at the same speed as in the fully coherent stimulus but the movement directions of the dots were progressively randomized. During the interstimulus interval, the subjects were required to respond by lifting either the right index finger or the right middle finger depending on whether they perceived a 3D object from the random-dot motion or not, respectively.

2.2. MEG acquisition

Neuromagnetic signals were measured using a 306-channel MEG system (VECTORVIEWTM, Elekta-Neuromag, Finland).

The signals were recorded with a band-pass of 0.03–150 Hz and sampling rate of 600 Hz and averaged starting 1000 ms before and ending 1000 ms after stimulus onset. More than 80 single epochs were averaged for each condition. Epochs where the simultaneously recorded electro-oculogram (EOG) exceeded 150 mV were discarded from averaging to eliminate artifacts related to eye blinks and movements. Subjects were asked to press a button as soon as the motion stimuli disappeared with their index finger if they perceived a rotating 3D sphere or with their middle finger if they saw random motion.

2.3. fMRI acquisition

Functional MRI (fMRI) data were collected using a 3-Tesla scanner (Siemens Trio, Erlangen, Germany). For functional imaging, single-shot echo-planar imaging (EPI)

sequence was used with the imaging parameters TR 3000 ms, TE 40 ms, Flip angle 90°, 40 axial slices, 3 mm thickness with 0 mm gap, 64×64 image matrix, and field-of-view (FOV) 220 mm covering the entire brain. Three 14 s functional scans were divided into 12 s segments, randomly alternating between different stimulus (coherency) conditions and resting (fixation) periods. Within each segment, motion stimuli were presented every 4 s. Subjects' task was the same as that in the MEG experiment.

2.4. Data processing

3D reconstruction of the cortical surface was performed using Freesurfer software (Dale *et al.*, 1999; Fischl *et al.*, 1999a) for each subject. Statistical parametric mapping (SPM) was used to infer statistical significance of the signal changes in fMRI data (Friston, 1998). The BOLD images obtained during fMRI scanning were realigned using the first image as a reference and spatially smoothed using a Gaussian kernel of 6 mm full-width-half-maximum. A boxcar wave function was applied as a reference function, and a statistical parametric map was generated for each voxel using the general linear model (GLM). The results of the fMRI analysis were used to impose plausible constraints on the MEG inverse calculation (Rosa *et al.*, 2010) using a "weighted" minimum-norm approach (Hamalainen *et al.*, 1993; Dale *et al.*, 2000) to improve spatial resolution of the spatiotemporal activity estimates. In this study, we introduced fMRI weighting, which was determined by thresholding the fMRI statistical parametric map for each condition vs. fixation condition with $p < 0.001$ (False Detection Rate (FDR) corrected), on the diagonal entries of the source co-variance matrix of the minimum L_2 -norm linear inverse operator to map measured MEG signal into estimated source distributions (Liu *et al.*, 1998).

2.5. Intersubject averaging

Spherical morphing (Fischl, 1999b) was used to bring the data from different subjects into a common anatomical space. The spatiotemporal activity estimates obtained by using fMRI-weighted MEG minimum-norm technique were transformed to the standardized cortical surface, temporally integrated over 25 ms, down-sampled at 10 ms, and averaged across subjects.

2.6. Granger causality analysis

In order to test the directional influences between the active regions detected in the spatiotemporal activity estimates, Granger causality (Granger, 1969; Geweke, 1982; Brovelli *et al.*, 2004) was calculated on the MEG time-series observed at the ROIs corresponding to (a) the primary visual area, (b) the MT area, (c) the PO junction, (d) the intra-parietal area (IP), and (e) the posterior infero-temporal area (pIT). These ROIs were defined by the results of fMRI group statistics in the standardized MNI coordinates calculated separately from fMRI-weighted MEG inverse procedure described above, in which fMRI data were analyzed in the subject-specific coordinates. MEG single-trial data from each ROI were extracted between 0.1 s and 0.5 s post-epoch periods and average waveforms were subtracted from the single trial data before applying the Granger–Geweke causality tests. In this study, Granger causality tests were applied to single trial data extracted from (i) 100% and 80% conditions (3D conditions) and (ii) 20% and 0% conditions (random motion conditions) separately to elucidate the differences in cortical functional connectivity between different 3D shape perception conditions. Granger causality is a statistical concept based on prediction as modeled by a vector auto-regressive (VAR) model. Causality from time series x_1 to x_2 is tested by comparing the residual error in the prediction of x_2 using x_2 alone vs. using x_1 and x_2 . If the prediction error is significantly decreased by including x_1 to the VAR model, x_1 is considered to cause x_2 . The order of the VAR model used in the Granger causality test was determined from minimizing the Akaike

Information Criterion (AIC) (Akaike, 1974) and the significance of each uni-directional causality was tested by using F -value of the model.

3. Results

3.1. Behavioral data

Figure 2 shows the behavioral results obtained during MEG and fMRI acquisitions. In the 100% and 80% coherent conditions, the subjects perceived a rotating 3D spherical surface in more than 90% of all trials, whereas a 3D object was rarely (<10%) perceived in the 0% and 20% conditions. Hereafter, we denote the 100% and 80% coherent conditions as “3D perception conditions” and the 20% and 0% conditions as “random motion conditions”.

3.2. MEG waveforms

Evoked MEG responses for the 100% and 60% coherence conditions measured in the typical subject are shown in Fig. 3. Increased amplitudes of the MEG event-related components were observed in the PO and bilateral inferior occipito-temporal channels after 200 ms from the onset of motion.

3.3. fMRI activation maps

Figure 4 shows the results of the fMRI experiment for all subjects, in which fMRI contrasts between the 3D perception conditions (100% and 80% coherent conditions) vs. the random motion conditions (0% and 20% coherent conditions) were depicted. Robust increases in brain activity were observed in the PO, IP and IT regions during the 3D perception condition. Results from the group statistics (Fig. 5) showed increased activities in the bilateral PO, IP and pIT regions, which directly reflected the results of the individual statistics. The primary visual area showed weaker activity during 3D than random motion perception.

3.4. Spatiotemporal activity estimates using fMRI-weighted MEG

Figure 6 shows the fMRI activations that were used for the weighted minimum-norm MEG inverse procedure, (contrasts between the motion conditions vs. baseline (resting) condition) in four typical subjects. In all subjects, the fMRI weighted areas included the bilateral primary visual, the MT, the PO, the IP and the infero-temporal cortices.

fMRI-weighted MEG spatiotemporal activity estimates in a typical subject are shown in Fig. 7. Increased neural activity in the PO area was observed both in the 3D perception (100% and 80% coherence) conditions and the intermediate (60% coherence) condition at 220–300 ms, while the activities in the IP and the inferior-temporal regions were observed only in the 3D perception conditions at 340–450 ms after the onset of motion. Figure 8 shows the results of the intersubject averaging of the activity estimates over all subjects. Again, the activity in the PO region at around 280 ms was observed in the 3D perception and the intermediate conditions while the activities in the IP and IT regions in the later latencies were observed only in the 3D perception conditions.

3.5. Causal interactions between regions

Figure 9 shows (a) time series of the estimated neural activities extracted from five regions-of-interest (ROIs) and (b) results of the Granger causality analysis to infer the directional interaction among the five ROIs. The thick blue arrows in Fig. 9 (b) show the pairs of ROIs and the directions where the directional causalities were observed above the statistical threshold of $p < 0.01$ in the 3D perception conditions (100% and 80% coherent conditions). The thin blue and red arrows denote the regions and the directions where the causalities

above $p < 0.05$ were observed in the 3D perception conditions (100% and 80% coherent conditions; blue) and the random motion perception conditions (20% and 0% coherent conditions; red), respectively. The directional causalities from MT to PO, from IP to pIT and from pIT to PO were statistically significant ($p < 0.01$) only in the 3D perception conditions but not in the random motion conditions.

4. Discussion

The results indicate that the PO, IP and inferior temporal regions play an important role in the perception of 3D object structure from 2D random-dot motion. These locations agree with previous fMRI studies of 3D SFM (Orban *et al.*, 1999; Paradis *et al.*, 2000; Beers *et al.*, 2009). Specifically, our ROI at PO ([38, -80, 32] in MNI coordinates) is in close proximity with the sites of activation reported as the parieto-occipital junction (POJ) in Paradis *et al.*, ([21, -78, 39]), or as ventral intraparietal sulcus (VIPS) in Beer *et al.*, ([26, -79, 31]) and Orban *et al.*, ([30, -78, 32]), which might include the human caudal intraparietal sulcus (CIP) reported in the previous study on spatial discrimination of surface orientation (Shikata *et al.*, 2001, 2003). The location of our ROI at IP ([30, -52, 60]) is in agreement with the dorsal intraparietal sulcus (DIPS) reported in Orban *et al.*, ([35, -42, 70]) and Beer *et al.*, ([30, -53, 53]) and is overlapped with the anterior intraparietal area (AIP) which is reported to be responsible for discrimination and manipulation of 3D objects both in humans (Shikata *et al.*, 2003) and monkeys (Verhoef *et al.*, 2011). Also, the ROI at pIT ([30, -56, -12]) corresponds to the inferotemporal activation observed in Orban *et al.*, ([46, -66, -18]) and Beer *et al.*, ([35, -68, -12]). The current results add further insight into the neuronal mechanisms by revealing the temporal characteristics of the neural activities in these regions. In addition, the results of our previous study (Iwaki *et al.*, 2006) showed significant suppression of alpha- and beta-band spontaneous activities over these regions, thus indicating the same regions in 3D SFM processing.

The observed change in the neural activity in area MT during perception of global motion has also been reported in previous fMRI studies (Vaina *et al.*, 1998; Castelo-Branco *et al.*, 2002; Peuskens *et al.*, 2004; Kolster *et al.*, 2010), and the PO areas have been known to be involved in the integration of spatial aspects of visual motion (Hotson & Anand, 1999). Other studies have also indicated that the IP regions process mental imagery (Iwaki *et al.*, 1999; Jordan *et al.*, 2001; Pelgrims, 2009), and that inferior-temporal region is responsible for object recognition (Haxby *et al.*, 1991). Together with these previous findings, our results suggest that the perception of moving 3D objects from 2D motion depends not only on the visuospatial processing in the dorsal visual pathway but also on the object recognition system in the inferotemporal cortex.

The interactions inferred by the Granger causality showed that there were significant directional influences from MT to PO, IP to pIT and pIT to PO only during the perception of 3D object structure with highly coherent random-dot motion conditions but not during the random motion perception. These results indicate that these regions were involved in a large-scale neural network underlying the perception of 3D object structure from 2D motion. In fact, synchronization of the neural activities between the intraparietal (AIP) and the inferotemporal (IT) areas of the monkey cortices during 3D shape discrimination was observed in a previous study using simultaneous recordings of local field potentials in IT and AIP (Verhoef *et al.*, 2011). The current results obtained from noninvasive measurements on humans are in agreement with the above findings on monkeys in which activities in the parietal region influence those in the IT area during 3D shape perception. The results also support the idea that PO, which was investigated in detail in the previous fMRI studies on 3D SFM (Orban *et al.*, 1999; Paradis *et al.*, 2000; Kolster *et al.*, 2010), receives feedback input from pIT as well as feedforward input from MT to form robust 3D percept by

integrating the global motion and the object information processed in the ventral visual system.

5. Conclusion

We combined neuromagnetic (MEG) and the hemodynamic (fMRI) measures to detect the dynamic brain responses underlying 3D structure perception from 2D motion in humans. This spatiotemporally accurate multimodal neuroimaging technique revealed the exact neural dynamics in the dorsal and ventral visual pathways. The results suggest that the perception of a rotating 3D object from 2D random-dot motion includes integration of global motion and object recognition, that are accomplished by the cooperative engagement of the ventral and the dorsal visual information processing streams.

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Fig. 1.

Examples of the random-dot motion stimuli used in this study. Coherence of the motion was changed from 100% to 0% to generate different 3-D object perception.

Fig. 2.

Subjects' behavioral performance during the MEG and fMRI experiments. In the 100% and 80% coherent conditions, rotating 3-D sphere was perceived in more than 95% of the trials, while 3-D object was not perceived in the most of the trials in the 0% and 20% coherent conditions.

Fig. 3. Averaged MEG waveforms corresponding to the 100% and 60% coherent conditions in the typical subject. Black triangles denote channels and latencies where differences between the conditions were observed.

Fig. 4. Results of the fMRI single subject statistics depicting the contrasts between the 3-D perception (100% and 80% coherent) conditions and the random motion (0% and 20% coherent) conditions.

Fig. 5. Results of the fMRI group statistics depicting the contrasts between the 3-D perception (100% and 80% coherent) conditions and the random motion (0% and 20% coherent) conditions.

Fig. 6. The distributions of the fMRI weighting for the weighted minimum-norm MEG inverse procedure in the four typical subjects overlaid on the each subject's inflated cortical surface.

Fig. 7.
 (Color online) The results of the fMRI-weighted MEG inverse analysis in the typical subject for 0%, 60%, and 80% coherent conditions. The blue circles denote the sites where we observed the major changes between the conditions.

Fig. 8.
(Color online) The results of the inter-subject averaging of the activity estimates over all seven subjects. The blue circles denote the sites where we observed the major changes between the conditions.

Fig. 9.

(a) Time-series of the estimated neural activities extracted from five ROIs (V1/V2, MT, PO, IP and pIT). (b) The results of the Granger causality analysis to infer the directional causality in the neural activities estimated in the five ROIs. Thick blue arrows denotes the pairs of ROIs and the directions where the directional causalities were observed above the statistical threshold of $p < 0.01$ in the 3-D perception conditions and thin blue and red arrows denote the regions and the directions where the causalities above $p < 0.05$ were observed in the 3-D perception conditions (blue) and the random motion perception conditions (red), respectively.