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Parallel motion signals to the medial and lateral motion areas V6 and MT+

Sabrina Pitzalis [a,b], Chiara Bozzacchi [a], Alessandro Bultrini [a], Patrizia Fattori [c], Claudio Galletti [c], Francesco Di Russo [a,b,*]

[a] Dept. of Education for Motor Activity and Sport, University of Roma "Foro Italico", Roma, Italy
[b] Laboratory of Neuropsychology, IRCCS Santa Lucia Foundation, Roma, Italy
[c] Dept. of Human and General Physiology and Dept. of Pharmacy and Biotechnology, University of Bologna, Bologna, Italy

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ABSTRACT

MT+ and V6 are key motion areas of the dorsal visual stream in both macaque and human brains. In the present study, we combined electrophysiological and neuroimaging methods (including retinotopic brain mapping) to find the electrophysiological correlates of V6 and to define its temporal relationship with the activity observed in MT+. We also determined the spatio-temporal profile of the motion coherency effect on visual evoked potentials (VEPs), and localized its neural generators. We found that area V6 participates in the very early phase of the coherent motion processing and that its electroencephalographic activity is almost simultaneous with that of MT+. We also found a late second activity in V6 that we interpret as a re-entrant feedback from extrastriate visual areas (e.g. area V3A). Three main cortical sources were differently modulated by the motion coherence: while V6 and MT+ showed a preference for the coherent motion, area V3A preferred the random condition. The response timing of these cortical sources indicates that motion signals flow in parallel from the occipital pole to the medial and lateral motion areas V6 and MT+, suggesting the view of a differential functional role.

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Introduction

In the primate visual system, motion is processed along a specialized pathway that begins in striate cortex (V1), extends through several extrastriate areas, and terminates in higher areas of the parietal and temporal lobes. Lateral areas V5/MT and MST are classically considered the key motion regions of the dorsal visual stream, being responsive to visual stimuli in motion and showing selectivity for the direction (e.g., Morrone et al., 2000; Smith et al., 2006; Tootell et al., 1995) and speed (e.g., Lebranchu et al., 2010; McKeefry et al., 2008; Pitzalis et al., 2012) of movement. Recent studies from our group have revealed the presence in the human dorsal stream of another key motion region, area V6, located medially in the parieto-occipital sulcus (Pitzalis et al., 2010). While lateral areas V5/MT and MST have been widely investigated and their role in motion processing is well grounded, the discovery of the medial motion area V6 is relatively recent and its functional role is still unknown. Human V6 has retinotopic organization, position, and neighboring relations similar to those of macaque area V6 (Galletti et al., 1999; Pitzalis et al., 2006). As in non-human primates, the human V6 is a motion area very sensitive to translational motion (Pitzalis et al., 2010; Sdoia et al., 2009), with a selective preference for fast speed of motion (Pitzalis et al., 2012), and a strong preference for coherent motion (Cardin and Smith, 2010; Helfrich et al., in press; Pitzalis et al., 2010; von Pföstl et al., 2009). Human V6 is also highly sensitive to flow fields (Cardin and Smith, 2010, 2011; Pitzalis et al., 2010) which is probably the most important visual cue for the perception of self-motion or 'egomotion' (i.e. the sensation to be moving in space).

Though motion perception in humans has been extensively studied with electrophysiological methods (e.g., see Kuba et al., 2007 for review), the effect of coherent visual motion has been less investigated. Two magnetoencephalographic (MEG) studies (Holliday and Meese, 2005; Wiest et al., 2001) found a consistent contribution of the lateral MT complex without reporting any electromagnetic activity in the medial parieto-occipital sulcus (POs). Another couple of MEG studies (Vanni et al., 2001; von Pföstl et al., 2009) suggested that the response in a medial parieto-occipital region, likely corresponding to human V6, occurred very early, with about the same latency as in V1. In contrast, a quite late activity (around 200 ms) has been reported in the same medial regions by other MEG (Urakawa et al., 2010), event-related potentials (ERP) (Mercier et al., 2009) and combined ERP/fMRI studies (Pitzalis et al., 2012). However, due to the low spatial resolution of the MEG data, past studies of this type could include in their maps some neighboring regions besides V6. Moreover, the response timing of area V6 in all these previous studies was evoked by visual stimuli that were not ideal to functionally activate V6, either for the type of the stimulus or for its size.

* Corresponding author at: University of Rome "Foro Italico", Piazza Lauro de Bosis, 15, 00135 Roma, Italy. Fax: +39 0636733387.
E-mail address: francesco.dirusso@uniroma4.it (F. Di Russo).
URL: http://digilander.libero.it/francesco.di_russo (F. Di Russo).

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The main purposes of the present study were (1) to find electrophysiological correlates of the motion area V6 using wide-field coherent motion stimuli intentionally designed to best activate the area based on finding in Pitzalis et al. (2010) and (2) to define the temporal relationship between the activity observed in the medial area V6 and that in the lateral area MT+. A third purpose of this study was to determine the spatio-temporal profile of the motion coherency effect on visual evoked potentials (VEPs) and to localize its neural generators. Given the low spatial resolution of VEP data, to improve spatial localization we used the combined VEPs/fMRI technique developed and utilized by our group in previous studies (e.g., Di Russo et al., 2002, 2003, 2005, 2007, 2011; Pitzalis et al., 2012). Cortical sources were identified using dipole modeling based on a realistic head model, taking into account the loci of cortical activation revealed by fMRI in response to the same stimuli. These sources were also localized with respect to classic visual cortical areas (including V6 and MT+) identified in flat maps of individual subjects by wide field retinotopic mapping (e.g., Pitzalis et al., 2006; Sereno et al., 1995) and functional localizers (Pitzalis et al., 2010; Tootell et al., 1995).

Material and methods

Subjects

Twenty-six paid volunteer subjects (mean age of 25.8, range of 19–36 years, 14 females) participated in the main VEP experiment. A subset of 13 of these subjects (mean age 26.4 range of 21–36 years, seven females) also received structural MRI and fMRI scanning. All subjects were right-handed and had normal or corrected-to-normal vision. All participants gave written informed consent prior to both electrophysiological and neuroimaging measures, and all procedures were approved by the ethics and human subjects committees of the Santa Lucia Foundation. Before scanning, subjects were allowed, if they desired, to consume caffeinated beverages to better maintain alertness during the scan session. Each subject participated in up to five scanning sessions.

VEP experiment

Stimuli

Visual stimuli consisted of 3D "star fields" composed by 150 high-contrast random dots (light dots on a dark background) simulating different flow patterns. Global patterns of optic flow were produced by controlling the coherency of local motion directions of the dots. Two kinds of motion were considered: coherent and incoherent motion. For the coherent motion condition a 3D spiral was used consisting in the combination of radial components (all dots moved outwards or inward ($p = 0.5$) at 30°/s along the radii to produce an impression of expansion or contraction) and rotational component of 180°/s (30 rpm) either clock- or counterclockwise ($p = 0.5$). For the incoherent motion condition, the dots randomly moved changing their local direction and speed at random. Average speeds were as in the other coherent motion condition. The purpose was to provide a control condition in which local motion was present in all directions at all locations, with no global flow structure. Both speed and size were logarithmically scaled with eccentricity (i.e., as a function of the distance from the center of the display). The dot diameter varied from 0.1 to 0.5°. In both conditions, each dot traveled along an appropriate trajectory for a limited lifetime of 300 ms, after which it disappeared to be regenerate at a new random position. The appearance of new dots was controlled to maintain constant dot density. A static pattern taken from a single frame of the coherent motion was also used. Stimuli duration was 500 ms showing, in a pseudo-randomized order, one of the three stimuli. Stimulus onset asynchrony varied from 1000 to 2000 ms to avoid motion after-effects. All stimuli were displayed on a 26″ CRT monitor (refresh rate 100 Hz) subtending 80°×60°. Stimuli were presented and synchronized to the electroencephalogram (EEG) using Presentation software (Neurobehavioral Systems, Inc. Albany, CA USA).

Electrophysiological recording and data analysis

The ERP experiment was conducted at the Psychophysiology Laboratory of the University of Rome "Foro Italico" (Rome, Italy). During the EEG recordings, subjects were comfortably seated in a dimly lit, sound-attenuated and electrically shielded room while stimuli were presented in binocular vision on a video monitor. Subjects were trained to maintain stable fixation on a central cross (0.4°) throughout stimuli presentation. The EEG was acquired using a BrainVision™ system (BrainProducts, Germany), with 64 electrodes placed according to the 10–10 system montage. This system and recording technique have already been detailed in previous papers by our group (Di Russo et al., 2005, 2007, 2011; Pitzalis et al., 2012). All scalp channels were referenced to the left mastoid (M1). Horizontal eye movements were monitored with a bipolar recording from electrodes at the left and right outer canthi. Blinks and vertical eye movements were recorded with an electrode below the left eye, which was referenced to site Fp1. The EEG was digitized at 250 Hz with an amplifier band-pass of 0.1 to 100 Hz including a 50 Hz notch filter and was stored for off-line averaging. Computerized artifact rejection was performed prior to signal averaging in order to discard epochs in which deviations in eye position, blinks, or amplifier blocking occurred. On average, 9% of the trials were rejected for violating artifact criteria.

Time locked ERPs to standard stimuli were averaged separately according to the displayed stimulus (coherent motion, incoherent motion, and static pattern). The EEG was segmented into 1100 ms epochs that began 100 ms prior the stimulus onset to establish a voltage baseline. In order to reduce high-frequency noise, the averaged ERPs were low-pass filtered at 35 Hz. Data were re-referenced to averaged mastoids. VEP latency and amplitude components were measured as peak voltage deflections within specified time intervals (see Results section); these measures were taken at the electrode sites where the components were maximal in amplitude.

One-way ANOVAs were used to evaluate the effect of stimulus type (coherent, incoherent and static) on each component, using peak amplitude and latency. The confidence level was set to 0.05 after Greenhouse–Geisser correction.

Modeling of ERP sources

Topographical mapping of scalp voltage and estimation of the dipolar sources of the VEP components in the grand-average waveforms were carried out using Brain Electrical Source Analysis (BESA 2000 v.5.1.8; Megis Software GmbH, Gräfelfing, Germany). The algorithm implemented in BESA estimates the location and orientation of multiple equivalent dipolar sources by calculating the scalp distribution obtained for a given dipole model (forward solution) and comparing it to the actual VEP distribution. Interactive changes in the location and orientation of the dipole sources lead to minimization of the residual variance (RV) between the model and the observed spatio-temporal VEP distribution. In the current study, this analysis used a realistic approximation of the head, with the radius obtained from the average of the group of subjects (81 mm). This realistic head model uses finite elements derived from an average of 24 individual MRIs and consists of three compartments: brain (including the cerebral spinal fluid), skull and scalp. A spatial digitizer recorded the three-dimensional coordinates of each electrode and three fiducial landmarks (the left and right preauricular points and the nasion). A computer algorithm was used to calculate the best-fit sphere that encompassed the array of electrode sites and determine their spherical coordinates. The mean spherical coordinates for each site averaged across all subjects were used for the topographic mapping and source localization procedures. In addition, individual spherical

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