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Research article

Direction of magnetoencephalography sources associated with feedback and feedforward contributions in a visual object recognition task

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HIGHLIGHTS

- Fusiform sources in a visual object recognition MEG experiment were examined.
- Directions of source currents were opposite for expected feedforward and feedback inputs.
- MEG and EEG source direction may depend on hierarchical organization.

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ABSTRACT

Identifying inter-area communication in terms of the hierarchical organization of functional brain areas is of considerable interest in human neuroimaging. Previous studies have suggested that the direction of magneto- and electroencephalography (MEG, EEG) source currents depend on the layer-specific input patterns into a cortical area. We examined the direction in MEG source currents in a visual object recognition experiment in which there were specific expectations of activation in the fusiform region being driven by either feedforward or feedback inputs. The source for the early non-specific visual evoked response, presumably corresponding to feedforward driven activity, pointed outward, i.e., away from the white matter. In contrast, the source for the later, object-recognition related signals, expected to be driven by feedback inputs, pointed inward, toward the white matter. Associating specific features of the MEG/EEG source waveforms to feedforward and feedback inputs could provide unique information about the activation patterns within hierarchically organized cortical areas.

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1. Introduction

Non-invasive methods such as magneto- and electroencephalography (MEG, EEG), and functional magnetic resonance imaging (fMRI) provide means to examine neural activity in various ways, for example, by determining locations, sequences, and connectivity patterns among regions in the human brain [39]. In addition to these measures, identifying inter-area communication in terms of the hierarchical organization of functional brain areas would be highly relevant in the quest for understanding the operation of the brain. Characteristic anatomical laminar distributions of input and output connections between cortical areas have been described as being of feedforward, feedback, or lateral type, thereby defining a hierarchical organization among the areas [15,36]. However, this type of information is not readily available in human imaging data. The spatial resolution of fMRI is approaching the level at which laminar distributions of cortical activity can be detected [35]. The direction of the MEG and EEG source currents is another piece of information that may help to characterize layer-specific input patterns into a cortical area, thereby providing cues about the flow and the function of the detected neural activity in terms of feedforward (bottom–up) and feedback (top–down) of inputs [18,23].

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MEG and EEG signals originate mainly from post-synaptic currents in cortical pyramidal cells [33], and the direction of the source current depends on the type and the dendritic location of the synaptic input [5,27]. In event-related response waveforms, an initial deflection can often be associated with feedforward input, followed by broader feedback-related activity [3]. In somatosensory, auditory, and visual evoked MEG data, early biphasic or triphasic responses, presumably driven by feedforward inputs, and later uniphasic feedback driven responses have been observed [18–20]. Given the different laminar distributions of feedforward and feedback type inputs, it is conceivable that the direction of the initial phase of a feedforward driven response is opposite to that of a feedback driven response. Biophysically realistic computational neural modeling incorporating detailed physiology of the laminar structure in cortical circuits has been successfully applied to interpret the directionality of neural current sources underlying MEG signals during a somatosensory detection task [22,23,41]. In the present study, we examined the direction in MEG source currents in the fusiform region in a visual object detection experiment in which there were specific expectations of activation being driven by either feedforward or feedback inputs [9].

2. Methods

The present results were derived from new analyses applied to previously published MEG data from a visual object recognition experiment [9]. In this experiment, the experimental evidence supported specific theoretical predictions regarding latency- and condition-dependent feedforward and feedback inputs to the inferior occipitotemporal (fusiform) region. According to the model of Bar [7,8] (Fig. 1A), low spatial frequency information about the visual object is quickly passed to the orbitofrontal cortex. Previously, activity associated with successful recognition of objects was found to occur earlier in the orbitofrontal cortex than in the fusiform region [9]. This is consistent with the orbitofrontal cortex enabling top–down facilitation of object recognition by sending predictions about the object identity to the fusiform cortex. Therefore, feedback-type input into the fusiform region is expected for those trials in which the subject recognized the object. The fusiform region is also expected to receive feedforward-type input through a bottom–up route along the ventral visual pathway. Thus, the fusiform region is expected to receive both top–down feedback-type input as well as bottom–up feedforward-type input. Here, we determined the direction of the MEG source current in these cases to evaluate whether the source direction is dependent on the input type.

Nine healthy volunteers (6 females, age range 22–30 years) performed a visual object recognition task during the MEG recordings. The protocols were approved by the Internal Review Board at Massachusetts General Hospital; written informed consent was obtained from all subjects. Line drawings of familiar objects were presented on a computer screen for 63 ms, preceded and followed by random-dot mask patterns for 27 ms and 108 ms, respectively. Subjects were instructed to recognize each of the objects and to indicate their level of knowledge about the identity of the object by pressing one of four response buttons. MEG signals were obtained using a 306 channel Vectorview system (Elekta Neuromag, Finland), comprising of 204 planar gradiometers and 102 magnetometers. The sampling frequency was 600 Hz with a 0.1–200 Hz band-pass filter. Responses were low-pass filtered offline at 20 Hz. Epochs were baseline corrected by subtracting the mean of the 500 ms pre-stimulus interval in each sensor. For details of the experimental setup, see [9].

The direction of the source currents was examined using a distributed source model, the minimum-norm estimate (MNE) [17]. The MNE-based estimates of the time course of the source currents in the left and right hemisphere fusiform gyrus regions-of-interest (ROIs) were obtained [9]. The MNE was computed by assuming that all sources were located on the cortical surface extracted from anatomical MR images; a loose orientation constraint and depth-weighting were applied [25]. To determine the direction of the source currents, the source components normal to the cortical surface was extracted. The MNEs were constructed for each individual subject; the waveforms were computed as the mean value of the amplitude of the discretized source elements within the ROIs. In addition to the MNE analysis, the location and the direction of the fusiform sources in individual subjects were illustrated with equivalent current dipoles.

For the practical estimation of the MEG and EEG source direction, it is helpful to make a distinction between the physiological direction and the physical orientation of the source current. MEG and EEG are highly sensitive to the physical orientation of the source [1], which usually can be reliably determined [29]. However, identifying the physiological direction of the source (i.e., outward vs. inward with respect to the white matter), accurate localization of the source with respect to the cortical anatomy is essential: if the source is mis-localized to the opposite bank of a sulcus, an erroneously reversed direction will be inferred. Here, the tangentially oriented fusiform source currents were mainly on gyral parts of the inferior surface of the occipitotemporal region [9]; thus, they were well suited for reliable determination of the physiological source direction using MEG.

Two specific cases of fusiform activation were examined. The first was non-specific early evoked activity, obtained from all recognized trials in the latency window 100–120 ms after the appearance of the first visual masking stimulus. This early activity is assumed to results from feedforward input to the fusiform region, presumably form the occipital visual cortices. The second case was the later, recognition-related activity, obtained from the difference between conditions (recognized minus unrecognized trials, 210–250 ms). This recognition-related would be consistent with resulting from feedback-type top–down facilitatory inputs from the orbitofrontal cortex, which showed activation around 130 ms in the previous study [9]. For statistical analysis, a *t*-test was performed for the MNE-amplitude of the left and right hemisphere fusiform ROIs for the two cases against the null hypothesis of the mean amplitude across the subjects being zero.

3. Results

Measured MEG field maps and the corresponding equivalent current dipoles for one subject are shown in Fig. 1B. The early visual evoked response at 110 ms suggested a source in the right inferior occipitotemporal cortex, pointing outward, i.e., away from the white matter. In contrast, the differential signals for recognized and not recognized trials at 260 ms suggested later bilateral inferior occipitotemporal sources pointing inward, toward the white matter.

Results from a distributed source analysis of the MEG data confirmed the reversal of the source direction between the two conditions. Source waveforms for the left and right fusiform ROIs, averaged over nine subjects, are shown in Fig. 1C. A *t*-test indicated significant positive (outward direction) source amplitude for the 100–120 ms latency window of the initial visual response (right hemisphere: $t_{\mathrm{df=9}} = 4.01$, $p = 0.003$, uncorrected; left: $t_{\mathrm{df=9}} = 5.26$, $p = 0.0005$), and negative (inward) amplitude for the 210–250 ms window of the recognition-specific subtraction data (right: $t_{\mathrm{df=9}} = 2.58$, $p = 0.03$; left: $t_{\mathrm{df=9}} = 4.21$, $p = 0.002$).

4. Discussion

The opposite directions of the estimated MEG source currents for the fusiform gyrus in the two experimental conditions are

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