



Oscillatory modulations in human fusiform cortex during motion-induced blindness: Intracranial recording

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HIGHLIGHTS

- High-gamma activity at 80–150 Hz was attenuated in a fusiform site around illusory disappearance of a visual target.
- The distribution of delta phases in the fusiform site became skewed immediately prior to the illusory disappearance of the visual target.
- High-gamma activity was augmented in the fusiform site around reappearance of the visual target.

ABSTRACT

Objective: Motion-induced blindness (MIB) is an illusory phenomenon, in which a static target surrounded by moving distracters is perceived to disappear. We determined the electrocorticographic (ECoG) correlates of MIB.

Methods: While undergoing intracranial ECoG recording, a patient with focal epilepsy was instructed to report the transitions of a visual target, which was designed to illusorily or physically disappear and reappear. We then determined the neural modulations associated with illusory and physical transitions of the target. We also tested whether the phase of local delta activity could predict exclusively illusory transitions.

Results: High-gamma activity at 80–150 Hz was attenuated in the fusiform region prior to the reports of illusory and real visual target disappearance. Conversely, such high-gamma activity was augmented prior to the report of real target reappearance. Exclusively around illusory disappearance but not around real one, the delta phases in the fusiform region showed a highly skewed distribution with preference of the negative peak.

Conclusions: Neuronal modulations in the fusiform region may be involved in visual awareness, while spontaneous fluctuations of neural states entrained on delta rhythm may be involved in generation of MIB.

Significance: Our study increases our understanding of the mechanisms of visual awareness.

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1. Introduction

Motion-induced blindness (MIB) is an illusory perception of visual disappearance, where a salient and static visual target becomes intermittently invisible when surrounded by a mask consisting of a field of moving distracters (Bonneh et al., 2001). To experience this phenomenon, the readers are encouraged to open the supplementary video file and *fixate* the central cross (Supplementary Video S1). You are expected to intermittently perceive

disappearance of a continuously present target on the upper right side of the peripheral visual field. The existence of such subjective perception unrelated to physical stimuli illustrates that our conscious perceptions are not simply a reconstruction of the external world, but also reflect internal processes in the brain that interpret sensory stimuli (Wilke et al., 2003). The neural substrates of MIB should provide insights about the internal processes as to how humans interpret physical stimuli.

Recent human studies using functional MRI (fMRI) attempted to determine what brain structures are involved in generation of MIB. Following subjective disappearance of a target, blood-oxygen-level-dependent (BOLD) signals were attenuated in V4 (Donner et al., 2008) and augmented in V1, V2, V3AB, MT, and posterior intraparietal sulcus (Donner et al., 2008; Schölvinck and Rees,

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2010). Yet, another fMRI study failed to replicate these observations (Hsieh and Tse, 2009). Since perceptual disappearance and reappearance of a target alternately occur in a short interval, the neural activities during each state could be difficult to strictly segregate using BOLD signals, which reflect changes in regional cerebral blood flow and metabolism occurring several seconds after a given event. Studies of monkeys using single unit recording from the V1 area and frontal eye field (FEF) revealed that a firing rate was increased slightly in V1 and significantly in FEF from 1300 until 300 ms prior to both reports of illusory and real disappearance of the target (Libedinsky et al., 2009; Libedinsky and Livingstone, 2011).

In the present study, we had a unique opportunity to sample electrocorticographic (ECoG) signals directly from the widespread regions including low- and high-level visual cortices in a patient with focal epilepsy. We determined the spatio-temporal dynamics of amplitude changes time-locked to overt reports of illusory and physical disappearance of a visual target. The measurements of interest included the amplitude of high-gamma activity at 80–150 Hz, which has been reported to be tightly correlated with firing rates (Ray et al., 2008) and BOLD signals (Niessing et al., 2005; Scheeringa et al., 2011). We specifically determined whether high-gamma amplitudes were altered in visual cortices at some level, prior to the reports of disappearance and reappearance of the target.

We subsequently determined the local oscillatory pattern which could predict the reports of spontaneous illusory transitions of the target exclusively and not those of externally-induced real transitions. We specifically tested the hypothesis that delta phases in visual cortex would show a skewed distribution prior to the report of illusory but not real disappearance of the target. A previous study of monkeys using single unit recording from the V1 area suggested that a delta phase could predict behavioral performance in a visual attention task (Lakatos et al., 2008).

2. Methods

2.1. Participant

The participant was a 14-year-old female with a history of focal seizures characterized by tingling of the right upper extremity as well as generalized tonic clonic seizures. She had a normal uncorrected visual acuity without visual field deficits. Her full-scale IQ was 99. MRI showed an area with increased T2 signal in the left parietal lobe, of which radiological diagnosis was ulegyria. No interictal epileptiform discharges were noted on scalp EEG or subsequent intracranial ECoG recordings; episodes of tingling of the right upper extremity failed to show significant evolution of epileptiform discharges. Resection of the parietal lesion was performed with sensorimotor, language and visual functions preserved; histological examination yielded a diagnosis of ganglioglioma without a surrounding cortical dysplasia. The study has been approved by the Institutional Review Board at Wayne State University, and written informed consent was obtained from the patient and her guardians.

2.2. Intracranial video-ECoG recording

Platinum subdural electrodes (10 mm intercontact distance, 4 mm diameter) were placed on widespread regions in the left hemisphere including the occipital region, fusiform region in the occipital-temporal junction and FEF. We attempted to minimize the risk of sampling errors, since Phase-I presurgical evaluation (Asano et al., 2009a) failed to identify the exact location of seizure onset zones. All electrode plates were stitched to adjacent plates

and/or the edge of dura mater, to avoid movement of subdural electrodes after placement (Wu et al., 2011). Video and ECoG were simultaneously and continuously recorded for 3 days using a 192-channel Nihon Kohden Neurofax 1100A Digital System (Nihon Kohden America Inc., Foothill Ranch, CA, USA). The sampling frequency was set at 1000 Hz with the amplifier band pass at 0.08–300 Hz. The averaged voltage of ECoG signals derived from the fifth and sixth intracranial electrodes of the ECoG amplifier was used as the original reference. ECoG signals were then re-montaged to a common average reference (Wu et al., 2011). No notch filter was used. All antiepileptic medications (oxcarbazepine and levetiracetam) were discontinued 2 days before the task. Surface electromyography electrodes were placed on the left and right deltoid muscles, and electrooculography electrodes were placed 2.5 cm below and 2.5 cm lateral to the left and right outer canthi.

2.3. Stimulus and task

The patient completed the following task while being awake, unседated, and comfortably seated on the bed in a dark room. She was instructed to report disappearance of the salient target surrounded by moving distracters by overtly saying “Gone” as well as reappearance of it by saying “Back”. Two blocks of tasks were given, while each block lasted 6 min.

Visual stimuli were binocularly presented on a 22-inch Dell P2210 LCD monitor (Dell Inc., Round Rock, TX, USA) with a pixel resolution of 1280 × 1024 and a refresh rate of 60 Hz, placed 60 cm in front of the patient. She was instructed to fixate on a central fixation cross on a black background during the task (Supplementary Video S1). The target was a high-contrast yellow dot presented in the right-upper diagonal, and the distracters consisted of scattered and constantly-moving small blue dots. The target intermittently disappeared for 2–4 s (average: 3 s) and appeared for 11–13 s (average: 12 s); thus, the target was designed to intermittently disappear and reappear illusorily sometimes and physically other times. The detailed specifications of target and distracters are described in the legend of Supplementary Video S1.

2.4. Time–frequency ECoG analysis

We determined ‘when’ and ‘where’ high-gamma amplitudes at 80–150 Hz were modulated relative to the responses of disappearance and reappearance. Only trials free of eye blinks during a 2-s period prior to the overt report of transitions were included into the time–frequency ECoG analysis, in order to exclude the potential effects of eye blinks on high-gamma amplitude measures (Nagasawa et al., 2011). Each ECoG trial was transformed into the time–frequency domain using a complex demodulation technique (Papp and Ktonas, 1977) incorporated in BESA® EEG V.5.1.8 software (BESA GmbH, Gräfelfing, Germany; Hoehstetter et al., 2004). A given ECoG signal was assigned an amplitude as a function of time and frequency at each trial (Fukuda et al., 2008; Wu et al., 2011). The time–frequency transform was obtained by multiplication of the time-domain signal with a complex exponential, followed by a low-pass filter. The low-pass filter used here was a finite impulse response filter of Gaussian shape, making the complex demodulation effectively equivalent to a Gabor transform. For assessment of high-gamma activity, the amplitude measure was sampled in steps of 5 ms and 10 Hz. The filter had a full width at half maximum of 2×7.9 ms in temporal domain and 2×14.2 Hz in frequency domain. The corresponding time–frequency resolution was ± 7.9 ms and ± 14.2 Hz (defined as the 50% power drop of the finite impulse response filter). For assessment of delta activity at 1 Hz (Nagasawa et al., 2011; Matsuzaki et al., 2012), the amplitude measure was sampled in steps of 100 ms and 0.5 Hz. The filter had a full width at half maximum of

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