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Frequency-dependent spatiotemporal profiles of visual responses recorded with subdural ECoG electrodes in awake monkeys: Differences between high- and low-frequency activity

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ABSTRACT

Electrocorticography (ECoG) constitutes a powerful and promising neural recording modality in humans and animals. ECoG signals are often decomposed into several frequency bands, among which the so-called high-gamma band (80–250 Hz) has been proposed to reflect local cortical functions near the cortical surface below the ECoG electrodes. It is typically assumed that the lower the frequency bands, the lower the spatial resolution of the signals; thus, there is not much to gain by analyzing the event-related changes of the ECoG signals in the lower-frequency bands. However, differences across frequency bands have not been systematically investigated. To address this issue, we recorded ECoG activity from two awake monkeys performing a retinotopic mapping task. We characterized the spatiotemporal profiles of the visual responses in the time-frequency domain. We defined the preferred spatial position, receptive field (RF), and response latencies of band-limited power (BLP) (i.e., alpha [3.9–11.7 Hz], beta [15.6–23.4 Hz], low [30–80 Hz] and high [80–250 Hz] gamma) for each electrode and compared them across bands and time-domain visual evoked potentials (VEPs). At the population level, we found that the spatial preferences were comparable across bands and VEPs. The high-gamma power showed a smaller RF than the other bands and VEPs. The response latencies for the alpha band were always longer than the latencies for the other bands and fastest in VEPs. Comparing the response profiles in both space and time for each cortical region (V1, V4+, and TEO/TE) revealed regional idiosyncrasies. Although the latencies of visual responses in the beta, low-, and high-gamma bands were almost identical in V1 and V4+, beta and low-gamma BLP occurred about 17 ms earlier than high-gamma power in TEO/TE. Furthermore, TEO/TE exhibited a unique pattern in the spatial response profile: the alpha and high-gamma responses tended to prefer the foveal regions, whereas the beta and low-gamma responses preferred the peripheral visual fields with larger RFs. This suggests that neurons in TEO/TE first receive less selective spatial information via beta and low-gamma BLP but later receive more fine-tuned spatial foveal information via high-gamma power. This result is consistent with a hypothesis previously proposed by Nakamura et al. (1993) that states that visual processing in TEO/TE starts with coarse-grained information, which primes subsequent fine-grained information. Collectively, our results demonstrate that ECoG can be a potent tool for investigating the nature of the neural computations in each cortical region that cannot be fully understood by measuring only the spiking activity, through the incorporation of the knowledge of the spatiotemporal characteristics across all frequency bands.

1. Introduction

Electrocorticography (ECoG) is a technique that uses subdural electrodes to record neural activity directly from the cortical surface and has been widely used in patients with epilepsy to localize the origin of epileptic seizures (Palmini et al., 1995; Zumsteg and Wieser, 2000). Recently, ECoG has gained attention as a tool for electrophysiological research in animals because it offers several advantages, including large spatial coverage, fine spatiotemporal resolution, and stable recordings

Abbreviations: BLP, band-limited power; ECOG, electrocorticography; FDR, false discovery rate; FP, fixation point; HGP, high-gamma power; MRI, magnetic resonance image; ND, normalized difference; PP, preferred position; RF, receptive field; RL, response latency; SRF, size of the receptive field; VEP, visual evoked potential.

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over weeks to months, which are impossible to attain simultaneously with other recording techniques (Bosman et al., 2012; Chao et al., 2010; Matsuo et al., 2011; Rubehn et al., 2009; Shimoda et al., 2012; Viventi et al., 2011). These advantages make ECoG a promising technique for neuroengineering applications, including brain machine interfaces (Graimann et al., 2004; Schalk et al., 2008).

Typically, ECoG signals are analyzed using the short-time window Fourier transform or its related spectral analysis techniques. The spectral decomposition of ECoG is critical, as it can isolate a putatively stable and informative aspect of the signal: the high-gamma power (HGP, 80–200 Hz). ECoG recordings in patients with epilepsy indicate that, compared to low-frequency band-limited power (BLP), HGP can better determine the timing and localization of motor-, sensory-, and task-related changes in neural activity (Canolty et al., 2007; Crone et al., 1998a, 1998b, 2001; Edwards et al., 2009, 2010; Kawasaki et al., 2012; Miller et al., 2007, 2010; Pei et al., 2011; Tsuchiya et al., 2008). Although HGP almost invariably shows event-related increments (but see Foster et al., 2012), event-related low-frequency BLP exhibits both increments and decrements in complicated temporal patterns over a few seconds that vary across subjects and recording sites (Canolty et al., 2007; Crone et al., 1998b; Fukuda et al., 2010; Harvey et al., 2013; Ohara et al., 2000). These observations have resulted in a view that, as far as event-related changes are concerned, the HGP reliably reflects local cortical functions at the cortical surface below the ECoG electrodes (Crone et al., 1998a, 2006; Jerbi et al., 2009), while it remains unclear what the lower-frequency BLP reflects, leading to less attention to event-related changes in the low-frequency BLP. Note that the functional roles of the low-frequency synchronized oscillations in steady states are a major issue in systems neuroscience (Engel and Fries, 2010; Ward, 2003).

However, detailed functional characterization of event-related changes in the low-frequency BLP might provide additional insights into local cortical processing. Although it is often assumed that electrical signals spatially propagate at different rates in the brain depending on their frequencies, the actual impedance spectra of cortical tissue are independent of frequency (Logothetis et al., 2007; Rank, 1963). This suggests that, in principle, low-frequency BLP might also reflect localized neural events. If this is true, it would be possible to learn the nature of the inputs and outputs of a given cortical area by analyzing both the HGP and low-frequency BLP, as output spikes and input synaptic activity are mainly correlated with HGP and low-frequency BLP, respectively (Bartos et al., 2007; Buzsáki et al., 2012; Logothetis, 2008). Furthermore, low-frequency BLP can reflect activity below the spiking threshold, which may not be reflected in HGP. To test this hypothesis, it is necessary to systematically investigate the differences between HGP and low-frequency BLP. In doing so, critical knowledge regarding what kind of information can be extracted from the different frequency bands can be obtained, which in turn will be useful for future ECoG applications in both basic neuroscience and applied neuroengineering.

In this study, we characterized the spatiotemporal profiles of visually driven ECoG responses across frequency bands using a retinotopic mapping paradigm, with a special focus on electrodes in the occipitotemporal cortex. Retinotopic responses have been investigated extensively for all known visual areas with various recording methods, the results of which facilitate the quantitative assessment and interpretation of our own results (Boussaoud et al., 1991; Brewer et al., 2002; Fize et al., 2003; Gattass et al., 1981, 1988; Van Essen and Zeki, 1978; Van Essen et al., 1984). Specifically, in two awake monkeys, we defined the spatial preference, size of the receptive field (RF), and response latency (RL) for each subdural ECoG electrode in the time-frequency domain, as well as time-domain visual evoked potentials (VEPs).

As to the response frequencies, we took an approach that is agnostic about the presence or absence of "oscillatory" responses (For this controversial issue in the field, see Miller et al., 2009 and Gaona et al., 2011). Following previous studies that identified functionally different subcomponents in the event-related changes of lower-frequency BLP (Canolty et al., 2007; Crone et al., 1998a, 1998b; Edwards et al., 2005; Harvey et al., 2013), we decomposed the spectral power change into the high-gamma band (80–250 Hz) and the alpha (3.9–11.7 Hz), beta (15.6–23.4 Hz), and low-gamma (30–80 Hz) bands. As we employed transient visual flash stimuli, which are typically used in a retinotopic mapping paradigm, we do not expect that changes in the power of these frequency band to reflect steady-state oscillations, which requires a longer duration of stimulation. Instead, we simply report the event-related changes in spectral power in different frequency bands as they are without giving too much interpretation. With these divisions of spectral power, we found similarities and striking differences in the spatial preference, RF size, and RL for HGP, each BLP, and VEPs, in the early (V1), middle (including V4), and high-level (TEO/TE) visual areas. Our findings constrain the models of how the measured ECoG responses are generated by a population of neurons, not necessarily from a perspective that presupposes oscillatory mechanisms in the brain.

2. Materials and methods

All experimental procedures were performed in accordance with the experimental protocols of the RIKEN Ethics Committee and the recommendations of the Weatherall report, "The use of non-human primates in research." All procedures were approved by the Committee for Animal Experiment at RIKEN (No. H24-2-2-3 (4)).

2. 1. Subjects and set-up for fixation training

Two macaque monkeys identified as Q (male, 8.1 kg) and B (male, 7.0 kg) were used in the experiments after brain magnetic resonance images (MRIs) were acquired. Before the monkeys were implanted with subdural ECoG electrodes, they were familiarized with the experimental settings and trained with a fixation task. During the fixation task, they sat in a primate chair with their head in a fixed position using a custom-made helmet for each monkey. Throughout the training and experiments, we used the same display and a custom-built computer control system (LabVIEW, National Instruments, Austin, TX) and measured horizontal and vertical eye positions at 500 Hz using an infrared video-based eye tracker (iView X^{TM} HiSpeed Primate, SMI). For visual stimuli, we positioned a liquid crystal display (Eizo, Japan) 30 cm from the eyes. We used MATLAB (Mathworks, Natick, MA) and Psychophysics Toolbox (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) to draw visual stimuli on the display. We wrote custom codes in LabVIEW running on a real-time PXI platform that controlled the flow of the experiment and synchronized the eye tracker, MATLAB, and other equipment (e.g., reward delivery).

2.2. Electrode implantation

Subdural electrodes were surgically implanted after the monkeys completed fixation training. To anesthetize the monkeys, we administered ketamine (5 mg/kg, intramuscular), atropine (0.05 mg/kg), and pentobarbital (20 mg/kg, intravenous). Throughout surgery, we continuously monitored their heart rate and sometimes checked their reflexive responses to noxious stimulation, adjusting the dose of pentobarbital accordingly. In the subdural space, we chronically implanted a customized multichannel ECoG electrode array (Unique Medical, Japan; Nagasaka et al., 2011) embedded with 2.1-mm diameter platinum electrodes (1-mm diameter exposed from a silicone sheet). The center-to-center inter-electrode distance was 5 mm. Both monkeys were implanted with 128 ECoG electrodes, a reference electrode in the subdural space, and a ground electrode in the epidural space above the right hemisphere (the reference and ground electrodes were 5×10 mm rectangular platinum plates). To localize the electrodes, we acquired post-operative X-ray images and co-registered them with the MRIs (Fig. 1A). We manually identified the locations of each electrode by projecting the electrodes in the X-ray images onto the cortical surface reconstructed from the MRIs. In Fig. 1A, we depicted some