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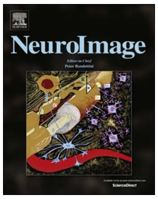

From intentions to actions: Neural oscillations encode motor processes through phase, amplitude and phase-amplitude coupling

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ABSTRACT

Goal-directed motor behavior is associated with changes in patterns of rhythmic neuronal activity across widely distributed brain areas. In particular, movement initiation and execution are mediated by patterns of synchronization and desynchronization that occur concurrently across distinct frequency bands and across multiple motor cortical areas. To date, motor-related local oscillatory modulations have been predominantly examined by quantifying increases or suppressions in spectral power. However, beyond signal power, spectral properties such as phase and phase-amplitude coupling (PAC) have also been shown to carry information with regards to the oscillatory dynamics underlying motor processes. Yet, the distinct functional roles of phase, amplitude and PAC across the planning and execution of goal-directed motor behavior remain largely elusive. Here, we address this question with unprecedented resolution thanks to multi-site intracerebral EEG recordings in human subjects while they performed a delayed motor task. To compare the roles of phase, amplitude and PAC, we monitored intracranial brain signals from 748 sites across six medically intractable epilepsy patients at movement execution, and during the delay period where motor intention is present but execution is withheld. In particular, we used a machine-learning framework to identify the key contributions of various neuronal responses. We found a high degree of overlap between brain network patterns observed during planning and those present during execution. Prominent amplitude increases in the delta (2–4 Hz) and high gamma (60–200 Hz) bands were observed during both planning and execution. In contrast, motor alpha (8–13 Hz) and beta (13–30 Hz) power were suppressed during execution, but enhanced during the delay period. Interestingly, single-trial classification revealed that low-frequency phase information, rather than spectral power change, was the most discriminant feature in dissociating action from intention. Additionally, despite providing weaker decoding, PAC features led to statistically significant classification of motor states, particularly in anterior cingulate cortex and premotor brain areas. These results advance our understanding of the distinct and partly overlapping involvement of phase, amplitude and the coupling between them, in the neuronal mechanisms underlying motor intentions and executions.

1. Introduction

The simple motor act of stretching out your arm to grab a cup of coffee is mediated by a rich and complex chain of neuronal processes. What, in essence, may seem as the execution of a straightforward motor command is, in fact, carried out by a cascade of events ranging from action selection and planning, to motor execution and monitoring. The neural mechanisms that mediate the transformation of a person's intentions into actions have been the subject of a thriving body of research for decades (Ariani et al., 2015; Brovelli et al., 2005; Desmurget and Sirigu, 2009; Jeannerod, 1994; Kalaska, 2009; Lau, 2004; Paus, 2001; Schwartz, 2016; Snyder et al., 1997). However,

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Table 1
Patient data: handedness, age, gender, and description of epilepsy type, etiology, as determined by the clinical staff of the Grenoble Neurological Hospital, Grenoble, France. The lesions (if any were observed) were determined based on the T1 images. Recording sites with epileptogenic activity were excluded from the analyses.

	Handedness	Age	Gender	Epilepsy type	Etiology	EZ localization	Lesion
P1	R	19	F	Frontal	Secondary	Precentral gyrus (RH)	Dysplasia
P2	R	23	F	Frontal	Cryptogenic	Precentral gyrus (LH)	Absent
P3	R	18	F	Frontal	Cryptogenic	Fronto-basal (RH)	Absent
P4	R	18	F	Frontal	Idiopathic	Fronto-central (RH)	Absent
P5	R	31	F	Insula	Secondary	Operculum (RH)	Cavernoma
P6	R	24	F	Frontal	Secondary	Supra-sylvian posterior (LH)	Vascular sequelae

because the neuronal processes at play can be observed at various spatial scales, and with different recording techniques, parallel streams of research have given rise to a rich but fragmented understanding of the local and large-scale integrative electrophysiological mechanisms that are involved in motor control.

Both human and non-human primate research provides solid evidence that goal-directed motor behavior is associated with changes in the patterns of rhythmic neuronal activity across largely distributed brain areas (Schnitzler and Gross, 2005). Movement initiation and execution are mediated by patterns of synchronization and desynchronization that occur concurrently across distinct frequency bands and within multiple motor cortical areas (Cheyne et al., 2008; Jurkiewicz et al., 2006; Pfurtscheller et al., 2003; Saleh et al., 2010).

To date, motor-related local oscillatory modulations are by and large examined by quantifying increases or suppressions in spectral power (Cheyne et al., 2008; Jurkiewicz et al., 2006; Pfurtscheller et al., 2003; Saleh et al., 2010). However, beyond band-limited oscillatory power, other spectral properties, namely phase and phase-amplitude coupling (PAC), are also thought to play a key role in neuronal encoding and information processing. The involvement of phase information in neuronal encoding has been extensively investigated in numerous perceptual modalities and higher-order cognitive tasks (Drewes and VanRullen, 2011; Dugue et al., 2011; Jensen et al., 2014; Klimesch et al., 2008, 2007; Montemurro et al., 2008; Palva and Palva, 2007; Sauseng and Klimesch, 2008; Sherman et al., 2016; VanRullen et al., 2011). In comparison, the role of phase and phase-based measures mediating motor processes are still insufficiently studied. Interestingly, a few studies provide evidence for the involvement of low-frequency phase and amplitude in the neuronal encoding of movement features (Hammer et al., 2016, 2013; Jerbi et al., 2011, 2007; Milekovic et al., 2012; Miller et al., 2012; Waldert et al., 2009, 2008). Nevertheless, the spatial, temporal and spectral dynamics of putative phase coding in the chain of processes are still largely unresolved: starting from goal encoding, to motor planning and motor command execution.

Recent years have witnessed a surge in interest in the putative mechanistic function of PAC (Cohen et al., 2008; Hemptinne et al., 2013; Lee and Jeong, 2013; Newman et al., 2013; Voytek, 2010, Bahramisharif et al., 2013), and numerous measures of PAC have been proposed (Canolty, 2006; Nakhnikian et al., 2016; Tort et al., 2010; Voytek et al., 2013, Özkurt, 2012). Conceptually, PAC may provide a flexible framework for information processing by means of cross-frequency synchronization (Canolty and Knight, 2010; Hyafil et al., 2015; Maris et al., 2011; Staresina et al., 2015; van der Meij et al., 2012; Weaver et al., 2016). However, despite important advances (Hemptinne et al., 2013; Özkurt and Schnitzler, 2011; Soto and Jerbi, 2012; Yanagisawa et al., 2012), the precise role of PAC in mediating motor planning and execution is not yet fully resolved. Specifically, the distinct functional roles of phase, amplitude and PAC estimates during motor behavior remain generally ill-defined.

In the present paper, we compare the involvement of all three of these features using multi-site intracerebral depth electrode recordings from human subjects performing a delayed motor task. Using high spatial, spectral and temporal resolution, we monitored modulations of neural activity, not only at movement execution but, also, during the delay time-window when motor intention is present but execution is withheld. In addition to standard statistical comparisons, we used a single-trial classification procedure (supervised learning) to identify the key contributions of three distinct oscillatory features (phase, amplitude and PAC) to the various motor-related processes along the chain of processes, from goal encoding to movement execution.

2. Material and methods

2.1. Participants

Six patients with medically intractable epilepsy participated in this study (6 females, mean age 22.17 ± 4.6). The patients were stereotactically implanted with multi-lead EEG depth electrodes at the Epilepsy Department of the Grenoble Neurological Hospital (Grenoble, France). In collaboration with the medical staff, and based on visual inspection, electrodes presenting pathological waveforms were discarded from the present study. All participants provided written informed consent, and the experimental procedures were approved by the Institutional Review Board, as well as by the National French Science Ethical Committee. Patient-specific clinical details can be found in Table 1.

2.2. Electrode implantation and stereotactic EEG recordings

Each patient was implanted with stereotactic electroencephalography (SEEG) electrodes. Each one of these had a diameter of 0.8 mm and, depending on the implanted structure, was composed of 10 to 15 contacts that were 2 mm wide and 1.5 mm apart (DIXI Medical Instrument). Intracranial EEG signals were recorded from a total of 748 intracerebral sites across all patients (126 sites in each participant, except for one patient who had 118 recording sites). At the time of acquisition, a white matter electrode was used as reference, and data was bandpass filtered from 0.1 to 200 Hz and sampled at 1024 Hz. Electrode locations were determined using the stereotactic implantation scheme and the Talairach and Tournoux proportional atlas (Talairach and Tournoux, 1993). The electrodes were localized in each individual subject in Talairach coordinates (based on post-implantation CT), and then transformed to standard MNI coordinate system according to standard routines and previously reported procedures (Bastin et al., 2016; Jerbi et al., 2010, 2009; Ossandon et al., 2011).

2.3. Delayed center-out motor task

After a rest period of 1000 ms, the participants were visually cued to prepare a movement towards a target in one of four possible directions: up, down, left or right (*Planning phase*). Next, after a 1500 ms delay period, a Go signal prompted the subjects to move the cursor towards the target (*Execution phase*). The Go signal consisted of a central cue changing from white to black. Fig. 1B shows the task design.