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Alpha power indexes task-related networks on large and small scales: A multimodal ECoG study in humans and a non-human primate

A. de Pesters [a,b], W.G. Coon [a], P. Brunner [a,c], A. Gunduz [d], A.L. Ritaccio [c], N.M. Brunet [e], P. de Weerd [f,g], M.J. Roberts [g], R. Oostenveld [g], P. Fries [g,h], G. Schalk [a,b,c,*]

[a] Nat Ctr for Adapt Neurotech, Wadsworth Center, NY State Dept of Health, Albany, NY, USA
[b] Dept of Biomed Sci, State Univ of New York at Albany, Albany, NY, USA
[c] Dept of Neurology, Albany Medical College, Albany, NY, USA
[d] Dept of Biomed Eng, Univ of Florida, Gainesville, FL, USA
[e] SUNY Downstate Med Ctr, Brooklyn, NY, USA
[f] Dept of Cogn Neurosci, Maastricht Univ, Maastricht, Netherlands
[g] Donders Inst for Brain, Cognition and Behaviour, Nijmegen, Netherlands
[h] Ernst Strüngmann Inst for Neurosci, Frankfurt, Germany

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ABSTRACT

Performing different tasks, such as generating motor movements or processing sensory input, requires the recruitment of specific networks of neuronal populations. Previous studies suggested that power variations in the alpha band (8–12 Hz) may implement such recruitment of task-specific populations by increasing cortical excitability in task-related areas while inhibiting population-level cortical activity in task-unrelated areas (Klimesch et al., 2007; Jensen and Mazaheri, 2010). However, the precise temporal and spatial relationships between the modulatory function implemented by alpha oscillations and population-level cortical activity remained undefined. Furthermore, while several studies suggested that alpha power indexes task-related populations across large and spatially separated cortical areas, it was largely unclear whether alpha power also differentially indexes smaller networks of task-related neuronal populations. Here we addressed these questions by investigating the temporal and spatial relationships of electrocorticographic (ECoG) power modulations in the alpha band and in the broadband gamma range (70–170 Hz, indexing population-level activity) during auditory and motor tasks in five human subjects and one macaque monkey. In line with previous research, our results confirm that broadband gamma power accurately tracks task-related behavior and that alpha power decreases in task-related areas. More importantly, they demonstrate that alpha power suppression lags population-level activity in auditory areas during the auditory task, but precedes it in motor areas during the motor task. This suppression of alpha power in task-related areas was accompanied by an increase in areas not related to the task. In addition, we show for the first time that these differential modulations of alpha power could be observed not only across widely distributed systems (e.g., motor vs. auditory system), but also within the auditory system. Specifically, alpha power was suppressed in the locations within the auditory system that most robustly responded to particular sound stimuli. Altogether, our results provide experimental evidence for a mechanism that preferentially recruits task-related neuronal populations by increasing cortical excitability in task-related cortical areas and decreasing cortical excitability in task-unrelated areas. This mechanism is implemented by variations in alpha power and is common to humans and the non-human primate under study. These results contribute to an increasingly refined understanding of the mechanisms underlying the selection of the specific neuronal populations required for task execution.

Introduction

Performing different tasks, such as generating motor movements or processing sensory information, requires the recruitment of specific networks of neuronal populations dispersed throughout distinct cortical areas. How the brain implements the recruitment of these networks is still largely unclear, but there is increasing evidence that oscillatory activity plays an important role in this process. For example, several

* Corresponding author at: National Center for Adaptive Neurotechnologies, Center for Medical Sciences 2003, 150 New Scotland Avenue, Albany, NY 12208, USA.
E-mail addresses: adepesters@neurotechcenter.org (A. de Pesters), wcoon@neurotechcenter.org (W.G. Coon), pbrunner@neurotechcenter.org (P. Brunner), agunduz@bme.ufl.edu (A. Gunduz), ritacca@mail.amc.edu (A.L. Ritaccio), nicolas.brunet@downstate.edu (N.M. Brunet), p.deweerd@maastrichtuniversity.nl (P. de Weerd), mark.roberts@donders.ru.nl (M.J. Roberts), r.oostenveld@donders.ru.nl (R. Oostenveld), pascal.fries@esi-frankfurt.de (P. Fries), gschalk@neurotechcenter.org (G. Schalk).

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studies involving different sensorimotor modalities have reported a decrease in the power of low-frequency oscillations (event-related desynchronization (ERD)) in the 8–12 Hz range (alpha band) in task-related areas (Pfurtscheller and Neuper, 1992; Crone et al., 2001; Potes et al., 2014). This phenomenon is frequently coupled with an increase in alpha power (event-related synchronization (ERS)) in areas unrelated to the task (Pfurtscheller and Berghold, 1989; Pfurtscheller and Neuper, 1992; Fu et al., 2001). Separately, alpha oscillations with higher amplitudes modulate the firing of neuronal populations more strongly than oscillations with lower amplitudes (Haegens et al., 2011), which establishes a link between modulations of alpha power and cortical excitability. Taken together, these findings suggest that modulations in alpha power may index the degree of inhibition in different cortical areas, and, by extension, the spatial representation of selected functional networks (Klimesch et al., 2007). These observations have been consolidated into the *gating-by-inhibition* (GBI) hypothesis (Jensen and Mazaheri, 2010), and most recently synthesized with the *communication-through-coherence* (CTC) hypothesis (Fries, 2005)) into the *function-through-biased oscillations* (FBO) hypothesis (Schalk, 2015). The view that emerges from this theoretical and experimental work is that the selection of functional networks is achieved by modulation of cortical excitability, and that cortical excitability is measured most directly by the instantaneous amplitude of oscillatory activity (that is influenced by oscillatory phase as well as oscillatory power) (Schalk, 2015).

If oscillatory activity indeed provides a general mechanism for the selection of cortical networks through modulation of cortical excitability, we can make three specific predictions. First, increases in population-level cortical activity in task-related areas should be accompanied by a decrease in alpha power irrespective of the task or the involved cortical areas, and alpha power should increase in all other regions. Second, in top-down preparation for a motor output, increases in cortical excitability as measured by a decrease of alpha power should occur prior to increases in population-level cortical activity. On the contrary, in a bottom-up response to a sensory stimulus, cortical excitability modulations may also be affected by the stimulus, and should thus trail stimulus-induced cortical activity. While the suppression in the alpha band has previously been reported to precede motor movements (Pfurtscheller and Berghold, 1989; Pfurtscheller and Neuper, 1992) and to follow auditory stimulation (Crone et al., 2001), such results remained to be demonstrated using single-trial analyses. Third, we should observe task-selective alpha modulations not only on large spatial scales, e.g., across motor and auditory regions, but also on smaller scales, e.g., within auditory regions. Such small-scale modulations of oscillatory activity are a prerequisite if they were to play a central role in regulating information flow within the brain. While there is solid evidence supporting the idea that alpha power may constitute a selection mechanism across large, spatially separated areas (Pfurtscheller, 1992; Pfurtscheller and Neuper, 1994; Foxe et al., 1998; Thut et al., 2006), evidence that it may also support selection of small and interwoven networks is scarce (Harvey et al., 2013). At present, the general consensus is still that modulations of alpha power are spatially widespread and only poorly informative of detailed delineations of the functional networks underlying the performance of different tasks (Crone et al., 2001; Pfurtscheller et al., 2003; Crone et al., 2006; Miller et al., 2009a).

To test these predictions and to better understand the dynamics between modulatory alpha band oscillations and population-level cortical activity, we recorded electrocorticographic signals (ECoG) during auditory and motor tasks in five human subjects and one macaque monkey. The high spatial and temporal resolution of these signals allowed us to study these dynamics not only across functional networks, i.e., auditory versus motor systems, but also within one functional network, i.e., the auditory system. In particular, we evaluated the spatial and temporal patterns of alpha power in response to different types of stimuli, over time, and in specific locations of auditory cortex, and related them to modulations of population-level activity as indexed by broadband gamma (70–170 Hz) (Manning et al., 2009; Miller et al., 2009b; Ray and Maunsell, 2011).

In agreement with the three predictions outlined above, we observed large modulations of alpha power across tasks: alpha power decreased in task-related areas and increased in a majority of task-unrelated areas. These results were common to the human subjects and the macaque monkey. Because alpha power has been linked to cortical excitability, these changes likely subserve the preferential recruitment of those functional networks necessary to perform a particular task. Furthermore, we found that alpha power suppression lagged population-level activity in auditory areas during the auditory task, but preceded it in the motor areas during the motor task. Finally, decreases in alpha power within auditory areas indexed regions where population-level activity increased the most in response to specific auditory stimuli. Similarly, increases in alpha power indexed regions where population-level activity increased the least. Taken together, our results add further evidence to a central role of oscillatory activity in regulating cortical excitability, and thus in regulating information flow within the brain. They also suggest that this modulating mechanism might operate even across small cortical populations.

Methods

Subjects

Five human subjects at Albany Medical Center (Albany, New York) and one macaque monkey at Radboud University (Nijmegen, Netherlands) participated in this study. The five human subjects (A–E) were patients with intractable epilepsy who underwent temporary placement of subdural electrode arrays to localize seizure foci prior to surgical resection. They included two women (A and B) and three men (C, D and E). The subjects' clinical profiles are summarized in Table 1. Language lateralization (LL) was established preoperatively using the Wada test (Wada and Rasmussen, 1960). Human subjects gave informed consent for the study, which was approved by the Institutional Review Board of Albany Medical College and the Human Research Protections Office of the US Army Medical Research and Materiel Command. All animal procedures were approved by the ethics committee of Radboud University, Nijmegen, Netherlands.

The subjects were implanted with electrode grids that were approved for human use (Ad-Tech Medical Corp., Racine, WI; and PMT Corp., Chanhassen, MN; for human subjects), or polyimide-based grids ((Rubehn et al., 2009), for the macaque) over one hemisphere of the brain. Electrodes for the humans consisted of platinum-iridium disks (4 mm in diameter, 2.3 mm exposed), embedded in silicon and spaced 6–10 mm apart; for the macaque, electrodes were 1 mm in diameter and spaced 2, 2.5 or 3 mm apart. The total numbers of implanted electrodes were 58–134 for the humans and 252 for the macaque. In the humans, the grids were implanted for about 1 week and their location varied across subjects. They were placed over the left hemisphere for subjects A, C, D, E and the macaque, and covered frontal, parietal and temporal cortices. Following the placement of the subdural grid, each human subject had postoperative anterior–posterior and lateral radiographs, as well as computer tomography (CT) scans to verify grid location.

Data collection

We recorded ECoG signals from the five human subjects at the bedside using the general-purpose BCI2000 software (Schalk et al., 2004; Schalk and Mellinger, 2010) connected to eight 16-channel g.USBamp biosignal acquisition devices (g.tec, Graz, Austria). Clinical monitoring occurred simultaneously with the use of a connector that split the cables coming from the patient into one set that was connected to the clinical monitoring system and another set that was connected to the amplifiers. This ensured that clinical data collection was not compromised