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Dorsal and ventral cortices are coupled by cross-frequency interactions during working memory

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ABSTRACT

Oscillatory activity in the alpha and gamma bands is considered key in shaping functional brain architecture. Power increases in the high-frequency gamma band are typically reported in parallel to decreases in the low-frequency alpha band. However, their functional significance and in particular their interactions are not well understood. The present study shows that, in the context of an N-back working memory task, alpha power decreases in the dorsal visual stream are related to gamma power increases in early visual areas. Granger causality analysis revealed directed interregional interactions from dorsal to ventral stream areas, in accordance with task demands. Present results reveal a robust, behaviorally relevant, and architectonically decisive power-to-power relationship between alpha and gamma activity. This relationship suggests that anatomically distant power fluctuations in oscillatory activity can link cerebral network dynamics on trial-by-trial basis during cognitive operations such as working memory.

Introduction

Rhythmic neuronal activity is a ubiquitous phenomenon that underlies the spectral components that can be readily observed in electrophysiological recordings. In recent decades, a large body of empirical evidence has been collected, providing a link between oscillatory activity in specific frequency bands and their functional role in cognition. For instance, amplitude fluctuations in alpha oscillatory activity (8–14 Hz) have been found to be related to cognitive processes such as perception, attention, and memory (Gevins et al., 1997; Cooper et al., 2003; Klimesch et al., 2007; Jensen and Mazaheri, 2010; Saalmann et al., 2012; van Kerkoerle et al., 2014; Bastos et al., 2015; Michalareas et al., 2016; Popov et al., 2017). Specifically, decreases in alpha amplitude have been proposed to index engagement of a cortical area, whereas increases mark reduced processing capabilities. This has been demonstrated in the visual (Adrian and Matthews, 1934; Foxe et al., 1998), sensorimotor (Haegens et al., 2010, 2011; van Ede et al., 2014), and auditory (Weisz et al., 2011; Mazaheri et al., 2014) domains, suggesting an overarching principle for effective neuronal resource allocation in a regionally specific manner.

Faster rhythms (gamma oscillations, >30 Hz), on the other hand, have been frequently linked to coherent stimulus processing (Tallon-Baudry and Bertrand, 1999; Fries, 2005), attention (Bauer et al., 2014; Marshall et al., 2015a, 2015b), and working memory (Tallon-Baudry et al., 1998; Roux et al., 2012). It is well known that fast and slow rhythms frequently co-occur and that they are often co-modulated (or anti-modulated) as a consequence of an experimental manipulation. This has led to the idea that dynamic interactions between slow and fast oscillatory activity might be a key mechanism shaping functional interactions in cortical networks (Buzsaki and Draguhn, 2004; Canolty and Knight, 2010; Lisman and Jensen, 2013).

One possible mechanism by which fast rhythms could interact with slower rhythms is by means of phase-amplitude coupling (PAC) (Jensen and Colgin, 2007; Canolty and Knight, 2010), where slow oscillations physically modulate the amplitude of faster rhythms. PAC has been identified in a variety of species, including rodents (Tort et al., 2009, 2010), nonhuman primates (Whittingstall and Logothetis, 2009; Spaak et al., 2012), and humans (Canolty and Knight, 2010). Moreover, PAC has been demonstrated during cognitive operations such as item-context binding (Tort et al., 2009), spatial navigation and decision making (Tort et al., 2008), working (Axmacher et al., 2010; Leszczynski et al., 2015) and episodic memory (Staudigl and Hanslmayr, 2013; Park et al., 2016), sleep (Staresina et al., 2015), and resting conditions (Florin and Baillet, 2015) and in a variety of clinical conditions such as Parkinson's disease (van Wijk et al., 2016),

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schizophrenia (Allen et al., 2011; Kirihara et al., 2012; Popov and Popova, 2015), autism (Berman et al., 2015), and affective disorders (Miskovic et al., 2011).

Another view of the relationship between slow and fast oscillatory activity comes from recent work investigating the network properties of directed oscillatory coupling [e.g. Granger causality (GC)] between brain regions in humans and non-human primates. Long-range inter-regional gamma synchronization has been shown to reflect feed-forward interactions within the visual cortical hierarchy, whereas slower alpha-beta synchronization reflects feedback interactions (van Kerkoerle et al., 2014; Bastos et al., 2015; Michalareas et al., 2016). These findings are in line with generic anatomical connection profiles between cortical layers, both within and between cortical areas, and with the cortical-layer-specific distribution of different neuronal rhythms.

A third type of interaction could involve a relationship between the oscillations' amplitudes. In contrast to the PAC and GC measures, this type of functional interaction does not require a strict relationship of the oscillations' phase between brain areas. In fact, a number of studies have reported stimulus-induced increases in gamma band activity with a concomitant decrease in alpha-beta power [e.g. (Schoffelen et al., 2005; Hoogenboom et al., 2006, 2010; Swettenham et al., 2009; Muthukumaraswamy and Singh, 2013; Perry et al., 2013; Bauer et al., 2014; Kujala et al., 2015; Michalareas et al., 2016)]. These empirical observations suggest a negative correlation between the task-induced amplitude modulations of slow versus fast rhythms.

Yet a functionally relevant mechanistic relationship between low- and high-frequency oscillatory activity, where a temporary increase in low frequency power leads to a temporary reduction in high frequency power, would suggest a negative correlation within trials. Reports of this nature are far less frequent in the literature (de Lange et al., 2008; Park et al., 2011; Popov et al., 2017; Wang et al., 2017), which may be a consequence of the fact that single-trial estimates of oscillatory amplitudes typically have low signal-to-noise ratio, in particular when estimated from non-invasively recorded data.

The present study leveraged the availability of a large number of participants (n = 83), analyzing MEG data from a publicly available dataset. Participants performed a visual working memory (WM) N-back task, which reliably induces modulations in both alpha and gamma activity (Roux and Uhlhaas, 2014). These data are well suited to investigate the relationship between WM-load-dependent local changes in low- and high-frequency oscillatory activity, both across time within trials and across participants. We hypothesized that WM demands would manifest as power-power interactions, where reductions in alpha activity would be associated with a spatially specific power increase in gamma activity. Second, these power fluctuations should be related to behavioral performance both within and between trials. Third, "top--down" influence within key network nodes should be reflected in low-frequency activity, whereas "bottom-up" communication should be evident in high-frequency activity.

Material and methods

Participants and experimental procedures

Publicly available data provided by the human connectome consortium (www.humanconnectome.org) were analyzed. Eighty-three participants (37 female, mean age 28.5 years, range 22–35) participated in the experiment. Most were right-handed as measured with the Edinburgh Handedness Inventory with an mean lateralization quotient of 65% and SD = 44% (Oldfield, 1971). Participants gave written informed consent for participation in accordance with the Declaration of Helsinki. In two runs, participants performed an N-back WM paradigm, memorizing pictures of faces and tools. Participants were presented with 16 blocks per run of 0-back and 2-back trials and were asked to indicate match and no-match responses via button press with their right index and right middle finger, respectively. An initial cue presented for 2500 ms signaled the beginning of either a 0- or a 2-back block. After this, a serial presentation of face or tool stimuli, each displayed for 2000 ms, was intermixed with an inter-stimulus intervals (ISI) of 500 ms. Participants were asked to respond as fast as possible via button press after the presentation of each stimulus, within the stimulus presentation window. Following a fixation interval of 500 ms, the next stimulus was presented. A schematic of the trial sequences is shown in Fig. 1.

Data acquisition and analysis

Data were recorded using a whole-head 248-channel magnetometer system (MAGNES 3600 WH, 4D Neuroimaging, San Diego, CA) with the participants in supine position. Data were continuously recorded with a sampling rate of 2034.5101 Hz and a bandwidth of DC-400 Hz. Digitization of the participants' head shape and of the locations of the fiducial coils was accomplished with a Polhemus 3Space Fasttrak system. The WM task was a part of a 3-h session, where both task and resting-state MEG data were collected. Participants performed a sequence of tasks, described in detail in the reference manual provided by the human connectome consortium (http://www.humanconnectome.org/documentation/S500/index.html). Just prior to the N-back paradigm the participant underwent three runs of approximately 6 min of resting-state MEG recording.

The analysis described below was performed on the 'minimally preprocessed' data that were downloaded from the human connectome database. In brief, epochs lasting from 1.5 s before to 2.5 s after each picture's onset had been extracted from the continuous recording. Epochs containing superconducting quantum interference device (SQUID) jumps, bad sensors, or bad segments, defined as excessive signal amplitude changes $> \sim 10^{-12}$ T, were excluded from further processing. Eye-movement-related signals and cardiac signals had been identified with independent component analysis (ICA) (Jung et al., 2001) and projected out of the data. All data was analyzed using custom scripts in MATLAB and the FieldTrip toolbox (Oostenveld et al., 2011).

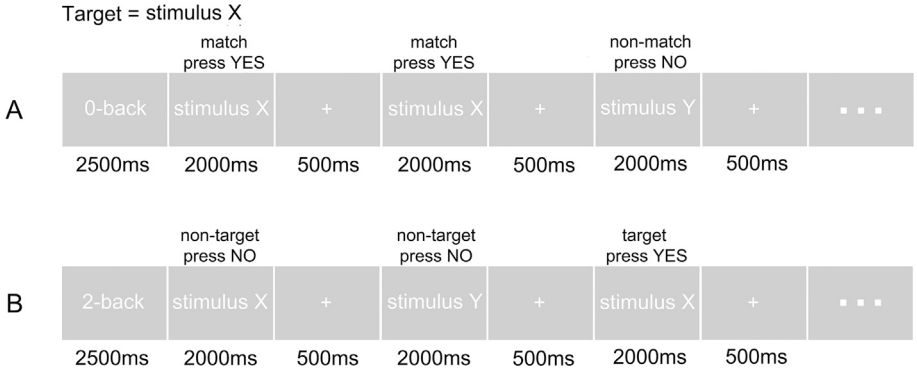

Fig. 1. Experimental task. A: Zero-back condition. At the beginning of a 0-back block, participants are presented with a target stimulus X. On subsequent trials, different stimuli are presented. After each of these stimuli, participants indicate via a button press whether the presented stimulus matches the target stimulus. **B**: Two-back condition. Two-back blocks were signaled by a presentation of "2-back" for 2500 ms. Participants indicated whether the presented stimulus matched the stimulus two trials earlier.