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Research Report

Amplitude and phase dynamics associated with acoustically paced finger tapping

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ABSTRACT

To gain insight into the brain activity associated with the performance of an acoustically paced synchronization task, we analyzed the amplitude and phase dynamics inherent in magnetoencephalographic (MEG) signals across frequency bands in order to discriminate between evoked and induced responses. MEG signals were averaged with respect to motor and auditory events (tap and tone onsets). Principal component analysis was used to compare amplitude and phase changes during listening and during paced and unpaced tapping, allowing a separation of brain activity related to motor and auditory processes, respectively. Motor performance was accompanied by phasic amplitude changes and increased phase locking in the beta band. Auditory processing of acoustic stimuli resulted in a simultaneous increase of amplitude and phase locking in the theta and alpha band. The temporal overlap of auditory-related amplitude changes and phase locking indicated an evoked response, in accordance with previous studies on auditory perception. The temporal difference of movement-related amplitude and phase dynamics in the beta band, on the other hand, suggested a change in ongoing brain activity, i.e., an induced response supporting previous results on motor-related brain dynamics in the beta band.

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1. Introduction

To investigate how the nervous system processes information to subserve human functioning, various techniques have been developed to study brain activity. Owing to its good temporal resolution and non-invasive nature, encephalography (electroencephalography, EEG; and magnetoencephalography, MEG) is a suitable tool for studying information processing sequences in the human brain (Näätänen et al., 1994). By averaging encephalographic signals with respect to an event, brain activity related to cortical processing can be extracted with high signal-to-noise ratio. Recently, further progress has been made in identifying the neural processes associated with

event-related activity (e.g., Cheyne et al., 2006; Serrien et al., 2006). In particular, it has become evident that differentiating between amplitude and phase changes allows for a distinction between evoked and induced changes (for a review, see Penny et al., 2002). The primary question governing this line of research is whether event-related components result from a stimulus-evoked activation that is superimposed on the ongoing background activity (evoked response), or whether the ongoing activity is altered by means of changes in amplitude and/or phase (induced response). The latter possibility is of particular interest, as it signifies interactions between response and ongoing brain activity, that is, genuine information processing (David et al., 2005).

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Similarly, encephalographic studies on motor behavior showed a shift in focus over the years (for a review, cf. Pollok et al., 2006). Early studies on the neural dynamics underlying action control focused on event-related potentials during motor tasks. A negative potential, the readiness potential, was measured above the supplementary motor area prior to movement execution, which was followed by various reafferent potentials (Kornhuber and Deecke, 1965; Cheyne and Weinberg, 1989). More recently, event-related desynchronization (ERD) was found during motor performance (e.g., Pfurtscheller, 1981; Gerloff et al., 1998a) followed by event-related synchronization (ERS) after movement termination (Pfurtscheller et al., 1996), both reflecting other aspects of cortical activation than the readiness potential (Feige et al., 1996). ERD and ERS appear primarily in the beta band (15–30 Hz) and increase with task difficulty (Gross et al., 2005). Interestingly, motor performance is also accompanied by ERD/ERS in the alpha band (Pfurtscheller and Aranibar, 1979), although the specific temporal and spatial properties of alpha and beta rhythms differ (Crone et al., 1998; Pfurtscheller and Lopes da Silva, 1999). In fact, induced changes in activity are neither restricted to alpha and beta oscillations nor to motor performance but have been found across frequency regimes and could be linked to various functional processes. For instance, gamma activity has often been related to attention (Tiitinen et al., 1993; Fries et al., 2001; Schoffelen et al., 2005).

The rapidly accumulating evidence regarding the functional role of oscillatory activity suggests that different brain processes occur simultaneously in different frequency bands. However, because these activities intermingle continuously and share frequency components, one has to look for additional parameters such as amplitude enhancement, time locking, phase locking, and so on, to further identify the function of specific oscillatory brain activities (Basar, 1998; Makeig et al., 2004). Phase locking to stimuli was already demonstrated for auditory responses several decades ago (Sayers and Beagley, 1974; Sayers et al., 1974) but regained interest when it became apparent that differences in event-related amplitude enhancement and time-locking of phases may help to discriminate between evoked and induced responses (Makeig et al., 2002; Penny et al., 2002; Fell et al., 2004; Hertrich et al., 2004; Klimesch et al., 2004; Mäkinen et al., 2005). Evoked responses generate simultaneous increases of amplitude and phase locking because they are superimposed on ongoing brain activity. Put differently, evoked responses are simply added onto ongoing brain activity so that the recorded event-related activity just displays the amplitude and phase of the response (apart from background ‘noise’). Because these event-related responses occur at the same instance and with the same phase, they yield simultaneous increases of amplitude and phase locking. In contrast, whenever event-related activities induce separate changes in amplitude and phase locking (i.e., concurrent increases are absent), one can conclude that these activities do not reflect simple evoked responses but a change of ongoing brain activity (induced responses) (Klimesch et al., 2004; Mäkinen et al., 2005). Note that we abandon the notion that all phase-locked responses are evoked responses (e.g., Tallon-Baudry and Bertrand, 1999) by differentiating between evoked responses and ‘pure’ phase resetting, which reflects different

underlying neural processes (see above; Penny et al., 2002; Fell et al., 2004; Klimesch et al., 2004; Makeig et al., 2004).

Against this background, we examined the phase and amplitude dynamics in brain activity associated with the performance of an acoustically paced synchronization task by reanalyzing data collected in an experiment on polyrhythmic tapping involving paced and unpaced unimanual fast repetitive finger movements as control conditions (Daffertshofer et al., 2000b). The primary objective of the study was to differentiate between auditory and motor-related processes by examining the phase and amplitude dynamics in the recorded MEG signals and to classify them in terms of evoked or induced responses. To this end, we compared phase and amplitude dynamics in various frequency bands. In general, fast repetitive finger movements are accompanied by distinct and thus discernible movement-related fields: a motor field and a post-movement field similar to the cortical fields recorded during single movements (Gerloff et al., 1997, 1998b; Mayville et al., 2001; Pollok et al., 2003). Hence, we examined whether rhythmic finger tapping was also associated with phasic changes in the beta band related with ERS/ERD as observed for single movements. Because metronome pacing might interfere with movement-related activity, particularly due to the sensitivity of MEG to tangential generators (Gerloff et al., 1998b), we first tried to differentiate between brain activity related to auditory and motor processes by means of principal component analysis (PCA) (Kelso et al., 1992; Daffertshofer et al., 2000a; Mayville et al., 2001; Boonstra et al., 2005). In view of the aforementioned studies, we expected that motor responses would be predominantly manifested as an integral modification of beta brain activity (i.e., induced responses), whereas auditory responses would be superimposed on ongoing brain activity (i.e., evoked responses).

2. Results

In the unpaced tapping condition, subjects were able to continue to tap at the required frequency. On average, the tapping frequencies in the unpaced tapping condition were 1.18, 1.33 and 1.99 Hz (left) and 2.00 and 3.07 Hz (right), compared to 1.20, 1.33 and 2.00 Hz (left) and 2.00 and 3.00 Hz (right) in the paced tapping condition. In the paced tapping condition, subjects anticipated the stimuli in that tap onsets preceded tone onsets (negative asynchrony; left 1.2 Hz, –17 ms; left 1.3 Hz, –15 ms; left 2 Hz, –14 ms; right 2 Hz, –15 ms; right 3 Hz, –17 ms; note that such anticipation is typically well pronounced in musically trained subjects; cf. Lang et al., 1990; Aschersleben, 2002).

The ARFs in the listening and paced tapping condition yielded comparable fields. The N1–P2 amplitude was reduced at higher pacing frequencies (Fig. 1A). Simultaneous with the N1–P2 component, there was an increase in the ARFs_{amp} and ARFs_{ph} in various frequency bands peaking roughly 100 ms after tone onset. The changes were present in a frequency range from 3 to 15 Hz and were most pronounced in the 3- to 9-Hz frequency band. At higher pacing frequencies, the increase of the ARFs_{amp} and ARFs_{ph} around 100 ms was

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