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Functional dissociation of brain rhythms in social coordination

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HIGHLIGHTS

- Spectral separation of sub-bands in the mu domain was used to identify neural processes in tasks requiring real-time social interaction: changes in the lower mu band were diffuse and non-specific; changes in the upper mu band were highly related to coupling measures of intentional social coordination.
- In the upper mu-band event-related synchronization was associated with uncoupled behavior whereas event-related de-synchronization denoted coupled behaviors.
- Coupled coordinated behavior displayed clear hemisphere predispositions: L > R in the in-phase and R > L in the anti-phase tasks.

ABSTRACT

Objectives: The goal of this research was to investigate sub-band modulations in the mu domain in dyads performing different social coordination tasks.
Methods: Dyads of subjects performed rhythmic finger movement under three different task conditions: *intrinsic* – maintain self-produced movement while ignoring their partner's movement; *in-phase* – synchronize with partner; and *anti-phase* – maintain syncopation with partner. Movement profiles of the dyads were used to estimate a synchronization index (SI) to verify differences in coordination according to each task. EEG was recorded during task performance and at baseline (partner's actions hidden from view). Log power ratios of mu band activity (active against baseline) were used to assess the relative levels of synchronization/de-synchronization in both the upper and lower mu bands.
Results: Results confirm a functional dissociation of lower (8–10 Hz) and upper (10–12 Hz) mu bands in social coordination tasks. Lower mu band activity was independent of specific modulations across tasks and hemispheric preferences. Upper mu band activity was sensitive to coordination tasks and exhibited marked differences between the hemispheres. Accentuated de-synchronization of right relative to left hemisphere in the anti-phase task appeared related to the greater demand of perceptual-motor discrimination. Left hemisphere de-synchronization in both in-phase and anti-phase coordination was interpreted in terms of successful production of imitation. Right hemisphere synchronization in the intrinsic task was interpreted as inhibition of an imitative response tendency.
Conclusions: Functional dissociation of lower and upper mu band and hemispheric preferences exists in real-time social coordination.
Significance: This research attests to the merit of analyzing sub-band activity in the alpha-mu domain in order to identify neural correlates of social coordination. Such 'neuromarkers' may be relevant for brain disorders such as apraxia and autism.

1. Introduction

The ability to understand the actions of another person and to be able to interact in a reciprocal manner is a central element in human social cognition. Perceptual-motor coupling is believed to be an important aspect of the neuro-physiological processes that permit interaction to proceed smoothly. Neuroimaging studies suggest that a network including the superior temporal sulcus, the inferior parietal lobule and inferior frontal gyrus is fundamental to action understanding (Rizzolatti and Luppino, 2001) and imitation (Iacoboni et al., 1999). In the broader context, imitation is a particular form of social interaction which depends upon the ability to infer or perceive the other's intentions (Kilner and Frith,

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2008). Such perception may be crucial for harmonizing with the actions of others. General motion as well as detailed properties of limb dynamics acquires importance in interactive motor coordination for learning and reproducing motor skills (Decety et al., 2002).

Motor activity in the brain is often studied from the perspective of modulations of mu oscillations in the alpha range (8–12 Hz) in EEG/MEG based paradigms. Changes in the mu spectral domain are associated with a wide range of motor events such as observation of movement, imagination of movement as well as performing an action (Pineda, 2005). The topography of modulations in movement-related processes is usually isolated to scalp areas over the sensori-motor cortex in the full mu range. However, the phenomenology of de-/synchronization in the mu band is not considered to be a unitary phenomenon: sub-bands within the mu domain are known to exhibit different modulations. The distinctive effect of sub bands in the alpha domain was reported in an extensive power spectral study (Lopes da Silva, 1993). Topographically widespread de-synchronization in lower mu band in conjunction with topographically specific changes in the upper mu band has been reported in cognitive and memory tasks (Klimesch et al., 1992; Klimesch, 1999). Pfurtscheller and colleagues (Pfurtscheller, 1989; Pfurtscheller et al., 2000) have demonstrated that de-synchronization of the upper mu (10–12 Hz) component reflects somatotopic and movement-specific processes, whilst de-synchronization of lower mu (8–10 Hz) is related to general levels of expectancy, engagement or attention (see also Matousek, 1973). Topographically distinct de-synchronization in upper and lower mu sub-bands has also been reported in tasks involving imitation learning (Marshall et al., 2009) at frontal and central sites, respectively.

The preferential employment of hemispheric resources has been noted in imitation and coordination-based processes. Goldenberg and colleagues (Goldenberg et al., 2001; Goldenberg and Strauss, 2002) have shown that the two hemispheres are responsible for different aspects of imitation or gesture generation. The inability to imitate gestures, a defining feature of Apraxia, has been correlated with lesions in the left hemisphere (Muhlau et al., 2005) whereas impairment in the right hemisphere is often associated with unilateral neglect or body awareness disorders (Decety et al., 2002). Some EEG investigations in the mu-domain have also shown hemispheric preferences in imitation paradigms. The dominance of the left hemisphere has been demonstrated in manual motor imitation tasks in the mu-range (Dawson et al., 1985). In contrast, a greater modulation of mu in the right hemisphere has been noted in tasks requiring body awareness (Perry and Bentin, 2009). However, the relevance of topographically specific spectral separation for imitation/coordination tasks has largely remained unexplored.

Previous studies have shown that spontaneous forms of social coordination between two people may occur as participants visually exchange information with each other through the medium of real-time movements and postures (Kelso, 1995; Oullier et al., 2008a,b; Oullier and Kelso, 2009; Schmidt and O'Brien, 1997; Schmidt and Richardson, 2008; Tognoli et al., 2007a). For example, various kinds of phase- and frequency-locking behavior have been observed. These behaviors tend to persist even after visual exposure to the other's movements have been blocked, suggesting a kind of social memory (Oullier et al., 2008a). Parallel electrophysiological studies identify a novel brain rhythm, a 'neuromarker' of *spontaneous* social interactions in the 10 Hz frequency range located over right centro-parietal cortex which modulates with the emergence/dissolution of coordinated behavior between the interacting individuals (Tognoli et al., 2007a). The present experiment follows previous work but asks a different question: what are the neural counterparts of *intentional* social coordination? (see also Tognoli et al., 2007b). Here, the degree of social coordination was manipulated experimentally by instructing subjects in a dyad to coordinate (in-phase or anti-phase) or ignore their partner's movements while maintaining their own self-produced movements. Relative levels of synchronization/de-synchronization in both the upper (10–12 Hz) and lower (8–10 Hz) mu bands were assessed. Currently, little is known about the effects of modifying the properties of social coordination on alpha band mu activity. For example, do the demands of imitation/social interaction modulate the way hemispheric processes are engaged? If they do, what are their particular signatures in the alpha-mu spectral domain? Based on previous literature, we hypothesized that upper, but not lower band modulations in the alpha–mu spectral domain may be sensitive to intentional social coordination which may be viewed as a form of imitation.

2. Materials and methods

2.1. Subjects, recording and tasks

Twelve subjects (mean = 30 and standard deviation = 6.5 years) in six pairs were instructed to interact in a simple motor task (raising and lowering of the right index finger in the frontal plane) in three different coordination tasks. The pairs consisted of 3 gender-mixed, 2 male–male and 1 female–female. All were right-handed with correct vision and reported no neurological disorder. Both finger movement and EEG data were recorded.

Simultaneous EEG was recorded with Ag–Ag Cl electrodes mounted on a whole head elasticated electrode cap (EasyCap, Germany) from each member of the dyad using 60 channels arranged following the 10% system (Chatrian et al., 1985). The signals from each EEG cap (measured with the respective grounds located at FPz sites and the references at the corresponding linked mastoids) were fed to a single amplifier (Synamp2; Neuroscan, TX) with impedances maintained below 10 kΩ. The signals were analog filtered (Butterworth), band pass from 0.05 Hz (−12 dB per octave) to 200 Hz (−24 dB per octave), amplified (gain of 2010) and digitized (24-bit) at 1 kHz in the range ±950 μV (vertical resolution of 0.11 nV). For finger movement data, the angular change at the metacarpophalangeal joint was recorded by means of light single-axis goniometers affixed to the right index finger of each subject, amplified (Neuroscan Synamp2 bioamplifier) on-line and band pass filtered at a common EEG analog filter setting of 0.05–200 Hz (Tognoli et al., 2007a).

Multiple trials were collected in pseudo random order with a resting period between trials of at least 30 s. A typical trial consisted of a 'baseline' segment followed by one of the 'active' coordination tasks. During the baseline partner's actions were obscured (opaque LC screen) from the field of view whereas in active segments dyads were instructed to visually couple their movement patterns (transparent LC screen) according to the tasks (Fig. 1). Tasks were labeled as: intrinsic (*I*) where subjects were required to produce their own movements at their preferred frequency and amplitude while ignoring their partner's self-paced movements; In-phase (*Ip*) where subjects were required to synchronize their finger movements; and Anti-phase (*Ap*) where subjects were required to syncopate with their partner's movement. Thus, if one member of the dyad extended his/her finger, the other flexed and vice versa. Total trial length was 40 s with baseline and active segments contributing 20 s each. Since the tasks were randomized across trials the subjects were unaware which trial type was upcoming at the time of the baseline period.

The beginning of each trial was indicated by auditory cues (pure tones) presented independently to each subject. This signaled dyads to initiate rhythmic right index fingers movements at their preferred frequency and amplitude while maintaining visual