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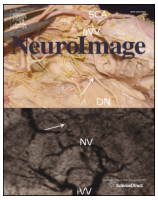

Frontal alpha oscillations distinguish leaders from followers: Multivariate decoding of mutually interacting brains

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ABSTRACT

Successful social interactions rely upon the abilities of two or more people to mutually exchange information in real-time, while simultaneously adapting to one another. The neural basis of social cognition has mostly been investigated in isolated individuals, and more recently using two-person paradigms to quantify the neuronal dynamics underlying social interaction. While several studies have shown the relevance of understanding complementary and mutually adaptive processes, the neural mechanisms underlying such coordinative behavioral patterns during joint action remain largely unknown. Here, we employed a synchronized finger-tapping task while measuring dual-EEG from pairs of human participants who either mutually adjusted to each other in an interactive task or followed a computer metronome. Neurophysiologically, the interactive condition was characterized by a stronger suppression of alpha and low-beta oscillations over motor and frontal areas in contrast to the non-interactive computer condition. A multivariate analysis of two-brain activity to classify interactive versus non-interactive trials revealed asymmetric patterns of the frontal alpha-suppression in each pair, during both task anticipation and execution, such that only one member showed the frontal component. Analysis of the behavioral data showed that this distinction coincided with the leader–follower relationship in 8/9 pairs, with the leaders characterized by the stronger frontal alpha-suppression. This suggests that leaders invest more resources in prospective planning and control. Hence our results show that the spontaneous emergence of leader–follower relationships in dyadic interactions can be predicted from EEG recordings of brain activity prior to and during interaction. Furthermore, this emphasizes the importance of investigating complementarity in joint action.

Introduction

When two people engage in social interaction, they exchange information with one another by producing actions and simultaneously adapting to the other person's actions via a tightly coupled alignment of perception and action within- and between-individuals (Hari and Kujala, 2009). It has been shown that both symmetrical and complementary motor adaptation of interacting partners is used when working toward a common goal (Kokal et al., 2009; Masumoto and Inui, 2013; Sacheli et al., 2013). However, the neural mechanisms underlying interpersonal real-time coordination remain largely unknown, as the methodological frameworks to study them have been underdeveloped (Hari et al., 2013; Konvalinka and Roepstorff, 2012).

Research in social cognition has only recently started to depart from studying individual minds in isolation responding to "social" stimuli, toward studies of interacting minds and brains (Sebanz et al., 2006). This movement was precipitated by the criticism that social cognition is fundamentally different when people engage in interaction, rather than remain mere observers (De Jaegher, 2009; Schilbach et al., 2013).

In particular, a number of recent studies have begun to investigate the interdependencies of neural processes in the brains of two people simultaneously as they interact (see Babiloni and Astolfi, 2012; Dumas et al., 2011; Konvalinka and Roepstorff, 2012 for reviews). These studies have provided insight into both individual neural processes during ongoing interaction, as well as interpersonal processes of two interacting brains, using hyperscanning techniques. One group of such studies has employed pseudo-interactive scenarios, scanning one person at a time in unidirectional interactions (Anders et al., 2011; Kuhlen et al., 2012; Schippers et al., 2010; Stephens et al., 2010), while others have measured two-brain processes during either turn-based or continuous,

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mutual interactions, employing fMRI (e.g. King-Casas et al., 2005; Montague et al., 2002; Saito et al., 2010), EEG (e.g. Astolfi et al., 2010; De Vico et al., 2010; Dodel et al., 2011; Dumas et al., 2010; Lindenberger et al., 2009; Yun et al., 2012), or fNIRS (e.g. Cui et al., 2012; Holper et al., 2012; Jiang et al., 2012) recordings.

More specifically, previous dual-EEG studies have consistently identified amplitude-modulation of oscillations around 10 Hz (alpha-band) over centro-parietal electrodes during joint attention and social coordination (Dumas et al., 2012; Lachat et al., 2012; Tognoli et al., 2007), which has also been reported in non-interactive experiments, during execution and observation of motor tasks (Caetano et al., 2007; Cochin et al., 1999) — corresponding to modulation in the rolandic mu rhythm (Gastaut, 1952). Interpersonally, two-brain studies have primarily focused on quantifying functional similarities or temporal synchronization between brains (Hasson et al., 2012) during interaction, showing evidence of inter-brain coupling when people engage in behaviorally coupled interactions (Dumas et al., 2010).

In addition to quantifying synchronized and symmetric brain-networks between brains, some dual-EEG studies have also shown asymmetric brain-coupling patterns between leader–follower participants of a dyad (Astolfi et al., 2010; Babiloni et al., 2007; Dumas et al., 2012; Sanger et al., 2012, 2013). This asymmetry has been reported either as functional connectivity (i.e. partial directed coherence) between different brain areas: prefrontal areas of a leader and ACC/parietal areas of the leader's partner in a card game (Astolfi et al., 2010); or as directed phase coupling in the alpha frequency band from frontal electrodes of leaders' brains to those of the followers' (Sanger et al., 2013). However, to what extent these phase-connectivity patterns might constitute a brain mechanism of social interaction (and in particular the establishment of leader and follower roles), and to what extent they may be linked to the difference in movement initiation times, remains unresolved. In contrast, we were interested whether two-brain analyses on oscillatory power – reflecting neuronal activation states – could reveal complementary patterns of individual, rather than coupled, brain mechanisms in a dyad, where the participants may take on symmetric or complementary roles.

We thus set out to investigate both the brain processes underlying mutual adaptation, and the potential inter-individual differences of interacting members within each pair. We employed a minimal interaction paradigm in order to investigate a simple interpersonal action–perception loop, whereby one person's action output became another's perceptual input, and vice-versa. This was done by asking pairs of participants to engage in a mutually interactive finger-tapping task with each other, or non-interactively with a computer metronome, while dual-EEG was recorded. While this synchronization paradigm typically engages symmetrical mechanisms between people when mutually adapting to each other during extended tapping (Konvalinka et al., 2009, 2010), it also allows the two members to spontaneously take on leader or follower roles, thereby potentially engaging complementary leader/follower behavioral and neural mechanisms.

A recent fMRI study investigated neural mechanisms underlying leadership, as participants engaged in a tapping paradigm with an adaptive stimulus (Fairhurst et al., 2013). The study revealed that leading and perceiving leadership correlated with right-frontal brain activity, areas engaged in self-initiated action. Here, we wanted to develop a two-brain analysis, which could pick out features that could be specific to leading or following behavior in an interactive dyad. To investigate within-pair inter-individual differences, we used a novel multivariate decoding approach, which allowed the classifier to pick up differences in brain activity during interactive versus non-interactive behaviors in either member of each pair.

The goal of our study was two-fold: to explore how ongoing brain-activity is modulated within-participants, when the task is done interactively with another person versus non-interactively with a computer; and second, to investigate how complementary forms of interactive behaviors are reflected in the brain activity of each member of a pair.

Materials and methods

Participants

Eighteen right-handed participants (15 male; 3 female), comprising nine pairs, volunteered for the study, recruited from Aarhus University, Denmark. They all gave written, informed consent. Ethics approval was obtained from the Science Ethics Committee for Aarhus County (Videnskabsetisk Komite for Aarhus Amt).

Task and procedure

The participants were seated with their backs to one another, and received no visual feedback from each other. The experiment explored 2 conditions, 1) an interactive and 2) a computer control condition. In the interactive condition, each participant received auditory feedback only of the beats generated by the other member of the pair. In the computer condition, both participants received auditory feedback of steady, computer-generated beats. The participants never received auditory feedback of self-generated taps. The computer control was chosen because the participants received the same auditory stimulation and performed the same motor task, hence controlling for these factors. Each condition was repeated 60 times, with the order randomized. Participants were informed of their auditory feedback prior to each trial. The experimental design is shown in Fig. 1 (a).

The trial was initiated by 5 steady beats from the computer, at a tempo of 120 beats per minute (bpm). The stimulus then ceased in the interactive condition, and the members only heard each other. In the computer condition, the stimulus continued at the steady tempo. The participants were given two instructions: to keep the given beat as precisely as possible, while at the same time synchronizing with their auditory feedback, by tapping with their right index finger for 10 beats following the 5 beat stimulus.

All participants tapped on response keys of Lumina response pads, connected to the computer via a serial port. The stimuli were sent using the Presentation software (Neurobehavioral Systems, Albany, NY, USA). One member of the pair was given two “right” earphones, and the other member was given two “left” earphones, which were connected to an earphone splitter. Therefore, tapping feedback of member one was sent to the left earphones, and feedback of member two to the right earphones, enabling the bidirectional interaction. The participants were asked to sit still, and avoid blinks and exploratory eye movements during tapping as much as possible.

EEG recordings

Simultaneous EEG was recorded from both members of each pair, using two 32-channel caps with Ag/AgCl impedance-optimized active electrodes (ActiCap, Brain Products, Gilching, Germany). The electrodes were placed at the positions of the international 10–20 system, with a nasal reference. Two identical Brainamp MR amplifiers with separate grounds were used, which were optically coupled to the computer and recorded through the same software interface, ensuring synchronization between the two sets of electrodes. The recording bandwidth was set at 0.16–250 Hz and the data were sampled at 1000 Hz.

EEG data preprocessing

The data were processed and analyzed using Fieldtrip (Oostenveld et al., 2011), a MATLAB software toolbox for MEG/EEG analyses, developed at the Centre for Cognitive Neuroimaging of the Donders Institute for Brain, Cognition and Behaviour. All the trials were epoched from −1 to 7.5 s. The trials were baseline corrected in the time domain, subtracting the mean of each entire epoch, in order to remove arbitrary DC offsets.

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