FMRI INVESTIGATION OF DYNAMIC COOPERATIVITY: SYNCHRONISED FINGER TAPPING WITH AN ADAPTIVE “VIRTUAL PARTNER”

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ABSTRACT

Cooperation is intrinsic to our ability to work together towards a common goal such as music making. The following study presents a novel approach for studying brain activity related to cooperative synchronization between a human and a virtual partner, an adaptively-paced auditory metronome. Using functional MRI (FMRI) and by varying the virtual partner’s level of cooperativity, we identify the neural correlates of dynamic, cooperative synchronization. Furthermore, overlap between cooperation and sensorimotor synchronization (SMS) is explored, and therefore a bridge between social cognition and simpler goal-directed action. This adaptively-paced tapping task provides a model with which to study the dynamic, cooperative relationship experienced when playing music in a group. Results presented both replicate previous findings and expand our understanding of the brain networks underlying SMS and cooperativity. These include shared fronto-parietal areas, implicated in executive function and variable activation of medial and lateral subdivisions depending on levels of cooperativity.

1. INTRODUCTION

As a prosocial species, humans have evolved to be able to cooperate with one another to work towards a common goal. It is assumed that this ability to participate in skilful social interactions depends on specific brain mechanisms which allow for these cooperative behaviors. Music making in groups is a key example of skilful cooperative behavior and, more fundamentally, a form of sensorimotor coupling (Janata & Grafton, 2003). Sensorimotor synchronization (SMS) is the coordination of a physical action in time with a rhythmic sequence, a function intrinsically linked to music making (Repp, 2005). As a novel approach to explore neural correlates of dynamic cooperation, we present a functional MRI (FMRI) study of SMS finger tapping with an adaptive “virtual partner” (Vorberg, 2005; Repp & Keller, 2008).

Previous neuroimaging studies of cooperation have employed various methods of inciting cooperative behavior including specially-designed computer games, variations of economic games and the Prisoner’s dilemma game (Rilling, 2002; Decety et al., 2004) to our knowledge, however, the link between cooperation-related brain activity and a measurable behavior has yet to be explored (Georgiou et al., 2007). Furthermore, the current study posits that, at least within the context of music making in groups, the relationship between cooperating individuals is a dynamic one. Therefore we use an adaptive SMS task which allows for the study of the dependence of participants’ tapping behavior on their partner’s variable level of cooperativity (Vorberg, 2005; Repp & Keller, 2008). The partner is a computer-programmed auditory metronome which simulates the potential behavior of a human partner in the task. The use of a “virtual partner” allows for the study of interpersonal cooperativity while controlling for the intrinsic limitations of human-human dyads in more realistic situations (Kelso et al., 2009).

One of these limitations is the adoption of leader-follower roles which, as observed in music making, can be a dynamic phenomenon (Maduell, 2007). The paradigm presented here does not directly manipulate role-taking, but the computer’s programmed behavior has been shown to have definite consequences in that regard (Repp & Keller, 2008). More specifically, while the computer metronome in this study dictated the overall pulse and was therefore, for all intents and purposes, the “leader”, the conditions of adaptive cooperativity allowed for variable give-and-take within the synchronizing partnership, with the computer adapting more or less to the human “follower”. The brain basis for leader-follower role adoption and the subsequent influence on cooperative behavior is still not fully understood (Chaminade and Decety, 2002). However, as discussed in other studies of and related to cooperation, these processes are expected to involve higher cognitive brain structures including prefrontal and parietal cortices, structures implicated in executive functions and mentalising (Chaminade and Decety, 2002; Blackwood et al., 2003; Decety et al., 2004; Kircher et al., 2009). The dependence of efficient SMS on these same or similar neural networks has been previously put forward with suggested roles in predicting/anticipating the behavior of one’s synchronizing partner (mentalising) as well as the ability to guide action based on both internal intentions and those of one’s partner (executive function). As such, we present a novel neuroimaging paradigm to test the hypothesis that action simulation (Keller et al., 2007) or the mirror neuron system (Overy, 2008) may provide the bridge between mechanisms underlying simpler internal models of goal-directed behavior (SMS) and social cognition such as cooperation (Blackwood et al., 2003).

2. MATERIALS AND METHODS

2.1 Subjects

The experiments were conducted at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany. Sixteen healthy volunteers (8 females and 8 males; age range: 21-33; mean age: 26.38 years, SD = 4.21) were recruited after screening for
absence of any prior neurological or psychiatric disorders, and not meeting any of the exclusion criteria for MR experimentation. All subjects had previous finger tapping task experience and some degree of musical training. Written informed consent was obtained for each subject before scanning.

2.2 Study Design

The study consisted of two successive scanning sessions. Each scan session included 30 pseudo-randomized task blocks. (For further details of study design, please refer to Figure 1.) The task blocks varied in the degree of cooperativity of the computer metronome during the adaptively paced sequence, with one of the five levels of computer cooperativity (non-adaptive, partially adaptive, optimally adaptive, highly adaptive, and completely adaptive) presented during each block. Each condition of computer cooperativity was repeated six times within a scan trial, and thus 12 repeats were presented overall. Subjects were instructed to synchronize their taps with the tones as accurately as possible and to maintain the initial tempo, to the best of their ability. Subjects were then cued to provide subjective visual analogue scale (VAS) ratings for the preceding cooperative tapping block using a two-button response box.

2.3 Stimuli

2.3.1 Auditory Stimuli

Tone sequences were generated by programs written in MAX 4.5.7. The adaptive metronome was programmed so that a negative registered asynchrony (participant’s tap preceded the tone) resulted in a shortening of the next sequence IOI (the next tone occurring sooner). Similarly, if the participant’s tap occurred after the tone, a positive asynchrony was registered resulting in a lengthening of the next IOI. The direction of this phase correction was the opposite of the correction expected in the participant’s taps, as it should be if the computer (controlling the tones) “cooperates” with the participant (controlling the taps). The degree of the correction was varied across five conditions ranging from no phase correction ($\alpha = 0$) to full correction ($\alpha = 1$) in .25 steps. Based on previous findings, optimal cooperation is expected at around $\alpha = 0.5$. It has been shown that, under normal circumstances, this cooperation improves the synchronization of the participant’s taps with the tones. (For further details, please refer to Repp & Keller, 2008.) The tones were specified to be 50 ms in duration played as synthesized “bongo drum” sounds. Participants listened over Siemens MR compatible headphones at a comfortable intensity.

2.3.2 Visual Stimuli

Visual stimuli included a black fixation cross displayed during rest periods (baseline). Starting with the first initiation tone, the fixation cross turned green and was displayed for the duration of the 12 second tapping task block. Visual analogue scales (VAS) for “influence” and “difficulty” were presented for five seconds each. The “Influence” (“Einfluß”) scale was anchored with no (“kein”) influence at the minimum and absolute (“absolut”) influence at the maximum. Similarly, “Difficulty” (“Schwierigkeit”) was anchored with very easy (“sehr leicht”) and extremely difficult (“sehr schwierig”). All visual stimuli were projected onto a screen visible to the subject via prism glasses. Visual stimulation was continuous throughout the experiment.

2.4 SMS Tapping Data acquisition

Participants were instructed and trained to tap with their right index finger on an in-house built, MR-compatible air-pressure tapping pad that was connected to the computer via a MIDI interface. Taps were recorded by MAX 4.5.7.

2.5 MRI Data acquisition

Functional imaging was conducted using a 3 Tesla Siemens Trio system. An echo-planar imaging (EPI) sequence was used with a TR = 2000 ms; TE = 24 ms; 36 x 3 mm axial oblique slices; 1 mm gap; voxel size = 3 x 3 x 3 mm$^3$; volumes = 699. Scans were acquired continuously throughout the experiment. High resolution, T1-weighted, structural scans (64 slices at 1 x 1 x 1 mm$^3$ voxel size) were obtained for each individual for anatomical overlay of brain activation.

2.6 Data Analysis

Behavioural Analysis

Online ratings for influence over the pulse and difficulty to synchronize during tapping tasks were grouped according to the degree of computer cooperativity and the individual means and standard deviations calculated. To do so, VAS ratings were converted into numerical 0-10 ratings. A group mean and standard deviation was calculated for the post-scan overall subjective rating of performance to be compared with objective measures of synchronised tapping.

Figure 1: Study design for adaptive SMS as a model for dynamic cooperativity. Each block consisted of two isochronous initiation 50 ms pacing tones (IOI of 500 ms). and, starting with the third tone, subjects were instructed to tap in synchrony with the then variably adaptive pacing signal programmed to adapt its timing to reduce asynchronies between human taps and computer tones. Following each task block, subjective ratings of “influence over the pulse” and “difficulty” were acquired.
Tapping Data

Recorded computer tone and human tap timings were analyzed in terms of asynchronies, or differences between tone and tap onsets. A measure of performance and a measure of error correction (explained in greater detail in the related study by Repp & Keller, 2008) are a standard deviation or an autocorrelation function, respectively, of tone tap asynchronies as a function of computer cooperativity. These tapping measures were explored both within and across subjects, across conditions of computer cooperativity and used here to further explore the FMRI data.

Imaging Analysis

Analysis of all neuroimaging data sets was performed using FEAT (FMRIB Expert Analysis Tool) Version 5.63, part of FSL (FMRIB's Software Library). Individual and group analyses was performed as per default procedures in the FSL FMRI data analysis stream (www.fmrib.ox.ac.uk/fsl). Contrasts performed explored activation during the five conditions of adaptive synchronisation compared to baseline. Each task block was modeled as three defined events: initiation (perception of initiation tones), pre-stabilization (first six tone-tap pairs) and stabilized tapping (subsequent 16 tone-tap pairs). Subtraction contrasts between conditions were also performed.

3. RESULTS

3.1 Behavioral Data

Tapping SMS measures

Behavioral tapping data replicate findings from previous SMS studies and, in accordance with preparatory behavioral studies, demonstrate that this adaptive SMS design can be effectively performed under MR conditions. Consistent with Repp & Keller (2008), the parabolic function of performance (SD asynchronies) observed across conditions describes how computer cooperativity has a variable effect on human tapping performance with a point of “optimal” cooperativity and poorer performance on either side of these conditions (mean ±SE of SD asynchronies across conditions: Non-adaptive 23.64±1.91; Partially adaptive 21.41±1.90; Optimally adaptive 22.09±2.21; Highly adaptive 24.09±2.55; Completely adaptive 28.74±3.10). Similarly, the observed negative linear decrease in the lag-1 autocorrelation across conditions of computer cooperativity replicates previous findings (mean±SE: Non-adaptive 0.42±0.04; Partially adaptive 0.20±0.05; Optimally adaptive 0.03±0.07; Highly adaptive -0.18±0.09; Completely adaptive -0.34±0.10).

Subjective ratings

Subjective ratings of task difficulty (ability to synchronize) and influence over the pulse were grouped by condition of computer cooperativity and averaged across subjects. As expected, perceived task difficulty mirrors acquired objective measures of task performance and a quasi-parabolic function across conditions of computer cooperativity is observed. Mean and SE of subjective difficulty ratings across conditions: Non-adaptive 3.19±0.33; Partially adaptive 3.05±0.34; Optimally adaptive 3.56±0.33; Highly adaptive 4.09±0.45; Completely adaptive 5.10±0.50.

3.2 Imaging Data

Neural activation during adaptively-paced synchronised tapping

All conditions of SMS across varying degrees of computer cooperativity (relative to baseline) result in increased activation of fronto-parietal cortical regions. To explore categorical differences between synchronization with a non-adaptive virtual partner and a completely adaptive one, a subtraction analysis showed significantly greater activity in the ventromedial prefrontal cortex (vmPFC) (Figure 2A, blue). A reverse contrast reveals activation of areas including the ventrolateral prefrontal cortex (vPFC) and premotor cortex (Figure 2A, red).
Neural activation during tapping with a variably cooperative partner

Contrasts used to explore the neural correlates of optimal cooperation included a comparison between optimal cooperativity and synchronization with a non-adaptive, uncooperative partner resulting in activation of the precuneus, visual cortex and parietal cortex (Figure 2B). A contrast of optimal cooperativity versus tapping with a completely adaptive (very “unhelpful”) partner revealed activity in areas including the pre-motor cortex, left hippocampus, vmPFC, posterior cingulate, primary motor cortex, primary somatosensory cortex, and posterior parietal cortex (PPC) (Figure 2C). To explore differences in neural activation while tapping with a dynamically adaptive “helpful” or “unhelpful” partner, a contrast comparing synchronizing with either a highly adaptive or a partially adaptive revealed right lateralized activity in the area of BA39 (superior temporal sulcus, STS) and/or BA40 (Figure 2D).

4. DISCUSSION

Cooperative synchronization is intrinsic to music making; however, the neural underpinnings of cooperativity generally and cooperation in adaptive synchronization specifically are still poorly understood. The present study employs an adaptively-paced finger tapping task to explore a dynamic cooperative partnership between a human and a virtual partner as a model for musical ensemble work. Use of this design in conjunction with functional imaging both replicates previous findings while proving a novel approach for expanding our understanding of the brain networks underlying SMS and cooperativity. Imaging data presented here identify task-related fronto-parietal activity and, more specifically, variable activation of medial and lateral subdivisions depending on levels of cooperativity. We therefore posit that activity seen in these areas is related to executive function, specifically mentalizing and action simulation.

4.1 Executive functions and the prefrontal cortex

The prefrontal cortex has been generally implicated in mediating different aspects of executive functions (Elliott, 2003). Results presented here show subdivision and laterality effects in line with and adding to previous findings identifying PFC activity in studies of social interaction and cooperativity. In particular, a contrast exploring complete versus no cooperation reveals activation of vlPFC. Previous neuroimaging studies have shown that activation of the VLPFC is greater as the temporal complexity of the sequence increases (Janata & Grafton, 2003). Alternatively, this structure has most recently been implicated in memory for music (Debas, 2009), possibly relating the current result to a greater reliance on memory of the initiation sequence in the condition where the subject had the greatest influence on the pulse (completely adaptive partner). By contrast, the subtraction exploring activity which is greater in the condition of no cooperation (non-adaptive partner) revealed vmPFC, an area identified by Decety and colleagues in a comparison of competition and cooperation (Decety et al., 2004). In an economics game scenario, ventromedial frontal cortex activation, lateralized to the right hemisphere, has also been reported when participants engaged in mutual cooperation (McCabe et al., 2001).

Exploring neural activity during optimal cooperation, a contrast was created to compare optimal cooperativity and synchronization with a non-adaptive (uncooperative) partner, resulting in activation of the visual and parietal cortex and the precuneus, an area implicated in visuo-spatial imagery and an experience of agency (Cavanna, 2006). A possible functional reason for observed frontal and precuneus activity in our cooperation study is that social interaction tasks rely on mentalizing and agency, executive functions systematically associated with these areas (Frith, 2003).

4.2 Mentalizing and agency

Mentalizing or simulating the actions of self or others, a key component of effective social interaction, is often attributed to fronto-parietal networks. In the present study, in all synchronization contrasts (relative to baseline), consistent activation was observed in prefrontal and parietal regions (Decety et al., 2004). In a contrast comparing “high” versus “low” cooperativity activation in the region of BA39: superior temporal sulcus (STS) / BA40 was observed identifying the neural difference between synchronizing with an unhelpfully adaptive (highly adaptive) and a helpful partner. We posit that this activation may be due to the fact that the STS has been shown to be activated by tasks involving agency, by representing the actions of others (Gallagher, 2003), in conjunction with determining that others are responsible for social events (Blackwood et al., 2003) and updating internal models of action performed by the self (Danckert et al., 2002). As mentioned above, the ability to understand and attribute both self and other actions is seen as part of a more general function of action simulation (Decety, 2003) and as such it is suggested that social cognition may be based on simpler internal models of goal-directed action (Blackwood et al., 2003). Our results show a right lateralization of activation which is consistent with findings that activity in the right hemisphere is greater when the self is imitated (being followed more by the adaptive metronome) and when subjects mentally simulate someone else’s actions (Decety et al., 2002).

4.3 Action simulation and SMS

As well as being observed in all conditions of adaptive synchronization (versus baseline), the contrast of optimal versus complete cooperativity (very “unhelpful”) results in widespread activation extending beyond fronto-parietal regions to include areas commonly identified in other neuroimaging studies of synchronization. Activation of MI, SI and premotor cortices may be attributable to evaluation, planning, programming, and guidance of simple and skilled motor tasks (Witt et al., 2008) but these areas are also activated by the observation and simulation of one’s own and others’ actions (Chaminade and Decety, 2002).
4.4 Conclusions and future studies

We therefore present further evidence that simulation networks act as a neural bridge between a simple goal-directed action such as SMS and higher level social cognition such as cooperation (Keller et al., 2007; Overy, 2008). Furthermore, by using a design where the “virtual partner” acted as group leader but where the human participant could influence the pulse to a greater or lesser extent, we present a method that is suitable for studying the dynamic leader-follower relationships observed in musical ensemble work. Although not covered in the current paper, supplementary analysis has been performed to explore the relationship between subjective ratings of influence and brain areas activated with variable degrees of virtual partner leading and following. Further studies employing variations of this adaptive SMS-model are currently underway. These will explore differences and overlap between the present paradigm and one in which the human participant is made responsible for maintaining rhythm and thus made to take over as leader. This may provide us with a better understanding of the neural underpinnings of role taking in group music making.

5. REFERENCES


