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Leading the follower: An fMRI investigation of dynamic cooperativity and leader–follower strategies in synchronization with an adaptive virtual partner

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ABSTRACT

From everyday experience we know that it is generally easier to interact with someone who adapts to our behavior. Beyond this, achieving a common goal will very much depend on who adapts to whom and to what degree. Therefore, many joint action tasks such as musical performance prove to be more successful when defined leader–follower roles are established. In the present study, we present a novel approach to explore the mechanisms of how individuals lead and, using functional magnetic resonance imaging (fMRI), probe the neural correlates of leading. Specifically, we implemented an adaptive virtual partner (VP), an auditory pacing signal, with which individuals were instructed to tap in synchrony while maintaining a steady tempo. By varying the degree of temporal adaptation (period correction) implemented by the VP, we manipulated the objective control individuals had to exert to maintain the overall tempo of the pacing sequence (which was prone to tempo drift with high levels of period correction). Our imaging data revealed that perceiving greater influence and leading are correlated with right lateralized frontal activation of areas involved in cognitive control and self-related processing. Using participants' subjective ratings of influence and task difficulty, we classified a subgroup of our cohort as "leaders", individuals who found the task of synchronizing easier when they felt more in control. Behavioral tapping measures showed that leaders employed less error correction and focused more on self-tapping (prioritizing the instruction to maintain the given tempo) than on the stability of the interaction (prioritizing the instruction to synchronize with the VP), with correlated activity in areas involved in self-initiated action including the pre-supplementary motor area.

Introduction

In any joint action task, one can imagine that a participating individual may take charge and dictate the timing or direction of the movement. In a musical performance, based on interpretation or skill the first violinist in a string quartet will dictate the tempo of the piece being played and the other players will attempt to follow. Who adapts to whom and to what degree will therefore depend on established leader–follower roles within the partnership and the respective behaviors of leaders and followers (Maduell and Wing, 2007; Shaw, 1971). Specifically, both anecdotal evidence and related research suggest the implementation of differing coordination strategies by leaders, followers, or even democratic equals (Davidson and Good, 2002; Goebl and Palmer, 2009; Goodman, 2002; Pecenka and Keller, 2011). Leaders and followers should differ in terms of the degree to which they adapt to or rely on the actions of their partner to successfully perform a shared task. This should result in biases towards greater self-focus or self–other focus, and therefore varying degrees of self-agency. The precise nature of this shift in focus in interactive social contexts and the underlying cognitive processes that allow for the variable give-and-take when either leading or following however are still poorly understood. In the fMRI study described herein, we employ a simple synchronized finger-tapping paradigm to simulate cooperative behavior and probe the behavioral and neural differences in leaders and followers.

The methods by which cooperative behavior has previously been elicited and studied include various interpersonal games and human–computer interfaces (Decety et al., 2004; Rilling et al., 2002, 2008). In

Abbreviations: fMRI, functional magnetic resonance imaging; VP, virtual partner; SD, standard deviation; SD ITI, standard deviation of inter-tap-intervals; β_c, period correction of the computer; LOC, locus of control; IOI, inter-onset-interval; ANOVA, analysis of variance; GLM, general linear model; BET, brain extraction tool; ROI, region of interest analysis; PE, parameter estimate; MIDI, musical instrument digital interface; LFr, leader follower correlation coefficient; IPL, inferior parietal lobule; TPJ, temporoparietal junction; IFG, inferior frontal gyrus; STG, superior temporal gyrus; preSMA, pre supplementary motor area; VAS, visual analog scale.

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order to simulate more temporally precise, dynamic interactions (Kelso et al., 2009), our group has focused instead on adaptive sensorimotor synchronization finger tapping paradigms in which individuals interact with and influence an adaptive "virtual" partner, or VP (Fairhurst et al., 2012; Repp and Keller, 2008). The VP, an auditory pacing signal, is programmed to vary its behavior (i.e., to adapt) as a function of human tapping performance and can be manipulated based on an algorithm including parameters of error correction (Large, 2008; Repp, 2005; Repp and Keller, 2004, 2008; Vorberg and Wing, 1996).

Previous behavioral studies have drawn a distinction between two types of error correction: phase correction and period correction. *Phase correction* is an automatic and obligatory process that adjusts the way in which the sequence of pulses generated by the human's internal timekeeper is aligned against the sequence of events in the pacing signal. *Period correction*, by contrast, involves consciously controlled adjustments to the duration of timekeeper pulses when the human intentionally adapts to a perceived timing change in the signal. Research that has used analytical methods to estimate the degree to which humans engage in these forms of error correction has revealed considerable individual differences (Repp and Keller, 2004, 2008; Repp et al., 2012; Schwartze et al., 2011). In our previous study (Fairhurst et al., 2012), we manipulated the level of phase correction employed by the VP so as to explore the neural basis of synchronization when coordinating in an optimal or more challenging partnership. We found that a small change in the degree of phase correction employed by the VP led to a large-scale switch in activated brain networks, which shifted from cortical midline structures associated with socio-affective processes to lateral prefrontal areas associated with cognitive control. Importantly, in that study the VP was always reliable in its ability to maintain a steady tempo (because phase correction does not affect the base interval generated by the VP's timekeeper). In the present study, we vary the degree of VP *period correction* and as such the magnitude of the adjustments made to the base time interval generated by the VP's internal timekeeper. High levels of period correction lead to a cumulative change in the base inter-onset-interval of the pacing signal tones, and in this sense the VP is less reliable. As the VP employs greater period correction, greater responsibility of maintaining the tempo is placed on the human participant. Our paradigm therefore manipulates the context of the interaction by varying the degree of influence the human can objectively exert over the more or less adaptive virtual partner, which, due to implemented period correction, is more or less prone to tempo drift (Repp and Keller, 2008).

Within the research field of group dynamics, behavioral work has explored factors that either result in the adoption of leader-follower roles or the effects leading has on group behavior (Shaw, 1961). Using our tapping paradigm, we define and describe leading in terms of a resulting pattern of behavior (Foti and Hauenstein, 2007; Goebl and Palmer, 2009; Konvalinka et al., 2010) and, based on personality traits and tapping behavior, categorize individuals as more or less prone to lead ("leaders" or "followers"). Specifically, by acquiring ratings of perceived influence and task difficulty, we identify individuals who find it easier ("leaders") or more difficult ("followers") to dictate the tempo within the partnership. Additionally, we assume behavioral differences between leading and following to reflect differential prioritization of two aspects of the tapping task: (1) to maintain the given tempo while interacting with the VP (lead) and (2)to tap in synchrony (follow). These two aspects of the task—which we explicitly instructed participants to fulfill—highlight potentially conflicting goals in sensorimotor synchronization (Repp, 2008; Semjen et al., 2000; Vorberg and Schulze, 2002), where an individual may aim either (1) to minimize the variability of asynchronies between their taps and events in the pacing signal (i.e., to stabilize synchronization) or (2) to minimize the variability of their inter-tap intervals (i.e., maintain a steady tempo). While following will entail greater self–other focus and prioritization of the instruction to synchronize, leading behavior will be evidenced by more stable self-paced tapping due to individuals focusing on the instruction to maintain the tempo in the attempt of setting a stable example (i.e., a temporal reference) for the VP to follow. These differences in strategy should be associated with less temporal error correction in the human (specifically, phase correction, which can be estimated from the time series data consisting of asynchronies between participant's taps and VP tones; Repp and Keller, 2008) in leaders than followers. We posit that this may be due to personality trait differences with leaders generally showing a stronger internal locus of control and therefore greater belief that outcomes are contingent on their personal behavior (Anderson and Schneier, 1978; Bass, 1981). Moreover, we expect that synchronization strategies will vary as a function of the reliability or adaptivity of the co-acting (virtual) partner.

Although efforts have been made to investigate the neural correlates of imitation and other following-like behavior (Iacoboni et al., 1999; Ocampo et al., 2011) there is little in the way of relevant studies exploring the neural underpinnings of leading. The only imaging study exploring the phenomenon of leading, per se, did so indirectly while investigating agency (Chaminade and Decety, 2002). By contrast, we aim to probe the effect of leading on interpersonal coordination. Two related neuroimaging studies have implemented reciprocal imitation tasks, comparing imitating versus being imitated (Decety et al., 2002; Nagy et al., 2010). While imitation requires following the example set by the experimenter, being imitated could be seen as a form of leading. Together these two studies implicate a fronto-parietal network and highlight the role played by these areas in agency attribution. In terms of our posited modulation of synchronization strategy, these brain regions may be differentially activated as a function of self or self–other focus. In our earlier study, we identified similar frontal activation when participants interacted with an overly adaptive VP and interpreted activation of right lateralized cognitive control areas (including the IFG and anterior insula) as a shift in attention towards maintaining the pulse based on an internal timekeeper.

In investigating the underlying cognitive processes that characterize our "leaders", we expect that our manipulation will identify brain structures more commonly reported in studies of sensorimotor synchronization (Fairhurst et al., 2012; Witt et al., 2008). In particular, we hypothesize that leading, by its very nature and as a function of our task, will rely on maximizing the stability of one's own actions. In conditions in which individuals, and specifically "leaders", exert more influence over the virtual partner, attention will be prioritized towards reducing the variability in their own tapping and as such will more strongly be dependent on an endogenous timekeeper (Semjen et al., 2000; Vorberg and Schulze, 2002) and self-initiated movement. Based on previous work, we would expect this to be reflected neurally by increased activation in areas including the midcingulate and supplementary motor area (Cunnington et al., 2002; Gerloff et al., 1998; Lau et al., 2004). More generally, based on previous coordination studies where context-based differences in both behavioral and neural responses were observed (Decety et al., 2004; Fairhurst et al., 2012), we expect differential neural activity depending on both the characterization of the participant (leader or follower) and the nature of the virtual partner in terms of its temporal (un)reliability (optimally versus overly adaptive).

Materials and methods

Participants

16 healthy volunteers (eight females and eight males; age range: 21–34; mean age: 27.27 years, SD = ±4.48) were scanned at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany. All participants were screened for prior neurological or psychiatric disorders and to ensure that they did not meet any of the exclusion criteria for MR experimentation. Participants had varying degrees of musical experience and all had previously participated in a related version of this finger tapping task. Specifically, 13 of the 16 subjects