



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



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ARTICLE INFO

Article history:

Accepted 12 September 2013

Available online 21 September 2013

Keywords:

Sensorimotor synchronization

Leading

Virtual partner interaction

Cooperation

Inferior frontal gyrus

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.

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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; Goebel 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; Goebel 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

from our previous study (Fairhurst et al., 2012) were re-tested for more direct comparison between paradigms. These comparisons will be discussed in a separate publication. The experiment was approved by the local ethics committee and informed written consent was obtained from each participant.

Study design and procedure

The procedure for each participant consisted of two successive scanning sessions. Each scan session included 30 pseudo-randomized task trials followed by a rest baseline period of between 12 and 15 s. Each task trial consisted of a sequence of 22 tones produced by the VP (Fig. 1A). Participants were instructed to synchronize their taps with the onset of the third tone as accurately as possible and to maintain the initial tempo, to the best of their ability. Specifically, as in our previous study (Fairhurst et al., 2012), participants were instructed with the following: “To mimic real-life ensemble performance, you will be synchronizing with an adaptive virtual partner who will adapt to the onset of your tapping. If you slow down or speed up, the virtual partner will adjust the following tone onset accordingly. The virtual partner will adapt its behavior to varying degrees in different conditions”. Accordingly, in each tapping trial, we implemented one of five levels of VP adaptivity (independent variable) during the adaptively paced sequence. As a function of this

manipulation of cooperativity, we explored objective tapping measures and subjective ratings that can be used to evaluate leader and follower behaviors. Each condition of VP adaptivity was repeated six times within a scan session and thus 12 repeats were presented overall. Following each tapping trial, participants were cued to provide subjective visual analog scale (VAS) ratings of perceived influence and perceived difficulty for the preceding tapping trial using a two-button response box (left button to move the cursor leftwards and right button to move the cursor rightwards along the scale). After scanning, participants completed the I-scale of the IPC locus of control (LOC) questionnaire (Krampen, 1981). This questionnaire assesses the individual's general belief about who or what has an influence on one's own life. Participants completed the German version of the questionnaire using a Likert response format. The so-called “internal” or I scale measures the extent to which people believe that they have control over their own life. A high score on the I scale indicates a strong control belief.

Stimuli

Auditory stimuli

Auditory sequences were generated online by programs written in MAX/MSP 4.5.7 (<http://www.cycling74.com>). The adaptive pacing signal had an initial inter-onset interval (IOI) of 500 ms but implemented period correction (β) and as such it accounted for and adjusted each subsequent IOI by a fraction of the calculated asynchrony (Δt) between tone and tap. A negative registered asynchrony (participant's tap preceded the tone) resulted in a shortening of VP timekeeper period and hence of the next sequence IOI (the next tone occurring sooner). Conversely, if the participant's tap occurred after the tone, a positive asynchrony was registered resulting in a lengthening of the next IOI (Fig. 1A). The direction of this 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). This period adjustment cumulatively affected the IOI between computer tones; specifically, shortening the period accelerated the tempo while lengthening the period decelerated the tempo. This places, with increasing degrees of period correction, greater responsibility on the human participant to maintain the initial given tempo. The degree of the correction was varied across five conditions in steps of 0.25, ranging from no period correction (0, i.e. non-adaptive) to full correction (1, i.e. overly adaptive). Varying the level of VP adaptivity also varies the reliability of this virtual partner's actions in the sense that high period correction settings make the VP prone to tempo drift. Based on previous work using this model (Repp and Keller, 2008), we know that there is a range within which the behavior of the VP that is more human-like (i.e., similar to estimates of human error correction), more reliable and more likely to result in optimized synchronization. Therefore, for the sake of simplicity we have concentrated on the effect of tapping with either an optimally (0.25) and overly (1) adaptive partner (Fig. 1B). The 22 VP tones in each tapping task trial were 50 ms in duration and played as synthesized “bongo drum” sounds. Participants listened over Siemens MR compatible headphones at a comfortable intensity.

Visual stimuli

Visual stimuli included a black fixation cross displayed on a white background 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 trial. VASs were presented to obtain online ratings for “sense of influence” and “difficulty” of the preceding tapping task trial. Each scale was presented for 6 s. The “Influence” scale (prompted with the word “Einfluss”: with the question “To what extent did your tapping influence the overall tempo?”) was anchored by no influence (“kein”) at the minimum and absolute influence (“absolut”) at the maximum. Similarly, “Difficulty”

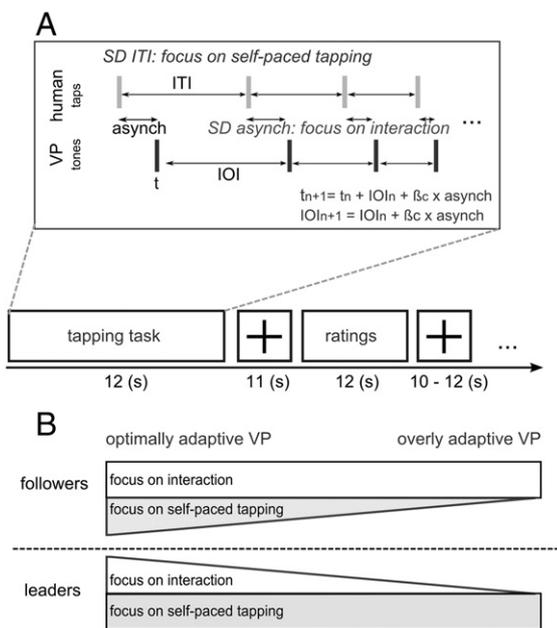


Fig. 1. Leading an adaptive virtual partner (VP) in a sensorimotor synchronization finger-tapping task. (A) Top - graphical description of the VP algorithm which adapts the timing of the pacing signal onset and therefore the inter-onset-interval (IOI) to reduce asynchronies (asynch) between human taps and computer tones by locally modifying the inter-onset-interval (IOI). Implementation of period correction by the VP can therefore lead to tempo drift. The degree to which the VP adapts to the behavior of the human tapping depends on the level of error correction (β_c) employed. Adaptation of the human tapping behavior is reflected in the change in inter-tap-intervals (ITIs). The standard deviations (SD) of the ITIs and asynchronies can be used as measures of prioritization of the instructed tasks to either focus on maintaining the prescribed tempo (self-focus) or focus on the stability of the interaction (self-other focus). Bottom - Functional MRI (fMRI) study design showing a sample trial including a 12 second tapping task (with a pseudo-randomized implemented level of VP adaptivity) followed by a rest period of 10, 11 or 12 s. (B) Hypothesis of task prioritization and thus synchronization strategy which should vary as a function of the participant leader-follower profile as well as the adaptivity of the virtual partner with whom they were interacting. Followers prioritize the interaction, while leaders prioritize self-tapping; the effect of this prioritization is most pronounced when the VP is overly adaptive.

(prompted with the word “Schwierigkeit”: with the question “How difficult was it to synchronize with the VP?”) was anchored by very easy (“sehr leicht”) and extremely difficult (“sehr schwierig”). All visual stimuli were projected onto a screen visible to the participant via prism glasses. Visual stimulation was continuous throughout the experiment.

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 using MAX/MSP. An empirically verified transmission delay of 46 ms (from the tapping pad to the processing software MAX/MSP) was subtracted from tap registration times before asynchronies were calculated by a computer algorithm (see Fig. 1A).

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 × 3 mm axial oblique slices; 1 mm gap; voxel size = 3 × 3 × 3 mm³; and volumes = 699. Scans were acquired continuously throughout the experiment. High resolution, T1-weighted, structural scans (64 slices at 1 × 1 × 1 mm³ voxel size) were obtained for each individual for anatomical overlay of brain activation.

Data analysis

Ratings data

Online ratings for influence over the pulse and difficulty to synchronize during tapping tasks were grouped according to the degree of VP adaptivity and the means and standard deviations per individual participant were calculated. To do so, VAS ratings were converted into numerical 0–10 ratings. A group mean and standard deviation were then calculated. The correlation of influence and difficulty ratings (LFr = $corr(influence, difficulty)$) across trials defined a subjective measure of leadership, which we refer to as the leader–follower correlation coefficient (LFr). The LFr provided us with a single parameter for each participant, which we used to classify individuals based on how challenging they found trials in which they perceived having greater influence over the tempo. Specifically, we used the LFr to sort our cohort into “followers,” those individuals who rated trials in which they felt greater influence to be more difficult (a positive correlation), and “leaders” who found trials where they perceived greater influence to be less difficult (a negative correlation). The LFr measure correlated significantly with the LOC-I scale questionnaire, thus linking subjective assessments of performance in a sensorimotor task with an established instrument for estimating degree of leadership and perceived locus of control (LOC I-scale). Although both the LFr and the LOC I-scale are continuously, as opposed to categorically, distributed we adopt common practice in behavioral and neuroimaging studies and used a median split based on the LFr to analyze both the objective tapping data and the neuroimaging data in terms of group differences (leader vs. followers).

Tapping data

To confirm that participants followed the instruction to synchronize and maintain a steady tempo, we calculated the mean asynchrony (mean ± SD: $\beta_c = 0$, -22.71 ± 11.02 ms; $\beta_c = 0.25$, -4.76 ± 5.01 ms; $\beta_c = 0.5$, -3.33 ± 3.72 ms; $\beta_c = 0.75$, -3.12 ± 3.66 ms; $\beta_c = 1$, -3.43 ± 4.40 ms) across our cohort. We found these and the values of mean ITIs of our cohort were within the usual range found in studies of SMS with musically trained participants (Repp and Keller, 2008). Our two primary measures of tapping performance,

however, were (1) the standard deviation (SD) of asynchronies between participants' taps and VP tones, and (2) the SD of participants' inter-tap intervals (ITIs). Asynchronies were computed by subtracting the onset time of each VP tone from the onset time of the nearest tap within each tapping task trial. The SD of asynchronies provides an (inverse) index of the stability of sensorimotor synchronization performance. We therefore assume that as SD asynchronies decrease, self-other focus increases (due to increased coupling strength between the human participant and the VP). The SD of ITIs provides an (inverse) index of the stability of the individual's tapping tempo. As such we assume that SD ITIs decrease as self-focus increases (Fig. 1B). In addition, we computed a measure of phase error correction based on the zero crossing point of functions describing the decrease in lag-1 autocorrelation of asynchronies across VP adaptivity conditions (explained in greater detail in the related study by Repp and Keller (2008), see Supplementary materials). These phase correction estimates were obtained to test whether leaders and followers (as defined by the LFr) differed in the degree of temporal adaptation that they used when interacting with the VP. Based on the behavioral results obtained, the three tapping measures described above were analyzed in a simplified mixed-model 2 × 2 ANOVAs that included the between-participants factor group (leaders vs. followers) and the within-participants factor VP adaptivity (optimally adaptive vs. overly adaptive).

Imaging data

Analysis of all neuroimaging datasets was performed using FEAT (FMRIB Expert Analysis Tool) version 5.63, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Pre-statistic processing included: motion correction using MCFLIRT (Motion Correction FMRIB's Linear Image Registration Tool (Jenkinson and Smith, 2001)), non-brain removal using BET (Smith, 2002), spatial smoothing using a Gaussian Kernel of 4 mm full width at half-maximum and non-linear high pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with $\sigma = 40.0$ s). Registration included co-registration of the functional scan onto the individual T1 high-resolution structural image and then registration onto a standard brain (Montreal Neurological Institute MNI 152 brain) using FLIRT (FMRIB's Linear Image Registration Tool (Jenkinson and Smith, 2001)). Statistical analysis at the individual participant level was carried out using a general linear modeling (GLM) approach (Friston et al., 1994). Time-series statistical analysis was carried out using FILM (FMRIB's Improved Linear Model) with local autocorrelation correction (Woolrich et al., 2001). The second level analysis grouped the data of each participant's two scanning sessions, using the data from the first level of analysis. For group statistics, analysis was carried out using FEAT (FMRIB Expert Analysis Tool) with higher-level analysis carried out using FLAME (FMRIB's Local Analysis of Mixed Effects). This analysis method allows for incorporation of variance within session and across time (fixed effects) and cross session variances (random effects). Cluster thresholding was performed with a Z-threshold of 2.3 and a corrected p-value of <0.05 with a cluster-based correction for multiple comparisons using Gaussian random field theory (Friston et al., 1994; Worsley et al., 1992).

Based on previous fMRI studies of SMS undertaken by our group (Fairhurst et al., 2012), in the present event-related design, the initiation tones (where participants were instructed to listen to the target tempo but not to tap) were modeled as a single separate event. Synchronized tapping (over the subsequent 20 tones of the trial) was modeled with one of five unique explanatory variables, each variable corresponding to one of the five levels of VP adaptivity ($\beta = 0$, $\beta = 0.25$, $\beta = 0.5$, $\beta = 0.75$ and $\beta = 1$). In these variables, the onset of the third tone defined the onset of each event, which was then assigned a duration of 11 s (thereby capturing activation related to the 20 tone-tap pairs per trial) with equal weighting of each event. We calculated basic contrasts of the initiation and the five tapping conditions relative to baseline. Separate contrasts for synchronized tapping at each level

of VP adaptivity were then compared (as in our previous study, Fairhurst et al., 2012) revealing the expected significant difference between the lower and upper ends of VP adaptivity. These subtractions confirmed an a priori assumption that a clear distinction can be seen between the behaviorally optimal and overly adaptive conditions (employed VP error correction: optimally adaptive = 0.25 and overly adaptive = 1). This was therefore followed by a simplified mixed 2×2 analysis: one within-participants factor of VP adaptivity (optimally adaptive [$\beta = 0.25$] vs. overly adaptive [$\beta = 1$]) and one between-participants factor of group based on the leader–follower profile (leaders vs. followers). Specifically, we implemented a two-stage model: the first model estimated the main effect of the within-subjects factor (VP adaptivity) and the interaction between VP adaptivity and leader–follower profile using an ANOVA. The second model used an unpaired two-sample *t*-test to explore the between-subjects factor (leader–follower profile), comparing differential activity dependent on the measure of leadership (median split based on the leader–follower correlation coefficient) across an averaged contrast of the two levels of VP adaptivity (optimally and overly adaptive). By separating the 2×2 analysis into two stages we account for both between-subject and within-subject error terms.

To better describe the directionality of the performed ANOVA, time course analyses and individual parameter estimates were extracted (PEATE – Perl Event-related Average Timecourse Extraction; see <http://www.jonaskaplan.com/peate/>) from functionally defined (based on the contrasts of the two main effects) regions of interest (ROIs) and analyzed using SPSS. We correlated these parameter estimates with the acquired behavioral data (tapping performance and subjective ratings) to establish a relationship between observed brain and behavioral responses. For exploratory purposes, based on our findings at a behavioral level, we probed the effect of group (leader or follower) depending on the nature of the partner (optimally or overly adaptive) by performing unpaired *t*-tests comparing leaders and followers at each of the two levels of VP adaptivity (tapping with an optimally adaptive partner or an overly adaptive partner). Regression analyses were then performed as in our previous study (Fairhurst et al., 2012) to explore correlated brain activity with the objective tapping measures and our subjective measure of leadership.

Results

Ratings data: Leaders and followers

Trial-by-trial difficulty ratings indicated that increases in VP adaptivity (and unreliability) lead to judgments of increased task difficulty (one-way ANOVA: $F(4,75) = 4$, $p < 0.01$). Subjective appraisal of degree of influence over the tempo, on the other hand, showed a slight inverse parabolic function with a peak at $\beta_c = 0.25$ despite the fact that influence is objectively greatest with the completely adaptive VP ($\beta_c = 1$). Neither the linear nor quadratic trends were statistically significant (one-way ANOVA: linear trend $F(4,74) = 0.056$ $p = 0.813$; quadratic trend $F(4,75) = 1.706$ $p = 0.196$).

The correlation of subjective difficulty and influence ratings within individual participants across trials showed that while some individuals rated trials in which they felt greater influence to be more difficult (“followers”), others showed an inverse correlation (greater influence trials were rated as less difficult, “leaders”). Furthermore, this correlation coefficient, which we refer to as the leader–follower correlation (LFr), was correlated negatively with results from the LOC-I scale ($r = -0.58$; $p < 0.05$), with leaders (negative LFr) scoring higher on the questionnaire measuring the degree to which they perceive events in their lives as being a consequence of their own acts (Fig. 2A). Based on this measure of leadership we divided our cohort, from this point onwards, using a median split of the LFr, giving us a set of eight leaders and eight followers. It should be pointed out, however, that our division between leaders and followers is not intended to establish a strict categorical

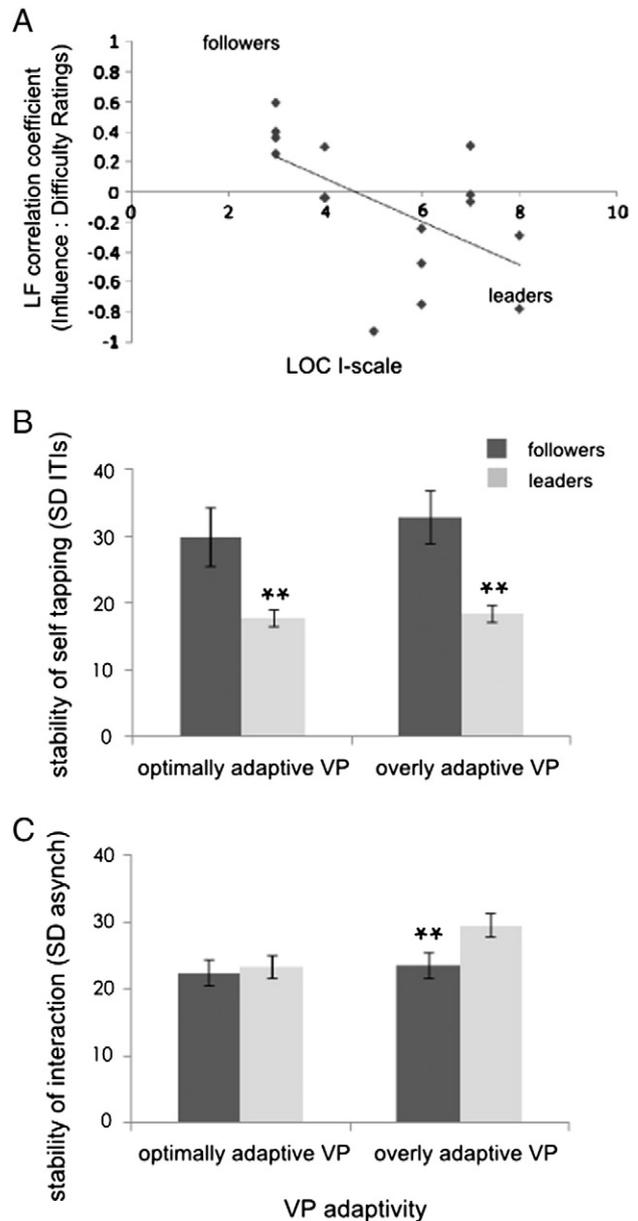


Fig. 2. Behavioral results. (A) Correlation between the leader–follower correlation coefficient (LFr) and individual scores on the I (internal) scale of the locus of control questionnaire. Measures of tapping performance showing (B) the variability in self-tapping (the standard deviation of the inter-tap-intervals or SD ITIs) as a function of VP adaptivity, and (C) the variability in the standard deviation of the asynchronies (SD asynchrony) as a function of VP adaptivity. The SD asynchrony measure indicates the stability of the interaction and thereby serves as an estimate of self–other focus, whereas the SD ITI measure indicates the stability of the participant’s behavior alone and thereby serves as an estimate of self focus. Asterisks indicate significance level of $p < 0.05$ of two-tailed *t*-test.

distinction. Rather, as implied by the fairly continuous distribution of LFr values in Fig. 2A, each individual may display a mixture of leader and follower characteristics, with some individuals being more prone to lead and others more prone to follow.

Tapping data: How to lead

From our objective tapping data we derived several measures that described the participants’ behavior. We saw a significant effect of VP adaptivity on standard deviation of asynchronies (SD asynchrony), a measure indicative of the stability of the interaction and, presumably, prioritization of instructed task to synchronize (main

effect: $F(1,14) = 22.045$, $p < 0.001$, with improved synchronization performance at the optimal level of VP adaptivity (mean \pm SD: *optimally adaptive VP* 22.94 ± 4.96 ; *overly adaptive VP* 26.56 ± 5.65). In line with Repp and Keller (2008), we saw no main effect of VP adaptivity on the standard deviation of inter-tap-intervals (SD ITI; $p = 0.45$), a measure indicative of the stability of self-tapping and prioritization of the task to maintain tempo. Mean individual SD ITI measures were shown to be significantly negatively correlated with mean perceived influence (*optimally adaptive VP*: $r = -0.051$, $p < 0.05$; *overly adaptive VP*: $r = -0.6$, $p < 0.05$) again highlighting the link between feeling in control and prioritizing stability of self-tapping.

As expected, the most profound differences were found between the lower and upper ends of VP adaptivity (employed VP error correction: *optimally adaptive* = 0.25 and *overly adaptive* = 1). As such from this point onwards, our analyses of both behavioral and imaging data were reduced to compare the responses at these two levels of VP adaptivity. We found a main effect of group (leader, follower) on our measure of self-focus (SD ITI): leaders proved to be more stable than followers across levels of VP adaptivity (Fig. 2B and Table 1; main between-subject effect $F(1,14) = 8.45$, $p < 0.05$; no significant effect of VP adaptivity and no significant interaction). When analyzing the measure of self-other focus (SD asynchrony in participant-VP coupling) we found no significant main effect of group but did find a significant interaction between VP adaptivity and group ($F(1,14) = 11.151$, $p < 0.01$) such that coupling was weaker in leaders when tapping with an unreliable, overly adaptive VP (Fig. 2C and Table 1; $t(7) = -3.40$; $p < 0.05$ two-tailed). We therefore saw an opposite relationship between the variability of ITIs (an index of self-timing stability), and asynchronies (an index of the stability of the interaction). Furthermore, we found that an estimate of error (phase) correction employed by the individuals (see Table 1, where values indicate the proportion of each asynchrony that is corrected for, on average) showed a significant difference in between the two groups ($t(7) = 2.707$; $p < 0.05$), with leaders correcting less than followers. Error correction was correlated positively with the leader–follower correlation (non-parametric correlation: $\rho = 0.516$, $p < 0.05$), that is higher error correction correlating with higher LFr (followers), suggesting that followers show a lesser tendency to lead.

fMRI data: Leading a variably adaptive VP

To explore the brain basis of the behavioral differences described above, we focused on the conditions presenting the two extremes of adaptivity and therefore a simplified 2×2 design with one within-subjects factor of VP adaptivity (optimally vs. overly adaptive conditions) and one between-subjects factor of group (leader or follower, based on the median split of the leader–follower correlation coefficient). We observed a main effect of VP adaptivity in right lateralized structures including the anterior insula, inferior frontal gyrus (IFG), superior temporal gyrus (STG) and the inferior parietal lobule (IPL) (Fig. 3A, Table 2). A contrast in which the activity estimate associated with tapping with an overly adapted partner was subtracted from the estimate associated with

tapping with an optimally adaptive partner showed that the right frontal activity (IFG, anterior insula) was greater when participants tapped with an optimally adaptive VP, $\beta_c = 0.25$ (Fig. 3B). Based on the main effect contrast, parameter estimates were extracted from functionally defined regions of interest showing activation of the IFG and IPL to be positively correlated with ratings of perceived influence (across conditions of VP adaptivity – IFG: $r = 0.51$, $p < 0.05$; IPL: $r = 0.53$, $p < 0.05$; Fig. 3C). Furthermore, IFG activation was positively and significantly correlated with the LOC I-scale ($r = 0.52$, $p < 0.05$).

The group (leaders vs. followers) main effect (see Methods for details) showed significant differences within a network of brain areas previously implicated in self-initiated movements. These structures included midcingulate, preSMA, premotor cortex, precuneus (both cognitive and sensorimotor functional subdivisions (Margulies et al., 2009)) and inferior parietal sulcus (Fig. 4, Table 2) which, based on a subsequent t -test and extracted parameter estimates (see Supplementary materials, Figure S1), showed greater activity in leaders than in followers. Moreover, individual parameter estimates extracted from the preSMA were shown to be significantly negatively correlated with the mean individual SD ITIs, specifically when participants tapped with an overly adaptive partner ($r(14) = 0.5$; $p < 0.05$). More generally, prioritizing stability of self-tapping or lower SD ITIs was seen to correlate with a network including the basal ganglia, IFG, parietal lobe and cerebellum (see Supplementary materials, Figure S2).

Despite a significant interaction observed in the behavioral measure of SD ITI, no significant interaction was observed at the brain level. It should be noted that participants were not necessarily recruited specifically to represent two distinct groups (a certain number of the participants were around the median). As such, perhaps the lack of a statistically significant interaction at a brain level may be due to insufficient statistical power. For exploratory purposes and based on the interaction observed at the behavioral level, we ran unpaired t -tests on our imaging data to compare leaders and followers at the two levels of VP adaptivity. In doing so, we found no significant difference at the optimal level but greater activity in the sensorimotor region of the precuneus in leaders (vs. followers) when tapping with an overly adaptive partner (see Supplementary materials, Figures S1 and S3).

Discussion

The first violinist in a string quartet and the leader in a ballroom dancing pair are examples of individuals who lead by influencing the action of their partners when cooperating to achieve a shared goal (Chemers, 1997). In the present study, we employed a sensorimotor synchronization paradigm in which individuals were able to exert more or less control over a virtual partner (VP) in a paced finger-tapping task. By varying the degree of power to dictate the overall tempo of the pacing sequence, we present a novel approach to probe the neural correlates of leading. More specifically, we investigated leading in terms of objectively dominating in the partnership – in this case interacting with a VP who, by varying the degree of employed period correction, adapted more or less across conditions – as well as the subsequent subjective appraisal of influence during the interaction. By defining leadership in terms of both subjective and objective behavioral measures, we identified a subgroup of individuals within our cohort who we were able to classify as more prone to lead (“leaders”). Moreover, we show that our context-specific, sensorimotor classification of leadership significantly correlates with the established and more general measure of locus of control.

Based on behavioral and neural data we then suggest a mechanism by which individuals lead in this type of dynamic interactive task by minimizing variability in their own actions while allowing the variability in joint-action to increase. Specifically, using functional imaging, we showed that leading is correlated with right lateralized activation of areas involved in cognitive control and self-related processing. Furthermore, we saw that leaders were more stable in terms of their self-

Table 1

Summary of behavioral tapping measures. Group mean \pm standard deviation for the measure of the stability of self tapping (standard deviation of inter-tap-intervals: SD ITI in ms), the measure of the stability of the interaction (standard deviation of asynchrony in ms) and estimates of human error correction for leaders and followers across levels of VP adaptivity.

	Leaders	Followers
SD ITI		
Optimally adaptive VP	17.67 \pm 3.37	29.81 \pm 12.55
Overly adaptive VP	18.42 \pm 3.87	32.85 \pm 13.72
SD asynchrony		
Optimally adaptive VP	23.36 \pm 4.89	22.53 \pm 5.33
Overly adaptive VP	29.53 \pm 4.91	23.57 \pm 5.13
Estimate of human error correction	0.26 \pm 0.11	0.45 \pm 0.14

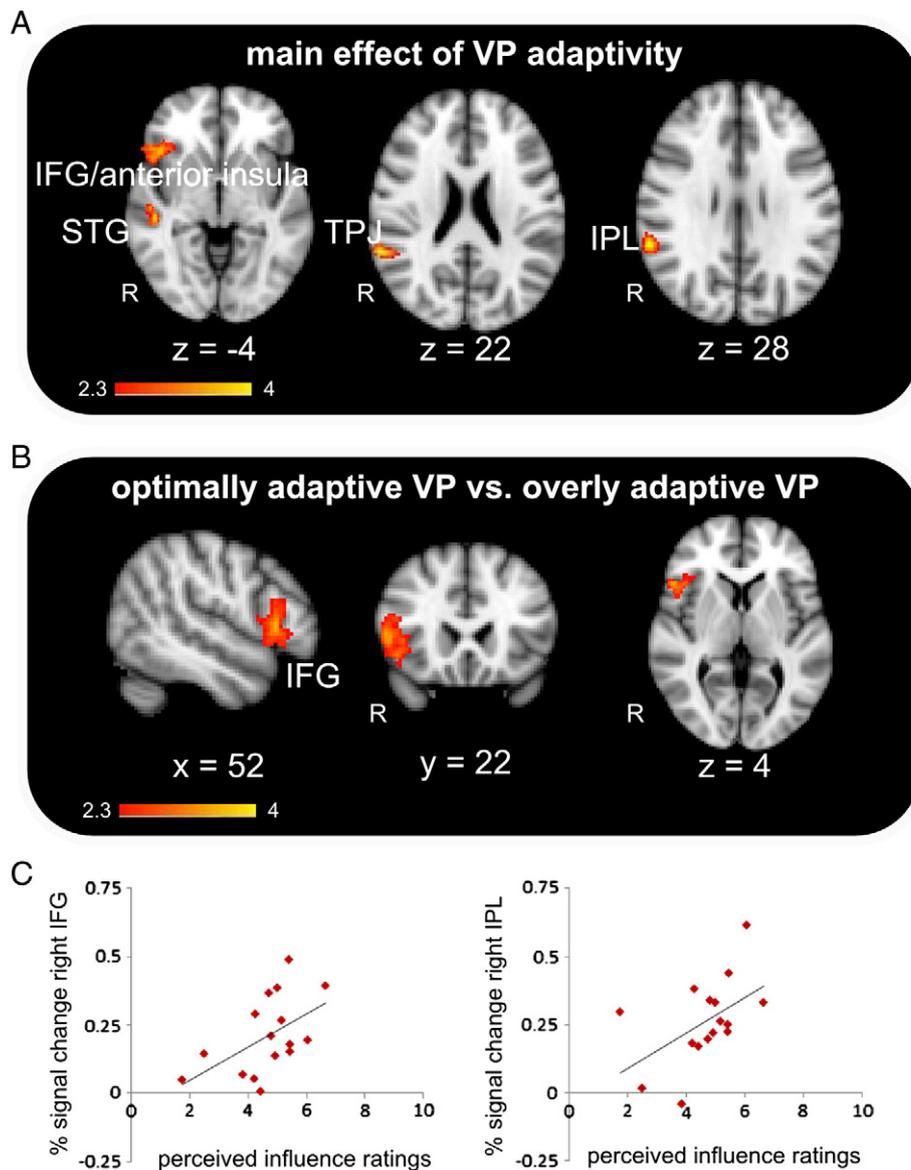


Fig. 3. Leading and influencing a variably adaptive VP. (A) Main effect of VP adaptivity (random effects, $Z = 2.3$; $p = 0.05$, corrected) indicating a right lateralized fronto-parietal network implicated in cognitive control and self-related processing. The network comprises the inferior frontal gyrus (IFG), anterior insula, superior temporal gyrus (STG), temporoparietal junction (TPJ) and inferior parietal lobule (IPL). See Table 2 for a full list of activation with MNI coordinates. (B) Subtraction of the optimally adaptive condition and the overly adaptive condition ($\beta_c = 0.25$ vs. $\beta_c = 1$) showing isolated IFG activity when participants tapped with an optimally adaptive VP. No significant differences were seen in the reverse contrast. (C) We show that extracted parameter estimates (% signal change) from these regions are significantly correlated with subjective ratings of perceived influence.

tapping performance and we showed that they lead in this finger-tapping task by differentially activating a set of structures previously shown to be involved in self-initiated (rather than externally triggered) movement. Together our data prompt us to suggest that leaders and followers implement different synchronizing strategies focusing to a greater or lesser extent on either self-tapping performance (prioritizing the instruction to maintain the given tempo) or the interaction (prioritizing the instruction to synchronize with the VP) depending on the nature of their partner.

Leading, perceived influence and agency

In a previous study, we demonstrated the benefit of this reduced sensorimotor synchronization model for the purposes of investigating the most basic level of social cognition, that is the interpersonal coordination of one's actions with another (Fairhurst et al., 2012). The present manipulation varied the degree to which the participant

could lead the VP. The main effect of varying VP adaptivity was seen to correlate with right lateralized activation of the anterior insula, the IFG, the STG, TPJ and IPL. Based on ROI analyses however, we see a dissociation between objective and subjectively perceived control, with both perceived influence ratings and percent signal change in these areas peaking at the optimal level of VP adaptivity (and not in the overly adaptive condition when objectively, participants had the greatest sway over the tempo). It is at this lower level of VP adaptivity that synchronization is optimized, suggesting that to feel in control (and to activate areas related to "leading") an effective exchange must exist. In other words, and in accordance with current theories on successful leadership, leaders lead more effectively and believe themselves to be more in control when a certain level of social exchange exists (Graen and Uhl-Bien, 1995). The lateralization observed is consistent with findings that activity in the right hemisphere is greater when the self is imitated (in our case, participants were followed more by the adaptive partner) (Decety et al., 2002).

Table 2

Main effects of factors. Coordinates in MNI space and associated peak voxel Z-scores. $p < 0.05$ corrected for multiple comparisons.

Regions		Z-max	Peak		
			x	y	z
<i>Main effect of VP adaptivity</i>					
Inferior frontal gyrus	R	4.18	52	20	4
Anterior insula	R	3.44	42	28	-2
Ventrolateral prefrontal cortex	R	3.78	46	22	-6
Superior temporal sulcus	R	3.26	56	24	-6
Temporoparietal junction	R	3.55	56	-46	20
Inferior parietal lobule	R	3.98	60	-44	26
<i>Main effect of group</i>					
Dorsolateral PFC	L	3.79	-32	54	8
(dlPFC extending into MFG)	R	2.06	44	16	40
Anterior insula	R	3.67	32	18	0
Inferior frontal gyrus	R	3.37	34	18	2
Premotor	L	3.02	-20	-2	50
Midcingulate	R	3.59	6	12	34
Pre-SMA		3.21	-2	14	50
Precuneus		2.80	14	-56	44
Cuneus	R	2.68	14	-76	34
IPL	L	2.31	-36	-82	28

Moreover, we have previously reported that the anterior insula and IFG were activated preferentially in conditions requiring greater cognitive control (Fairhurst et al., 2012). Specifically, our previous results suggested that observed IFG activation was related to the proposed role of this region in switching between default and central executive networks (Sridharan et al., 2008), with the latter being recruited during the more challenging exchanges with the VP. In the present study, we additionally show that activity in the IFG and IPL is significantly correlated with subjective ratings of perceived influence (subjectively feeling in control). We propose that increased perceived influence is indicative of increased awareness of self or greater self-agency. Our activation pattern may therefore be related to participants focusing on controlling the constancy of their own actions when trying to lead or when they subjectively felt more in control (Derrfuss et al., 2005). Specifically, we find that IFG activity is significantly correlated with individual measures on the LOC I-scale. Our data could also be seen as a result of inhibitory control (Garavan et al., 1999; Hampshire et al., 2010) and greater response control (Dodds et al., 2011). This may be necessary for the suppression of automatic, entrainment-like imitative responses – following the fluctuating tempo produced by the adaptive VP (Brass et al., 2009).

Alternatively, increased activity in the anterior insula, which is functionally connected to the IFG, has been reported in studies of cooperation (Decety et al., 2004) and more pertinently has been implicated in

agency processing including attribution of actions to self (Farrer and Frith, 2002; Farrer et al., 2003) and self-awareness (Craig, 2009). Similarly, we identify posterior activation in the IPL and TPJ areas which, based on the two related reciprocal interaction studies (Decety et al., 2002; Nagy et al., 2010), have been linked to the attribution of agency, necessary for imitation. Our findings are more in line with those of the earlier study (Decety et al., 2002) both in terms of the right lateralization of the cluster and the position, which sits more inferior to those of Nagy et al. (2010).

Our pattern of activation overlaps with several other reports which suggest that the neighboring regions including the STG and TPJ, possibly in conjunction with fronto-insular areas, are involved in agency processing, whether self or external (Spengler et al., 2009). However, it is possible that the posterior activation we observe extending into the STG is more specifically linked to the understanding or predicting of the intentions, goal or strategies of another in a socially relevant context (Schultz et al., 2004). Leading, at least within this context, may be synonymous with taking control, that is, prioritizing the instruction to maintain the tempo rather than to focus on synchronizing or imitating (Phillips-Silver and Keller, 2012). This is presumably done in conjunction with monitoring the intentions of co-acting other(s), that is, complying with the other part of the instructed task (namely to synchronize). Based on our behavioral data, however, how individuals prioritize the two parts of our task seems to depend firstly on their leader–follower classification and secondly on the nature of the VP.

Leaders, followers and synchronization strategies

Using various forms of synchronous tapping tasks, our group has explored and identified inter-individual differences based on measures of tapping performance (Pecenka and Keller, 2011). Specifically, and related to the present study, Pecenka and Keller (2011) identified a tendency in individuals to either predict or track the actions of their partner to varying degrees, and thus differentially respond in an interactive coordination task. In a similar fashion, the present data suggest that our cohort can be divided into individuals more or less prone to leading (or so-called “leaders” and “followers”) based on both objective measures of tapping behavior and subjective appraisal of the interaction. Based on the latter, we define leaders as individuals who find conditions of the tapping task in which they perceive the greatest influence to be less difficult and we provide additional evidence for a correlation between perceived locus of control and this measure of leadership (Anderson and Schmeier, 1978).

Our objective tapping measures reinforce the distinction between our subgroups and suggest a difference in synchronization strategy. Based on the deviation in self-tapping (SD ITIs), “leaders” are significantly more stable than followers at both low and high levels of VP adaptivity

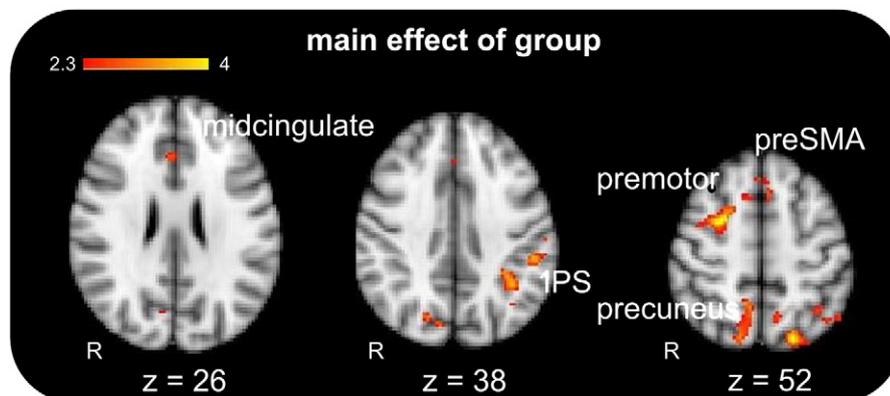


Fig. 4. Leaders vs. followers. The main effect of group profile (an unpaired two-sample t -test; random effects, $Z = 2.3$; $p = 0.05$, corrected) showed modulation of activity in areas implicated in self-initiated actions, including the pre-supplementary motor area (pre-SMA), precuneus, mid-cingulate and inferior parietal sulcus (IPS).

(Fig. 2C). This result agrees with the data reported by Konvalinka et al. (2010) showing that participants adjusted their ITIs as a function of the auditory feedback from their partner. It should be noted that in our setup, firstly auditory feedback was unidirectional (no tone was produced when participants tapped) and secondly we were able to exercise experimental control over mutual adaptive timing. Furthermore, our paradigm differs from others in that our instructions and our manipulation encourage a leadership role and identify individuals who lead by focusing on the stability of self timing rather than the stability of the interaction. In other words, within the context of this task, to lead is to provide a stable example for the VP to follow. As such, for leaders the primary goal is to minimize the variance of their inter-tap intervals, while followers instead aim to minimize the asynchronies between their taps and the tones of the VP (Repp and Keller, 2008). This difference is manifested in a difference in the degree of sensorimotor coupling strength in leaders and followers, as reflected in the higher estimates of phase correction in followers than leaders. We posit that the observed stability of leaders' own tapping is thus due to prioritization of the second component of the instructed task, which was to maintain the given tempo. Furthermore we suggest that this observed bias for leaders to "lead" by focusing more on their own internal timekeeper is at the expense of the stability of their interaction with the VP, especially when the computer is highly adaptive and thus unreliable. We therefore hypothesize and provide evidence that to lead is to correct less (employ less error correction) and therefore not to follow.

An exploration of the brain basis of the group bias revealed activation in brain areas previously implicated in self-initiated movement including midcingulate and pre-SMA (Cunnington et al., 2002; Gerloff et al., 1998; Lau et al., 2004), with leaders showing greater activity in these structures than followers (with no interaction between group and VP adaptivity). The negative correlation between activity in the pre-SMA (during the "overly adaptive" condition) and SD ITI measures leads us to suggest that this activation is related to individuals focusing on the stability of their own tapping behavior which is enhanced (at least neurally relative to followers) when tapping with an erratic partner. In line with this, Lau et al. (2004) highlight that, in particular, activity in the pre-SMA is indicative of internally initiated responses when external stimuli do not adequately specify the appropriate action. A similar but more extensive network was also seen when probing the imaging data for activity which correlated with the objective tapping measures of stable self-tapping.

Although the instructed task for all individuals involved focusing on both the stability of the interaction and the stability of self-paced tapping, based on our behavioral data, our subgroups appear to have prioritized these tasks differently, depending on the reliability of their partner. A more reliable VP ($\beta_c = 0.25$) allows for greater stability (low SD asynchronies) of the dynamic interaction and allows the leader to lead. An unpaired *t*-test of the imaging data suggests that at this optimal point of VP adaptivity "leaders" and "followers" do not perform this leadership task differently. However, in conditions in which the VP is more unreliable ($\beta_c = 1$), we see the partnership between participant and VP uncouple (higher SD asynchronies), specifically when leaders are interacting with the more erratic partner. Neurally, no significant interaction was observed but for exploratory purposes the difference observed at a behavioral level was explored. A comparison of leaders and followers tapping with an overly adaptive partner, the contrast revealed greater activity in leaders isolated to the precuneus. Both cognitive and sensorimotor regions of the precuneus showed this effect (Margulies et al., 2009). The precuneus is believed to integrate external and self-generated information and to help resolve issues of agency and perspective taking when interacting with or thinking about interactions with other individuals (Cavanna and Trimble, 2006). This may be particularly necessary when leaders are struggling to lead an overly adaptive, unreliable partner.

To summarize, our findings suggest that leading is related not only to implementation of a task specific strategy, but also to the adjustment

of this strategy depending on the nature of the partner with whom one is interacting. This description of leading stands out amongst numerous neuroimaging studies which have focused on imitation and other strategies implemented when "following."

Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2013.09.027>.

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