

Being and Feeling in Sync with an Adaptive Virtual Partner: Brain Mechanisms Underlying Dynamic Cooperativity

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Cooperation is intrinsic to the human ability to work together toward common goals, and depends on sensing and reacting to dynamically changing relationships between coacting partners. Using functional magnetic resonance imaging (fMRI) and a paradigm in which an adaptive pacing signal simulates a virtual partner, we examined the neural substrates underlying dynamic joint action. A single parameter controlled the degree to which the virtual partner adapted its behavior in relation to participant taps, thus simulating varying degrees of cooperativity. Analyses of fMRI data using objective and subjective measures of synchronization quality found the relative balance of activity in two distinct neural networks to depend on the degree of the virtual partner's adaptivity. At lower degrees of adaptivity, when the virtual partner was easier to synchronize with, cortical midline structures were activated in conjunction with premotor areas, suggesting a link between the action and socio-affective components of cooperation. By contrast, right lateral prefrontal areas associated with central executive control processes were recruited during more cognitively challenging interactions while synchronizing with an overly adaptive virtual partner. Together, the reduced adaptive sensorimotor synchronization paradigm and pattern of results illuminate neural mechanisms that may underlie the socio-emotional consequences of different degrees of entrainment success.

Keywords: cognitive control, cooperation, entrainment, fMRI, virtual partner

Introduction

Successful interactions among individuals require a certain degree of adaptivity. From everyday experience we know that interacting with an adaptive partner is generally easier than with a rigid one. However, one individual might be overly adaptive, overcompensating for variability in the other's behavior, and therefore unhelpful also. Ideally, a partner modifies his or her performance by a certain optimal degree in order to facilitate fluid interaction. Imagine two individuals carrying a sofa. If one adjusts to the other's slowing and speeding up either too little or too much it makes for difficult carrying and increases the chances of dropping the sofa or running over the person in front. Thus, successful cooperative joint action depends on flexible and reliable give-and-take (adaptation) between coacting individuals (Schmidt and Richardson 2008).

An integrated understanding of the links between the levels of social interactions, behavioral contexts and mechanisms, and the supporting neural mechanisms has not yet been achieved. In this paper we link the three levels (Fig. 1). Specifically, we utilize a simple novel sensorimotor synchronization (SMS) paradigm, which has emerged as a powerful reduced model system for studying entrainment, to show that

objective and subjective performance parameters predict the degree to which brain activity will be biased toward components of a large-scale network involved in automatic and socio-emotional processing instead of components of a network associated with cognitive control (Fig. 1).

Paradigms for Studying Interagent Dynamics at Various Timescales

Methods for examining cooperative behavior have focused on different timescales and interaction partners. Most common have been various interpersonal turn-taking games that transpire on a relatively slow timescale (Rilling et al. 2002; Decety et al. 2004). However, many dynamic interactions, such as those employed by cooperating musicians and dancers, occur at faster timescales and require a high degree of temporal precision. Studies of such interactions have involved SMS paradigms in which a person synchronizes movements, for example finger taps, with a stable isochronous pacing signal (see Repp 2005 for review) or, more recently, with human partners (Tognoli et al. 2007; Kelso et al. 2009; Konvalinka et al. 2010). More generally, SMS refers to the coordination of a physical action in time with a rhythmic sequence, a function intrinsically linked to group music making (Repp 2005).

Sensorimotor Synchronization with a Virtual Partner

Here we implement a virtual partner (VP) using an adaptive auditory signal (Repp and Keller 2008) with which a person is asked to tap a finger in synchrony while attempting to maintain the given tempo (see also Vorberg 2005). One crucial element of this paradigm is that a computer-programmed auditory pacing signal simulates the potential behavior of a human partner by dynamically adapting its timing based on the individual's performance. The VP is adaptive in that it varies the onset of its tones by a given proportion (α) of the amount of asynchrony between its tones and the taps of the participant (Fig. 2A). Variation across a range of α ($\alpha = 0, 0.25, 0.5, 0.75, \text{ or } 1$) simulates a range of flexible adaptivity and corresponds to differing degrees of coupling between the VP and the human participant (Fig. 2B). Measures of individual synchronization performance, such as the standard deviation of asynchronies between taps and tones (SD asynchrony), provide an objective measure of the success of dynamic cooperation. Lower SD asynchrony indicates more stable performance, and varying the level of VP adaptivity results in a systematic pattern of synchronization variability (Repp and Keller 2008). This pattern is captured by a parabolic function and highlights that VP adaptivity varies on a continuum rendering synchronization more or less difficult (Fig. 2C).

A second important aspect of the paradigm is the instruction to synchronize while also maintaining the initial tempo.

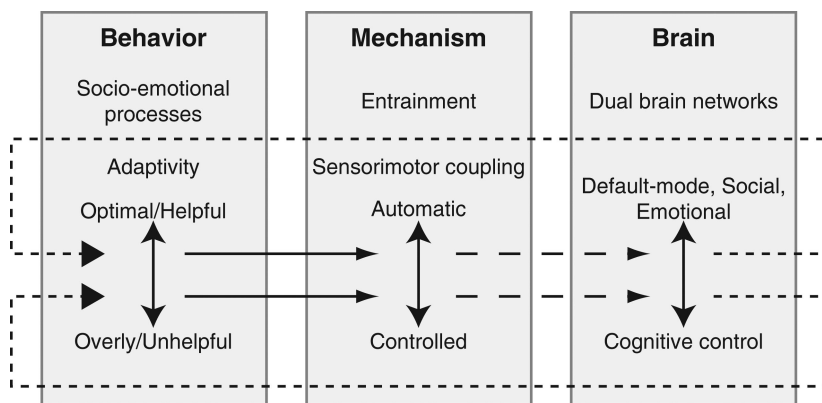


Figure 1. Links between social interaction, behavioral mechanisms, and brain networks. At each level exists a process that varies on a continuum (vertical arrows) and is capable of interacting with a process at the neighboring level, thereby influencing its position along the continuum. For example, adaptivity in social behavior varies from helpful to unhelpful, which in turn influences (solid horizontal arrows) the degree to which entrainment, a process of sensorimotor coupling between agents, is easy and automatic or difficult and requiring of mental effort (cognitive control). We postulate (dashed horizontal arrows) that the ease and quality of entrainment biases the relative prevalence of activity in two large-scale brain networks, one of which is more active during effortful perceptual and cognitive tasks that require interaction with external stimuli, and the other of which is more active during quiescence, self-reflection, and social cognition. Specifically, as sensorimotor synchronization becomes easier, as a result of interacting with an optimally adaptive partner, the brain network more strongly associated with socio-emotional processing should become more active, which in turn may influence subsequent social interactions (looping dashed arrows).

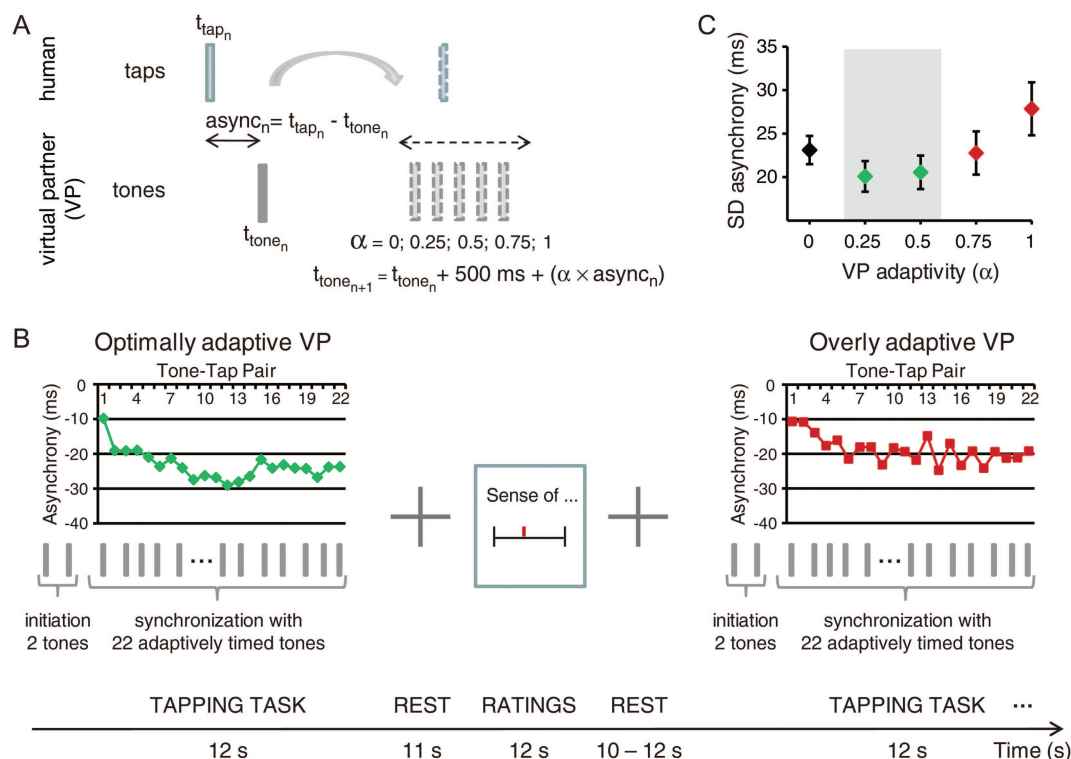


Figure 2. Study design for adaptive SMS as a model for dynamic cooperativity, and associated behavioral data. (A) The VP's algorithm for adapting its timing to reduce asynchronies (async) between human taps (t_{tap}) and computer tones (t_{tone}) by locally modifying its base interonset interval (500 ms) depending on the level of phase correction (α) employed. (B) At the bottom is a sample of a tapping trial which consisted of two isochronous 50 ms initiation tones and, starting with the third tone, the participant was instructed to tap in synchrony with the then variably adaptive pacing signal that was programmed to vary its tone onsets by a fraction (α) of the measured asynchrony. The data plots show examples of a single participant's measured asynchronies in either an optimally adaptive ("helpful") or overly adaptive ("unhelpful") trial. (Negative asynchronies indicate that taps preceded VP tones.) Following each task trial, subjective ratings of "sense of influence over the pulse" and "difficulty" were acquired. (C) Objective measure of tapping performance (SD asynchrony) across conditions of VP adaptivity. Less variation in the tap-tone asynchronies is indicative of more successful self/partner coupling. Green dots highlight "helpful" levels of adaptivity and red dots highlight conditions of unhelpful adaptivity. Gray area denotes range of human error correction which overlaps with conditions of optimized synchronization. The plotted data are the mean SD asynchronies across all individuals and trials in the experiment. Error bars are 1 SEM.

The emphasis on both the phase relation (synchronization) between the human and VP and the periodicity of the interaction (tempo) is integral to collaborative joint action goals in contexts such as musical ensemble performance. In addition,

specifying precise goals allowed us to take into account subjective, as well as objective, measures of participants' performance on the task. While tapping performance provided an objective measure of cooperation or "being in sync,"

subjective ratings of perceived task difficulty (acquired after each trial) served as an indirect measure of how in sync participants felt with their VPs.

The association between variation in VP adaptivity (α) and variation in objective and subjective measures of performance is mediated by the relative balance of two error correction mechanisms that operate during SMS: phase and period correction (Repp 2005). Phase correction, the tendency to adjust the alignment of one's taps relative to a pacing sequence in order to compensate for timing deviations is automatic and hence easy, whereas period correction, the ability to adapt to tempo changes or to maintain a steady tempo in the presence of deviations from that tempo, is a more effortful controlled process (Repp 2005). The difficulty of the interaction therefore varies as a function of coupling strength between the VP and human. Coupling is optimal—in the sense that SD asynchrony is minimized—when both parties employ similar, moderate degrees of phase correction, and synchronization can be maintained automatically under such circumstances (Repp and Keller 2008).

Synchronization, Music, and Two Brain Networks

How might the brain of an individual respond as a partner's behavioral adaptivity during SMS varies from being easy to synchronize with to being difficult to synchronize with? Our predictions emerged from considering several different lines of evidence. The first concerns the concept of entrainment, that is, the biological phenomenon that describes the temporal coordination of rhythmic behaviors across interaction partners in diverse species (e.g. fireflies, frogs, fiddler crabs, and humans) (Schmidt and Richardson 2008; Oullier and Kelso 2009; Phillips-Silver et al. 2010). The human ability to engage in highly complex forms of both physical and social entrainment is suggestive of specialized neural and cognitive mechanisms. These mechanisms may elucidate how entrainment (e.g. when walking or rocking in chairs) increases interpersonal affiliation and prosocial behavior (Valdesolo et al. 2010), and SMS in musical interactions fosters prosocial behavior (Hove and Risen 2009). Spontaneous sensorimotor engagement with music increases when music is perceived as having more groove (an attribute of music associated with the positive urge to move along with music) and the amount of experienced groove and enjoyment is greater when sensorimotor coupling with the music is easier and better (Janata et al. 2012). One of the features of strong experiences with music, sometimes associated with feeling in the groove, is a sense of a loss of agency (Gabrielsson and Lindstrom Wik 2003), which can also be induced in SMS tasks (Repp and Knoblich 2007).

Strong experiences with music have been considered in relation to the functioning of two large-scale brain networks (Janata 2009) that have typically been regarded as serving opposite roles, as exemplified by the labels afforded them: “task-positive” and “task-negative” (Fox et al. 2005; Fransson 2006). The task-negative network, often referred to as the default-mode network (DMN) (Raichle et al. 2001; Fox et al. 2005) is less active during cognitively demanding tasks (Fransson 2006; Weissman et al. 2006; Congdon et al. 2010), but becomes transiently more active during lapses in performance (Weissman et al. 2006; Congdon et al. 2010). Separate from the cognitive load perspective, a view of the DMN has

emerged that associates increases of activity within the network with tasks that increase self-referential, social, and emotional processing (Northoff et al. 2006; Van Overwalle 2009). Both of these perspectives are integrated in the entrainment phenomenon considered here.

On the basis of the panoply of observations described above, we expected the adaptive VP paradigm to manipulate the relative balance of activity within the two anticorrelated networks. Specifically, we predicted that optimal synchronization should result in activation of those areas that are recruited when externally driven perceptual and cognitive control demands are low, that is, the self-referential, social, and affective regions along the cortical midline. We expected to observe more activity in cognitive control areas as the degree of adaptivity of the VP increased to the point of being unhelpful.

Materials and Methods

Participants

Sixteen healthy volunteers (eight female and eight male; age range: 21–33 years; mean age: 26.38 years, $SD = \pm 4.21$) were scanned at the Max Planck Institute for Human Cognitive and Brain Sciences in Leipzig, Germany. None of the participants had any prior neurological or psychiatric disorders, and none met the exclusion criteria for magnetic resonance (MR) experimentation. Our cohort consisted of both musically active and less musical individuals, but all were thoroughly screened for relevant musical experience. Factors of musical experience included instrument type and duration of active participation in musical activities, ensemble experience, and starting age. However, no significant differences based on musical experience were seen for any of our measures of interest. This may presumably be due to the fact that all participants had previous finger-tapping task experience and had all participated in at least one behavioral version of the experiment prior to scanning. The experiment was approved by the local ethics committee and informed written consent was obtained from each participant.

Study Design

The study consisted of two successive scanning sessions separated by a short rest break. Each scan session included 30 pseudo-randomized task trials followed by a rest baseline period of between 10 and 12 s (Fig. 2B). The task trials varied in the degree of adaptivity of the VP controlling the adaptively paced sequence, with one of the five levels of VP adaptivity (nonadaptive, optimally adaptive, moderately adaptive, highly adaptive, and completely adaptive) presented during each. Specifically, phase correction (α) was implemented by the programed pacing signal and as such it accounted for and adjusted each subsequent interonset interval (IOI) by a fraction ($\alpha = 0, 0.25, 0.5, 0.75, 1$) of the calculated asynchrony between tone and tap (Fig. 2A). Adaptivity is not synonymous with helpfulness, however. Thus, we also distinguish between optimally adaptive (“helpful”) or overly adaptive (“unhelpful”) (Fig. 2B,C). Each condition of VP cooperativity was repeated six times within a scan session and thus 12 repeats were presented overall. Despite all participants having previously participated in a behavioral version of the experiment, prior to scanning, the paradigm was clearly explained. Participants were explicitly told that they would be interacting with a human–computer interface but that the VP would adapt its timing relative to their performance. Participants were instructed to synchronize their taps with the tones of the VP as accurately as possible and to maintain the initial tempo to the best of their ability. Participants were then cued to provide subjective visual analogue scale (VAS) ratings of the preceding cooperative tapping trial using a two-button response box. After scanning, participants were requested to rate how “in sync” they felt with the VP on a numerical scale anchored from 0 (not in sync) to 10 (completely in sync) on a verbal, numerical ratings scale.

Stimuli

Auditory Stimuli

The VP was implemented as an auditory pacing signal generated online by a program written in MAX 4.5.7 (<http://www.cycling74.com>). The signal in each tapping task trial comprised a sequence of 22 tones. This sequence was programmed in such a way that it had a starting IOI of 500 ms, which could then vary (if $\alpha \neq 0$) based on the relative timing of the participant's previous tap. In adaptive conditions, a negative registered asynchrony (i.e. participant's tap preceded the tone) resulted in a shortening 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 and the next IOI was lengthened (Fig. 2A). The direction of this phase correction was the opposite of the correction expected to be applied in the participant's taps, as it should be if the VP (controlling the tones) "cooperates" with the participant (controlling the taps). The degree of the correction was varied by a fraction of the calculated asynchrony across five conditions in 0.25 steps, ranging from no phase correction ($\alpha = 0$, i.e. nonadaptive) to full correction ($\alpha = 1$, i.e. completely adaptive). It has been shown that, under normal circumstances, moderate degrees of cooperation improve the synchronization of the participant's taps with the tones, as evidenced by a reduction in the variability of the asynchronies. Specifically, a quadratic trend is usually observed across conditions with an optimal point of VP adaptivity described at approximately $\alpha = 0.25$, that is optimal adaptivity. For further details, please refer to Repp and Keller (2008). The tones 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-s tapping task trial. VASs were presented to obtain online ratings for "sense of influence over the tempo" and experienced "difficulty" of the synchronization task during of the preceding tapping task trial. It should be noted the instructions for the second of these ratings specified that participants should rate how difficult it was to synchronize with the VP. As we directly manipulated the coupling factor between the human-VP dyad, we expected an effect on the perceived difficulty of the interaction, measurable by this rating. Each scale was presented for 6 s. The "Influence" ("Einfluss" in German) scale was anchored by no influence ("kein") at the minimum and absolute influence ("absolut") at the maximum. Similarly, "Difficulty" ("Schwierigkeit") 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 to tap with their right index finger, starting with the third tone of the pacing signal, on an MR-compatible air-pressure tapping pad built in-house that was connected to the computer via a musical instrument digital interface. Participants received training on this task prior to scanning. Taps were recorded using MAX. A calculated transmission delay of 46 ms (from the tapping pad to the processing software MAX) was subtracted from tap registration times before asynchronies were calculated by the algorithm that controlled VP adaptivity.

MRI Data Acquisition

Functional imaging was conducted using a 3-Tesla Siemens Trio system. An echo-planar imaging sequence was used with a time repetition = 2000 ms; time echo = 24 ms; 36×3 mm axial oblique slices; 1-mm gap; voxel size = $3 \times 3 \times 3$ mm³; volumes = 699. Scans were acquired continuously throughout the experiment. High-resolution,

T1-weighted, structural scans (64 slices at $1 \times 1 \times 1$ mm³ voxel size) were obtained for each individual for anatomical overlay of brain activation.

Data Analysis

Ratings Data

Online ratings for influence over the tempo and difficulty to synchronize during tapping tasks were grouped according to the degree of VP adaptivity and the individual means and SDs calculated. To do so, VAS ratings were converted into numerical 0–10 ratings. A group mean and SD were calculated for the post-scan overall subjective rating of performance to be compared with objective measures of synchronized tapping. The threshold for statistical significance in analyses of ratings data was set at $P = 0.05$.

Tapping Data

Computer tone and human tap timings were analyzed (using SPSS) in terms of asynchronies, or differences between tap and tone onsets (i.e. tone onset times were subtracted from tap onset times, yielding negative asynchronies when taps preceded tones). A measure of performance stability and a measure of error correction (explained in greater detail in Repp and Keller 2008; see Supplementary Materials) are a SD and an autocorrelation function, respectively, of tap–tone asynchronies as a function of VP adaptivity. These data also provide information pertaining to the stability and subsequent predictability of the pacing signal onset. These tapping measures were compared both within and across participants, across conditions of VP adaptivity, and used here to analyze the functional magnetic resonance imaging (fMRI) data. The degree of error correction implemented by the human can be estimated based on the zero crossing point of lag-1 autocorrelation of the asynchronies across conditions. On the basis of the parabolic function across conditions of the SD asynchronies, one is able to derive the minimum x- and y-coordinates describing the point at which synchronization performance is optimized. As depicted in Figure 2C, performance is best when VP adaptivity is moderate and within the range of estimated human adaptivity. To ensure that this behavioral effect, reported previously by Repp and Keller (2008), would not be perturbed by scanner noise, a pilot study of the tapping task was performed under various background noise conditions (Supplementary Fig. 1). The threshold for statistical significance in analyses of tapping data was set at $P = 0.05$.

Imaging Data

Analysis of all neuroimaging data sets was performed using FMRIB Expert Analysis Tool (FEAT) version 5.63, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl). Pre-statistic processing included motion correction using "Motion Correction FMRIB's Linear Image Registration tool" (Jenkinson and Smith 2001), nonbrain removal using brain extraction tool (Smith 2002), spatial smoothing using a Gaussian Kernel of 4 mm full width at half-maximum and nonlinear high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with $\sigma = 40.0$ s). Registration included coregistration 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 "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 approach. Time-series statistical analysis was carried out using "FMRIB's Improved Linear Model" with local autocorrelation correction (Woolrich et al. 2001). Second-level analysis grouped the data of each participant's two scanning blocks, using the data from the first level of analysis. For group statistics, analysis was carried out using FEAT with higher-level analysis carried out using "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 (Worsley et al. 1992;

Friston et al. 1994). Contrasts performed explored activation during the five conditions of adaptive synchronization compared with baseline. Paired *t*-tests of the various levels of VP adaptivity were also compared (the results of which are reported in the Supplementary Materials). Each task trial was modeled as two defined events: initiation (perception of initiation tones where participants were instructed to listen to the desired tempo but not to tap) and synchronized tapping. Regression analyses were conducted to explore covariance of blood oxygen level-dependent signal change during tapping with acquired behavioral measures. Specifically, additional explanatory variables of objective task performance (SD of asynchrony) and subjective ratings of experienced difficulty were incorporated into the model. This was done by inputting individual means per condition and entering these as separate regressors. In one model we included both of these regressors, so as to explore the effect of the objective measure of task performance (being in or out of sync) while accounting for and removing the effect of the subjective assessment of synchronization difficulty. In two other separate analyses we explored the effect of each of these variables individually.

Results

Tapping with Differentially Helpful Partners: Manipulations of VP Adaptivity

On the basis of the dynamic interchange between the human participant and VP, we can extract information pertaining both to how and to what degree the human adapts to the VP and also how VP adaptivity affects human tapping behavior. Measures of mean asynchrony demonstrate that participants were able to maintain synchrony across conditions of VP adaptivity (VP adaptivity $F(4.60) = 2.882$, $P = 0.094$, repeated measures analysis of variance [ANOVA]—see Supplementary Table 1). Moreover, the behavioral variability data replicated the findings of Repp and Keller (2008)—a parabolic function of performance instability (SD asynchronies) across levels of α (Fig. 2C, Supplementary Table 1)—tracing the effect of varying VP adaptivity on human tapping performance. Using SD asynchrony as a measure of task performance, we observed that task performance is “optimal” (i.e. instability is lowest) around $\alpha = 0.25$ – 0.5 with poorer performance on either side of this range (VP adaptivity main effect $F(4.60) = 7.708$, repeated measures ANOVA, $P = 0.005$; polynomial trend contrasts in the ANOVA detected a significant quadratic trend $F(1.15) = 40.655$, $P < 0.0001$). From this we see that synchronization performance was facilitated by a small amount of VP adaptivity. By contrast an overly adaptive and therefore unreliable partner impeded task performance. Therefore, from this point onwards, data will be described in terms of “helpful” or optimally adaptive conditions ($\alpha = 0.25$ and 0.50) and “unhelpful” or overly adaptive conditions ($\alpha = 0.75$ and 1). Additionally, from the tapping data we were able to explore the nature of human adaptivity in response to the VP by estimating the amount of error correction employed by the human tapper (human α : mean and SE = 0.54 ± 0.09 ; range: 0.24 – 0.63). It is interesting to note that the range of human error correction within our cohort matches the range of VP adaptivity where performance was optimized (i.e. SD asynchrony was lowest).

To explore the more subjective appraisal of the human–VP interaction, we collected and analyzed VAS ratings of perceived task difficulty. Trial-by-trial subjective ratings of task difficulty (perceived difficulty of synchronizing) were grouped

by condition of VP adaptivity and averaged across participants. Group mean perceived task difficulty differed significantly across conditions (see Supplementary Table 1). As expected, the subjective ratings mirrored objective measures of task performance and a quasi parabolic function across conditions of VP adaptivity was observed (VP adaptivity main effect $F(4.60) = 20.181$, $P < 0.0001$; repeated measures ANOVA, quadratic trend $F(1.15) = 23.581$, $P < 0.0001$). Furthermore, synchronizing with an overly adaptive partner was perceived to be more difficult than synchronizing with an optimally adaptive partner ($\alpha: 1 > 0.25$, $t(15) = 5.372$ $P < 0.001$).

Being and Feeling in Sync: Objective and Subjective Measures of Task Performance and Task Difficulty

An advantage of the present design was that the effect of a variably adaptive partner on entrainment success was reflected in both objective and subjective measures. Therefore to identify the neural correlates of being and feeling in sync, we incorporated both objective and subjective measures of task performance (averaged SD asynchronies per condition and subjective VAS ratings of task difficulty, respectively) into analyses of the fMRI data. The first analysis identified areas activated as a function of the objective measure of being in sync with the VP. Specifically, this regression analysis identified brain areas in which activity varied as a function of SD asynchrony at each level of VP adaptivity, that is each participant’s parabolic function. Positive correlations were indicative of regions that increased in activity when the participant and VP were “out of sync” (higher SD). This contrast revealed an extensive network, including the anterior insula, inferior and superior frontal gyri (IFG and SFG, respectively), the

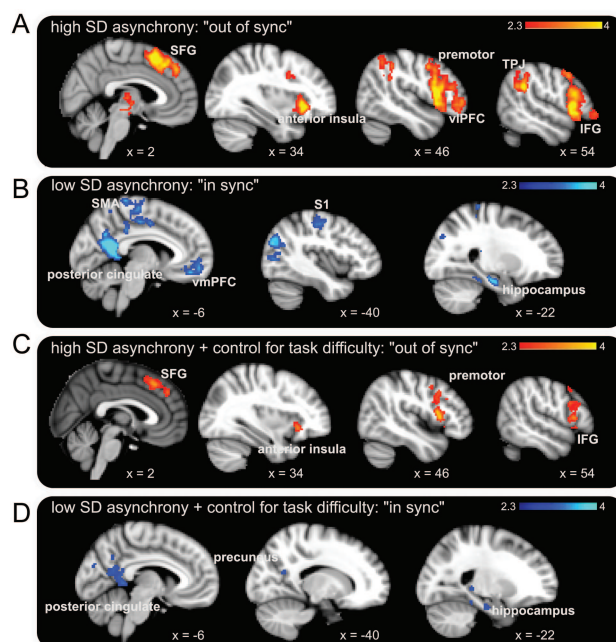


Figure 3. In or out of sync with an adaptive virtual partner. Group mean contrast (mixed effects, $Z = 2.3$; $P = 0.05$, corrected) of covariance with objective task performance measure (SD asynchrony): (A) “out of sync” or high SD asynchrony, (B) “in sync” or low high SD asynchrony, (C) “out of sync” while controlling for task difficulty and (D) “in sync” controlling for task difficulty.

ventrolateral prefrontal cortex (vlPFC), and inferior parietal lobe (Fig. 3A, Table 1). By contrast, being “in sync,” that is lower SD of asynchronies, correlated with increased midline activation of structures including the ventromedial prefrontal cortex (vmPFC), hippocampus, supplementary motor area (SMA), primary somatosensory cortex (S1, extending into primary motor cortex, M1), posterior cingulate (PCC) and precuneus (PCu) (Fig. 3B, Table 1).

Given the parabolic trend across conditions of perceived task difficulty ratings, we repeated the SD asynchrony regression while controlling for experienced difficulty. Overall, we again observed two distinct patterns of activation with right hemispheric activation of the anterior insula, SFG, IFG and dmPFC correlated with being “out of sync,” that is higher SD of asynchronies (Fig. 3C, Table 1) and a more restricted network associated with being “in sync.” The latter network consisted of midline PCu, PCC, and hippocampus (Fig. 3D, Table 1). When pairwise contrasts were calculated between different levels of VP adaptivity, as opposed to each subject’s parabolic function as in the analysis presented above, largely similar results were obtained (see Supplementary Tables 1–4 and Supplementary Fig. 2).

Finally, we performed a regression analysis to identify brain regions whose activity correlated with subjective ratings of task difficulty. Consistent with the other analyses, we found increases in perceived synchronization difficulty to correlate with greater activation of the right IFG, right AI, posterior dmPFC, bilateral vlPFC, SFG and inferior parietal activity in the region of the temporoparietal junction (TPJ), whereas decreases in perceived task difficulty activated the SMA, S1/M1, vmPFC, and the hippocampus (Table 2).

Table 1

Neural correlates of objectively being more or less in sync with the VP

VP adaptivity	Regions	Z-max	Peak MNI coordinates				
			x	y	z		
Controlling for task difficulty							
Low SD async	Hippocampus	L	3.69	−34	−34	−12	
	Precuneus	L	2.70	−12	−58	18	
	Posterior cingulate	R	2.88	6	−58	20	
	Cuneus cortex	L	2.71	−14	−94	24	
High SD async	Inferior frontal gyrus	R	3.95	48	14	8	
	Anterior insula	R	3.57	2	28	46	
	Dorsomedial PFC	R	2.62	46	6	44	
	Superior frontal gyrus	R	3.05	2	44	38	
		L	3.25	−2	28	44	
Without controlling for task difficulty							
Low SD async	Hippocampus	L	3.95	−26	−24	−18	
		R	4.96	34	−26	−16	
	Posterior cingulate	L	4.2	−2	−54	22	
	Precuneus	L	3.17	−2	−56	62	
		L	2.67	−6	−58	34	
	Anterior cingulate	R	3.1	6	28	−10	
	SMA	R	3.98	0	−4	46	
	Ventromedial PFC	R	3.2	10	54	−6	
	S1 (extending into M1)	L	3.4	−40	−24	52	
		R	2.72	40	−24	52	
	Cuneus cortex	L	3.59	−14	−92	26	
	High SD async	Anterior insula	L	4.08	−30	26	−4
			R	5.22	36	22	−4
		Superior frontal gyrus	R	4.81	4	20	52
Temporoparietal junction		L	4.09	−62	−48	36	
		R	4.39	54	−42	28	
Thalamus		R	4.46	10	−12	6	
Ventrolateral PFC		R	4.53	8	−12	6	
Inferior frontal gyrus		R	4.64	50	14	2	

Coordinates in MNI space and associated peak voxel Z-scores. $P < 0.05$ corrected for multiple comparisons.

Discussion

Cooperative synchronization is intrinsic to most social physical interpersonal interactions. However, the neural underpinnings of cooperation in a dynamic, two-person context are still poorly understood (Schilbach 2010). This study therefore examined the neural substrates of cooperativity in a task that captured the temporal demands of dynamic joint action by scanning individuals as they tapped in synchrony with an adaptive VP. By varying coupling strength (by varying $VP\alpha$) between the interacting dyad, we found effects on objective measures of tapping performance, subjective evaluations of task difficulty, and concomitant activation of two distinct brain networks.

We replicated a previous finding that synchronization is best at certain (optimal) degrees of adaptivity (Repp and Keller 2008; Konvalinka et al. 2010) that correspond to levels of α that are within the typical human range (thus “like me” from the perspective of a human agent). Under such circumstances, timing variations across agents are well matched and relatively easy to predict based on mechanisms related to internal models and the covert mental simulation of action (Keller 2008). We took advantage of the fact that the social implications of synchronization ability, that is how easy or “like me” someone is to synchronize with, can be implemented in the simplest of SMS tasks—tapping to a quasi-stable-pacing signal, and manipulated by a single parameter that governs how adaptable a synchronization partner (the pacing signal) is, to explore the brain’s responses to variation in the social implications of a VP’s synchronization style.

Our manipulation of VP behavior across a range from helpful to unhelpful revealed that objective and subjective measures of synchronization quality were positively correlated and varied with how adaptable the VP was. At a neural level, the relative activation of each of two, typically anticorrelated, brain networks depended on the level of adaptivity of the VP. As elaborated below, one of these networks, often referred to as the DMN, is associated primarily with self-referential, social, and emotional processes while the other is commonly associated with cognitive control. As such, we posit that the paradigm employed here allows us to link basic

Table 2

Neural correlates of perceived difficulty of the interaction

VP adaptivity	Regions	Z-max	Peak MNI coordinates				
			x	y	Z		
Increasing task difficulty	Anterior insula	R	4.52	38	22	−2	
		L	3.42	−36	26	−6	
	Posterior dorsomedial PFC	R	4.55	4	16	52	
		L	3.75	−30	26	−6	
	Temporoparietal junction	L	3.95	−62	−48	36	
		R	4.37	54	−44	28	
	Inferior frontal gyrus	R	3.98	56	20	−4	
		R	2.40	56	38	8	
	Decreasing task difficulty	Superior frontal gyrus	R	4.41	4	16	56
			R	4.18	2	−6	46
Ventromedial PFC		L	3.99	−4	42	−16	
		R	3.63	48	−76	6	
Inferior parietal lobule		L	3.23	−28	−30	−16	
		R	4.78	34	−26	−18	
Hippocampus		L	3.28	−38	−30	54	
		R	3.01	36	−28	56	
S1 (extending into M1)		L	3.28	−38	−30	54	
		R	3.01	36	−28	56	

Coordinates in MNI space and associated peak voxel Z-scores. $P < 0.05$ corrected for multiple comparisons.

mechanisms of entrainment to the dual brain networks observed in a manner that has implications for understanding socio-emotional aspects of interpersonally coordinated behavior (Fig. 1). Behavioral studies have shown that engaging individuals in synchronized activity, be it walking, singing, playing musical games, or rocking, is a remarkably simple and effective way of increasing subsequent cooperation between those individuals (Wiltermuth and Heath 2009; Kirschner and Tomasello 2010; Valdesolo et al. 2010). Music often generates an almost compulsive urge to move, and is a particularly effective vehicle for synchronizing actions of many individuals because it provides a temporal scaffold, a pulse, with which to synchronize. Thus, important aspects of human culture and social functioning appear to be linked by the remarkably simple phenomenon of synchronization and its basis in entrainment (Merker et al. 2009).

Being in Sync and Socio-emotional Processing

Integration of Motor and Default-Mode Network Areas

Of particular interest was the activation of the SMA and S1/M1 that accompanied the cortical midline activations during the optimally adaptive condition (Fig. 3B; Supplementary Fig. 2). Activation of the SMA is usually not observed in association with DMN activation; thus the activity of these sensorimotor regions in conjunction with the midline frontoparietal network may highlight a critical link between the action component of the dyadic interaction and the socio-affective components of cooperation.

The relevant link may be via the PCu (Margulies et al. 2009). The anterior dorsal zone of the PCu is regarded as a sensorimotor region of the PCu, being linked anatomically and functionally to both the SMA and auditory cortex in the posterior superior temporal gyrus. Within the DMN, we observed activation in a part of the transitional zone between the PCC and PCu that exhibits a “limbic” pattern of connectivity with the ventral medial prefrontal cortex, medial temporal lobe, and the rest of the PCu (Margulies et al. 2009).

The PCu 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). Thus, activations restricted to the functional networks associated with sensorimotor and limbic zones of the PCu/PCC regions during successful coupling with a VP suggest that their coactivation is part of a mechanism supporting the mental state that permits well-synchronized (entrained) action between individuals to translate to (positive) socio-emotional processing.

It is interesting to note that these additional components, both sensorimotor and affective, are correlated with perceived difficulty of the interaction task. An important distinction regarding the concept of “difficulty” should be borne in mind when interpreting the fMRI results, namely, the difference between task difficulty and the difficulty of the interaction between the participant and the metronome. Throughout our experiment, the nominal task difficulty of synchronizing taps with a quasi isochronous sequence of tones remained constant. Task difficulty would have increased had we asked participants to tap along with nonisochronous sequences, that is rhythmic patterns that varied in metric complexity as determined by the ratios of the durations between successive

tones. Instead, our manipulation varied the difficulty of the interaction of the simplest possible SMS task. This variation in difficulty manifest itself in correlated objective and subjective measures, allowing us to identify those brain areas involved in the sensorimotor-coupling task that were less and more reflective of the experiential states of the participants.

Entrainment, Imitation, and Social Cognition

Entrainment is typically thought of as a low-level mechanism that allows individuals to coordinate their actions with others. As such, in the following study we present a novel method for exploring at the most basic level of social cognition how individuals (in a cooperating dyad) might temporally adapt to one another so as to synchronize their movements. Entrainment and behavioral imitation have potentially related implications for social cognition (Phillips-Silver and Keller 2012). Given the extensive literature on imitation, we briefly contrast the two concepts. While entrainment is largely restricted to situations in which there is a discernible steady pulse with which a person synchronizes—in that sense imitating the time intervals in the pacing signal, imitation encompasses a broader range of relationships that do not necessarily conform to a rigid temporal scaffold, for example imitating someone’s facial expression at some later point in time. Although our focus in this paper is on entrainment, interpreting our findings in relation to neuroimaging studies of imitation and shared mental representations is of some utility.

In general, action synchronization and social interaction rely on executive and evaluative functions that are consistently associated with the network of regions functionally connected to the PCC/PCu (Cavanna and Trimble 2006; Margulies et al. 2009). Here we focus in particular on PCC/PCu and the vmPFC component of this network. Across studies, activations within the region of the vmPFC that we found to be more active during successful coupling with the VP are consistently observed when individuals make judgments about items in relation to themselves (self-referential processing), judgments about close others, and sequence learning (Van Overwalle 2009). Specifically, the activations we found have been observed in studies of cooperation (McCabe et al. 2001; Decety and Chaminade 2003), perspective taking and shared task representation (Ruby and Decety 2001; Sebanz et al. 2007), and mental simulation of action (Ruby and Decety 2001). Activation of the vmPFC during conditions (“optimal”) when synchronization was most precise may be associated with an assessment of “rightness” of the behavior (Moscovitch and Winocur 2002). This is consistent with an interpretation that the vmPFC is sensitive to the subjectively experienced difficulty of the interaction, as suggested by our observation that activity in the vmPFC is not further modulated by objective task performance once the subjective component is removed. This prefrontal area has also been shown to be conditionally activated during mentalizing when the postscanning ratings of self/other similarity were highest (Mitchell et al. 2005). Interestingly, it has been shown that this mentalizing or perspective taking can result in self-other merging and that this overlap may be an effective means of increasing behavioral mimicry (Galinsky et al. 2005). The process of self/other merging is also of interest in that it is commonly reported to occur during strong experiences with music (Gabrielsson and Lindstrom Wik 2003; Becker 2004).

It was noteworthy that synchronization was optimized when the degree of adaptivity (error correction) of the human was within the range of adaptivity programed into the VP (human α range: 0.24–0.63 vs. VP α optimal conditions: 0.25–0.5, see Fig. 2C). We posit that it is within this range that the partner who is being synchronized with can be assessed as “like-me.” In other words, sensorimotor coupling becomes a form of shared mental representation (Meltzoff 2007), and a vehicle to self-other merging.

Being Out-of-Sync

As many musicians know, the ecstatic feelings that often arise when each person’s part in an ensemble interweaves seamlessly with the others—when all the players are “in sync” or in “the groove”—are difficult to come by when the coordination of timing between the players is not quite right. Even if not an outright “train wreck” characterized by the total loss of coordination, the experience is one of struggle to make the parts fit, and the socio-emotional experience is diametrically opposed to the desired one. Perhaps unsurprisingly, we found the neural signature of the struggle to synchronize with an overly adaptive partner to be reflected in engagement of components of a network that exists in an anticorrelated relationship to the DMN (Fox et al. 2005).

As SMS shifted from an automatic mode to a more difficult controlled processing mode, a number of cognitive control areas became active (Stephan et al. 2002). These included the right anterior insula, lateral prefrontal cortex, and the SFG in the posterior medial prefrontal cortex. Paradigms involving response conflict routinely engage these areas (Amodio and Frith 2006; Van Overwalle 2009), and the lateral prefrontal cortex generally serves strategic action planning needs (Tanji and Hoshi 2008). It is thought that cooperating with an overly adaptive (unhelpful) partner may elicit effortful albeit intermittent period correction, adjustments which result in a focus on maintaining the pulse based on an internal timekeeper (Repp and Keller 2008). To focus on the pulse under such conditions there is a need to inhibit, or dampen automatic phase correction responses to some degree (Repp and Keller 2004). Thus, activation of the right anterior insula and vIPFC could be seen as a form of inhibitory control (Hampshire et al. 2010).

The region around the right anterior insula and adjacent inferior frontal gyrus has been shown to be engaged during cooperative and competitive games (Decety et al. 2004). Within our theoretical framework (Fig. 1), it has also been suggested that these areas play a central role in switching of brain activity between default-mode and cognitive control networks (Sridharan et al. 2008). This region, along with the TPJ, is part of a ventral stimulus-driven attentional orienting network (Corbetta and Shulman 2002) that we found to become more active as the synchronization task became more difficult and performance deteriorated. These same areas are engaged as a person recovers from an attentional lapse during a selective attention task, that is, during a shift from transient activation of the DMN to activity in attentional control areas (Weissman et al. 2006).

Conclusions

To summarize, we find that synchronizing with an optimally adaptive VP allows the shared sensorimotor coordination goal

to be realized with greater ease, leading to reduced need for cognitive control resources. The reduction of activity in cognitive control areas is associated with a concomitant increase in activity in cortical midline regions associated with self-referential and socio-emotional processes. We posit that the shift of brain activity to these regions allows for reflection on the seemingly effortless quality of the ongoing interaction with the partner and other prosocial thoughts. This may be akin to the state of being in the groove. Similarly, optimal adaptivity of the synchronization partner may imbue the interaction with a heightened sense of flow, which is experienced when a person succeeds at performing a task that is at the limit of his or her ability (Csikszentmihalyi 1990). Although isochronous tapping may not meet the criterion of a challenging activity, one can imagine that any action on the part of the partner that reduces perceived discrepancies in the interaction could be misattributed to one’s own improved performance on the task, thereby inducing a sense of flow. Taken together with the related constructs of groove and flow, our results pave the way for future studies aimed at understanding the dynamics of temporally precise, deeply rewarding interpersonal entrainment that characterizes joint activities such as group music making (Hove and Risen 2009).

We end with a commentary on the concept of optimal task performance in cognitive neuroscience. The prevailing concept of good performance on psychological tasks that require interaction with an external stimulus is closely linked to cognitive control. Influential labels for the two networks discussed here have been task-positive (cognitive control) and task-negative (DMN, socio-emotional), a view that is reinforced by the fact that lapses in performance on attention demanding tasks are associated with increased activity within DMN structures (Weissman et al. 2006; Congdon et al. 2010). Although cognitive control appears to be important for mediating sensorimotor interactions in which the adaptivity of partners to each other is not optimal and synchronization becomes more difficult, optimal performance in SMS is characterized by a state in which activity in cognitive control areas is reduced and activity within socio-emotional areas increases. We suggest that this type of task–brain coupling may help explain why activities in which the actions of individuals are synchronized well and seemingly without effort promote positive affect and greater social cohesion.

Supplementary Material

Supplementary material can be found at: <http://www.cercor.oxfordjournals.org/>.

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