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An fMRI-study of leading and following using rhythmic tapping

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ABSTRACT

Leading and following is about synchronizing and joining actions in accordance with the differences that the leader and follower roles provide. The neural reactivity representing these roles was measured in an explorative fMRI-study, where two persons lead and followed each other in finger tapping using simple, individual, pre-learnt rhythms. All participants acted both as leader and follower. Neural reactivity for both lead and follow related to social awareness and adaptation distributed over the lateral STG, STS and TPJ. Reactivity for follow contrasted with lead mostly reflected sensorimotor and rhythmic processing in cerebellum IV, V, somatosensory cortex and SMA. During leading, as opposed to following, neural reactivity was observed in the insula and bilaterally in the superior temporal gyrus, pointing toward empathy, sharing of feelings, temporal coding and social engagement. Areas for continuous adaptation, in the posterior cerebellum and Rolandic operculum, were activated during both leading and following. This study indicated mutual adaptation of leader and follower during tapping and that the roles gave rise to largely similar neuronal reactivity. The differences between the roles indicated that leading was more socially focused and following had more motoric- and temporally related neural reactivity.

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Lead; follow; Functional magnetic resonance imaging; tapping; synchronizing

Introduction

Leading and following is a relationship where the leader and follower are synchronizing and joining actions in accordance with what they aim to do together. The complementation is more than mere synchronization of the two roles (Koban et al., 2019; Sacheli et al., 2013a). In order to investigate social interaction, the use of music and rhythms have emerged as a promising method as they form the base for social behavior (D'ausilio et al., 2015). Most social actions are rhythmic, such as turn-taking in a conversation or adaptation in timing when singing together (de Reus et al., 2021; Warner & McGrath(ed), 1988). Rhythms, mostly tapping, have been widely used for research purposes with the participants interacting with a computer (Repp & Su, 2013; Repp, 2005). Joint tapping with other persons promotes prosocial behavior such as being more helpful in children (Kirschner & Tomasello, 2010) and to help pick up dropped items in adults (Kokal et al., 2011). In this study, two participants at the time take turns in leading and following each other in simple rhythms using finger tapping.

To lead during a tapping exercise has previously been shown to activate the right anterior insula, the inferior frontal gyrus (IFG), the superior temporal gyrus (STG), the temporo parietal junction (TPJ) and the inferior parietal lobule (IPL), which have been associated with cognitive control and adaptation (M. Fairhurst et al., 2014). Skilled dancing leaders engage areas for motor control and planning (supplementary motor area (SMA), cingulate motor area, premotor cortex, and cerebellum) (Chauvigné & Brown, 2018) and leaders seem to combine modeling a task with identifying the strategy of the follower (M. Fairhurst et al., 2014). To follow is not merely to synchronize with, but also to complement and foresee the leaders' actions (Aschersleben, 2002; Koban et al., 2019; Sacheli et al., 2013b). In line with this, skilled followers have been shown to activate neural areas known to be recruited during mentalizing, such as medial prefrontal cortex, posterior cingulate cortex, TPJ and superior temporal sulcus (STS) (Chauvigné & Brown, 2018).

In this fMRI (functional Magnetic Resonance Imaging) study, a new minimal model for social interaction is used, finger tapping of a simple rhythm to explore leading and following. Two persons form a couple and take turns in leading and following each other. The roles have different responsibilities. The leader initiates action

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tapping her/his pre-learnt rhythm and the follower taps along in the rhythm. This new model allows for all participants, which are non-experts, to both lead and follow as well as to adopt to each other. It also opens a way to measure the neural reactivity of leader and follower relative to the other.

The aim of the study is to define similarities and differences in neural activations representing leading and following. Our hypotheses are that activations will be mostly similar for leading and for following, during both tasks with increased reactivity in the STG, the TPJ and IPL and possibly IFG but lead rendering higher reactivity in the STS and follow in the STG.

Materials and Methods

Participants

Twenty-one right-handed persons (7/14 females/males, mean age 30.7 (SD $\pm$10.6)) took part in the study. All participants reported themselves to be healthy, without formal musical education or documented professional leadership expertise.

The participants gave their written consents for taking part in the experiment, in accordance with the regulations of Tokyo Institute of Technology and all procedures were in accordance with protocols approved by the local institutional review board (dnr. 2019002). Processing of the data in Sweden was approved by the Swedish ethical review authority (dnr. 2021–0548–01)

Procedures

Questionnaires

All participants filled out questionnaires (see supplementary information) about their prior experience of informal leadership and followership, exemplified with what role the person takes when enjoying a hobby or during leisure time with friends. They rated their experience of each situation on a scale from 1 to 5. They also rated how comfortable they were in a leading and following role, exemplified by the same kinds of situations, on a scale from 1 to 5. After the experiment, the participants filled out another questionnaire about how it was to lead and follow in these circumstances, again on a scale from 1 to 5.

Tapping together

The day before the MRI session, each participant received an e-mail with instructions to learn to tap a 5 sec simple rhythm with the right-hand index finger, as shown in an example in Figure 1. The rhythms consisted of 10–12 beep-sounds in compositions of short (0.3 sec) and long (0.6 sec) beats. The participants received one personal rhythm both in writing and as a 30 sec sound-file where the rhythm was repeated 6 times, seamlessly. The sound files were recorded with 90 bpm. The personal 5 sec rhythm was to be repeated over and over all through the experiment. All personal rhythms were different.

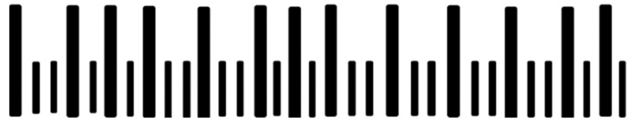

Figure 1. A schematic representation of a rhythm. Large bars indicate a tap and small bars indicate silence.

Participants were instructed to practice to tap the rhythm on a table, or the like, using their right index finger until they felt sure that they know the rhythm by heart.

On the day of the experiment, two participants took turn in tapping the respective rhythms together, one person tapping his/her pre-learnt rhythm and the other one trying to follow. In every block each participant performed all tasks: lead, follow, tap alone and listen to the other participant tapping. Each experiment was divided into 3 sessions (Figure 2), composed of pseudo-randomized trials within which each person acted both as leader and as follower (Figure 3).

The participants did not want to see each other, as one was placed inside the MR-scanner and the other was in an adjacent room (Figure 3), but identical visual instructions were presented on computer screens using Presentation® (Neurobehavioural systems Inc.). They used their right index finger to tap on a fiberoptic response pad system adapted for use with MRI (Current Designs Inc.) which recorded the time of pressing and releasing the buttons of both participants during the experiment. The participants heard the sound of the others´ tapping in their headphones but did not hear their own tapping. Thus, in the condition of tap alone there were no sounds in the headphones.

Synchronicity in tapping

For all participants, double taps (taps interspaced with less than 0.2 sec) and extreme outliers (inter-tap-intervals longer than 2 sec) were excluded from the analysis. For each task, the string of taps for the leader was used as a model for the correct rhythm. The taps of the follower were then matched to this rhythm and the relative difference between each tap calculated. Thus, synchronicity is defined as the time

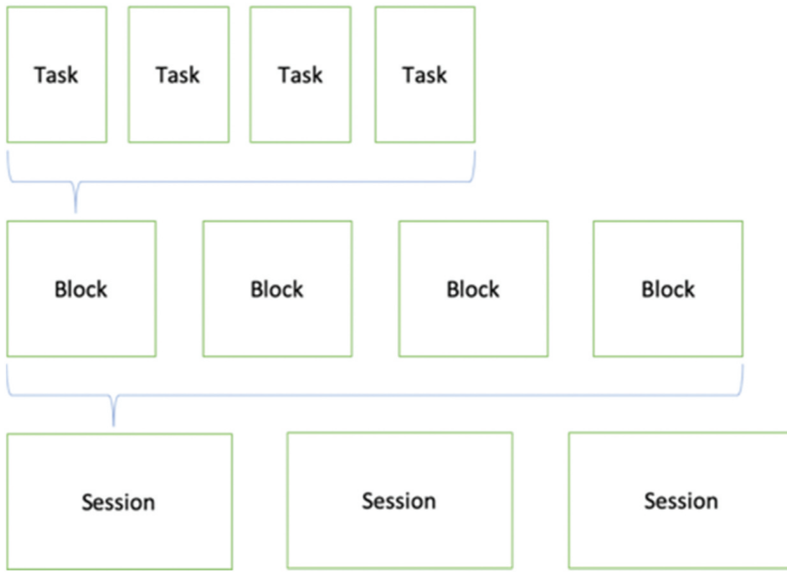

Figure 2. The experimental design. Tasks are lead, tap alone, follow and listen.

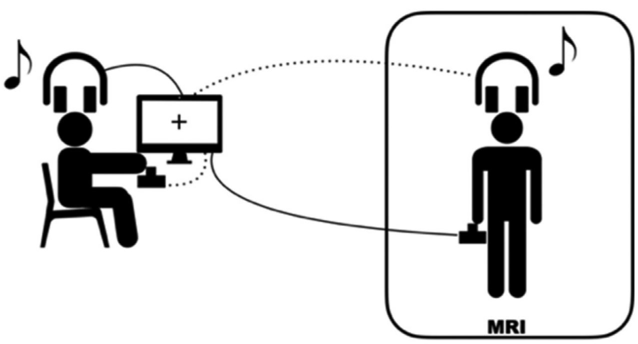

Figure 3. Two participants at the time were interacting using the rhythms. One person sat in front of a computer and tapped the rhythms with the right-hand index finger on a button. The sound of the other persons tapping was heard via the headphones. The other person lay in the fMRI-scanner in the next room, with the same set-up.

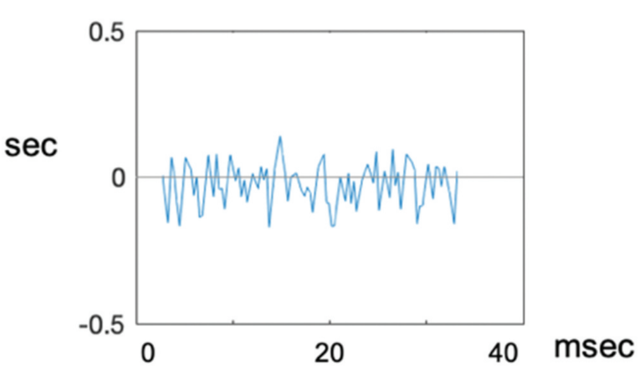

Figure 4. An example of temporal synchronicity in milliseconds between a leader and a follower during tapping.

difference between the tap of a leader and a follower, i.e., the relative adaptation of the follower to the leader´s tapping rhythm. Figure 4 is an example of a follower's temporal synchronicity with the leader, depicted with the blue line. The x-axis shows duration of task in milliseconds and the y-axis shows relative time between taps in milliseconds (msec). The leader is assumed to have perfect tapping, represented by the x-axis. The blue line thus represents the follower´s tapping in relation to the leader.

Data acquisition

fMRI data was acquired using a 3T Signa scanner with a 9-channel array coil (General Electric Company, Fairfield, USA). The scanning took place at the Tokyo Institute of Technology, Tokyo, Japan.

For the T1-weighted structural image, we used an SPGR Pulse-sequence with an echo time of 3.1 msec, a repetition time of 7.7 ms and a flip angle of 11°. The field of view was set to 260 × 260 × 240 mm^3 and an in-plan matrix of 256 × 256, with a voxel size of 1 × 1 × 1.2 mm^3. The 200 slices had slice gaps of 0.8 mm. Slices were acquired in an ascending order in the axial plane. For functional MRI, we used the blood-oxygenation-level dependent T2*-weighted image sequence with a single-shot gradient echo planar imaging (EPI) sequence. Imaging was performed with an echo time (TE) of 30 msec, repetition time (TR) of 2500 msec and a flip angle of 80°. The field of view was set

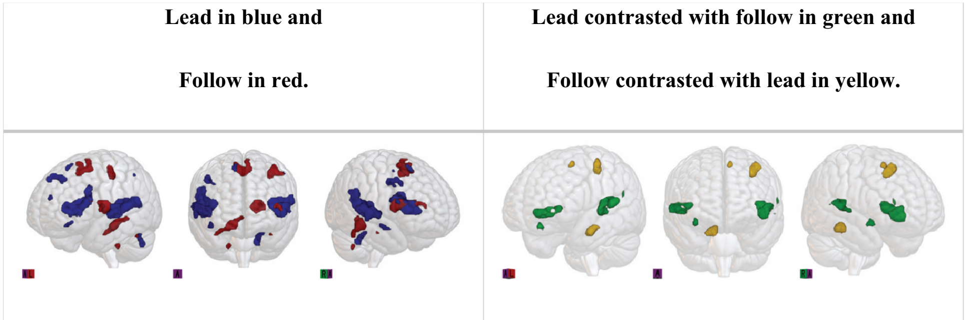

Figure 5. In the left panel, neural reactivity for lead(blue) and follow(red), respectively. p=0.05 (FWE). In the right panel, contrasts of lead and follow, with the neural reactivity for lead (lead-follow) >(follow-listen) in green and for follow (follow-listen) >(lead-tap) in yellow. p = 0.05 (Fwe).

to 212 × 212 mm^2 with a voxel size 3.3 × 3.3 × 3.2 mm^3, 40 slices with a slice gap of 0.8 mm. Two hundred and sixty-six dynamic scans were acquired per session.

MRI data

Preprocessing

Preprocessing of data was performed in Statistical Parametric Mapping 12 (SPM 12, Welcome Center for Neuroimaging, UK), running on MATLAB R2018b (MathWorks Inc., Massachusetts, USA). First, the functional images were realigned to the mean functional image to correct for head movement during scanning. Participants that moved more than 2 mm or 2° was excluded from further analyses. The realigned images were then slice-time corrected using the middle slice as the reference slice. The functional images were then co-registered to the structural T1-weighted image and the structural images segmented into gray matter, white matter, CSF, soft tissue and other, using SPM's segmentation routine. Both structural and functional images were subsequently spatially normalized to Montreal Neurological Institute (MNI) standard brain-space, using the forward deformation field obtained during segmentation. Finally, the images of voxel size 2 × 2 × 2 were smoothed using an 8 mm full-width at half maximum Gaussian smoothing kernel.

Statistical analyses

For each participant, the following contrast-maps were created: the tasks of lead and follow, respectively; leading without the activity for tapping (i.e., lead minus tap) and following without the activity for listening to the leader tapping (i.e., follow minus listen). Finally, lead minus tap and follow minus listen were contrasted against each other. The six contrast maps per participant were then used in the whole brain, random effect, group-level analysis. Group analysis was done using two sample t-tests with a p-value of 0.05, family-wise error (FWE)-corrected. A conjunction analysis of lead and follow was conducted with a p-value of 0.05 (FWE). Brain region identification for cluster peaks was done in SPM using Anatomical Automatic Labeling (AAL) (Tzourio-Mazoyer et al., 2002). To asses cluster spread MRIcroGL (Rorden & Brett, 2000) was used, with atlases AAL3 (Rolls et al., 2020), Atlas of Intrinsic Connectivity of Homotopic Areas (AICHA) (Joliot et al., 2015) and spmMorphometrics. All results are presented in MNI-coordinates.

Results

Among the 21 participants, one male participant could not enter the MR-scanner for medical reasons and one female was excluded due to excessive head movements, leaving 19 participants in the fMRI analysis. The average self-rated leadership experience was 3.4 and the participant reported levels of comfort in leading to 3.3 and partaking as a follower at 4.0. After the experiment, they rated the degree of their own success in leading, with a mean of 3.7, and in following 4.1. See Table 1 for the demographic information.

Tapping synchronicity

The mean relative synchronicity between leaders and followers was 0.0026 sec, with a standard deviation of 0.169 sec.

Brain activity

For all participants lead and follow resulted in largely similar activations. See supplementary Table S1 for details. In a conjunction analysis, Table 2, reactivity

Table 1. Demographic information of participants in this study.

Participants					Questions prior to experiment			Questions after experiment	
Number of participants	*Age (years)*	*Level of education*	*Handedness*	*Formal Musical and Leadership education*	*Self-rated leadership experience (1= not experienced, 5= very experienced)*	*Self-rated comfortability in leading (1= not comfortable, 5= very comfortable)*	*Self-rated comfortability in following (1= not comfortable, 5= very comfortable)*	*Self-rated degree of success in leading (1=low, 5=high)*	*Self-rated degree of success in following (1=low, 5=high)*
21 (7 women)	21–53, mean 30.9	High school graduates	17 right handed, 2 left handed.	None with formal education in music or leadership.	Mean 3.4 (SD 1.2)	Mean 3.3 (SD 1.4)	Mean 4.0 (SD 0.82)	Mean 3.7 (SD 1.2)	Mean 4.1, (SD 0.78)

Table 2. Conjunction analysis lead and follow.

Conjunction of lead and follow				
Conjunction: Lead ∩ Follow, $p < 0.05$ (FWE)				
Brain area	Right (R) or Left (L) hemisphere	Nbr of voxels	Peak Z-value	Peak Cluster MNI-coordinates
Superior Temporal gyrus	L	1196	6.36	−44–32 12
Postcentral gyrus	L	276	6.03	−50–12 52
Supplementary motor area	L	183	5.71	−4–4 62
Superior Temporal gyrus	R	480	5.65	44–30 16
Cerebellum IV, V	R	18	5.44	8 -58 -8
Supramarginal gyrus	R	2	4.95	64–18 18
Rolandic operculum	L	1	4.69	−48 4 8

Table 3. Brain reactivity during leading contrasted to tapping and following contrasted to listening.

Lead Contrast: Lead > Tap, $p < 0.05$ (FWE)					Follow Contrast: Follow > Listen, $p < 0.05$ (FWE)				
Brain area	Right (R) or Left (L) hemisphere	Nbr of voxels	Peak Z-value	Peak Cluster MNI coordinates	Brain area	Right (R) or Left (L) hemisphere	Nbr of voxels	Peak Z-value	Peak Cluster MNI coordinates
Superior temporal gyrus	L	1535	6.20	−44–32 10	Cerebellum IV, V	R	322	6.01	16 -58 -14
Superior temporal gyrus	R	1080	5.60	48–36 14	Thalamic VPL	L	322	5.80	−20–24 10
Middle frontal gyrus	R	78	5.11	48 26 44	Precentral gyrus	L	207	5.42	−40–16 56
Cerebellum crus II	L	7	4.76	−18 -80 -42	Supplementary motor area	L	255	5.37	−8–6 58
Inferior frontal gyrus, triangular part	R	3	4.66	50 22 18	Rolandic operculum	L	43	5.26	−44–2 10
Supramarginal gyrus	R	2	4.65	58–46 30	Cerebellum VIII	R	23	5.26	20 -64 -44
					Cerebellum crus I	L	8	4.90	−36 -60 -30
					Putamen	L	3	4.81	−24 4 16

during leading and following showed shared areas in the superior temporal gyrus – spreading into the STS and TPJ, the left post central gyrus (somatosensory cortex), the left SMA and right cerebellum, as well as smaller activations in the right supramarginal gyrus and the left Rolandic operculum.

Lead

When contrasted to tapping (Table 3 and Figure 5), leading still showed the most activity in the left and right STG, spreading over the superior temporal sulci and planum temporale in both hemispheres. On the right-side reactivity also spread over the TPJ to the angular gyrus. Clusters were also present in the right middle frontal gyrus (MFG) and the left cerebellum, crus I and II, as well as in the triangular part of the right IFG and the right supra marginal gyrus in the inferior parietal cortex (IPC).

Follow

To follow, as contrasted to listening (Table 3 and Figure 5), the result was predominantly activity within the right cerebellum IV, V, the left thalamus, the left precentral gyrus (motor cortex), the left SMA, the left Rolandic operculum, the right cerebellum VIII, the left cerebellum, crus I and putamen.

Comparing lead and follow

In order to further single out the activity associated with leading, the contrast lead vs. tapping was contrasted against follow vs. listening, and vice versa, as shown in Table 4 and Figure 5. This showed that leading was more associated with reactivity in the right anterior insula and the right and left STG. These large clusters spread into the superior temporal sulci and planum temporale in both hemispheres.

Comparison of the contrasts follow to listen with lead to tap gave activity in the right cerebellum IV and V, the left somatosensory cortex and the left SMA.

Discussion

In this explorative fMRI-study, two persons were taking turns in leading and following each other in finger tapping. There was close relative temporal synchronicity between leader and follower, which is potentially also reflected in the rather high self-rated success of both leading and following.

Table 4. Brain reactivity for lead contrasted to follow and follow contrasted with lead.

Lead contrasted with Follow Contrast: (Lead > Tap) − (Follow > Listen), $p < 0.05$ (FWE)					Follow contrasted with lead Contrast: (Follow > Listen) − (Lead > Tap), $p < 0.05$ (FWE)				
Brain area	Right (R) or Left (L) hemisphere	Nbr of voxels	Peak Z-value	Peak Cluster MNI coordinates	Brain area	Right (R) or Left (L) hemisphere	Nbr of voxels	Peak Z-value	Peak Cluster MNI coordinates
Insula	R	35	6.21	32 10–14	Cerebellum IV, V	R	153	5.68	14 -56 -14
Superior temporal gyrus	L	531	5.63	−50–32 8	Postcentral gyrus	L	161	5.60	−34–22 48
Superior temporal gyrus	R	334	5.44	60–16 6	Supplementary motor area	L	27	5.08	−8–6 56
Superior temporal gyrus	L	9	4.84	−66–36 16					
Middle temporal gyrus	L	2	4.73	−62–18 0					
Superior temporal gyrus	R	1	4.71	42–38 14					

In line with previous research, STG, TPJ and STS were activated for all contrasts except for follow contrasted with lead, which could indicate cognitive control and adaptation (M. Fairhurst et al., 2014). In particular, activations in the STS are suggested to relate to social cognition such as cognitive empathy, perspective taking and detecting social cues regarding intentions and biological motion (Beauchamp et al., 2008; Frith & Frith, 2010). The STS has also been reported to be involved in social activities (Behrens et al., 2008). In this study, it could be expected that the leader and follower feel an affective response related to the social connection with the other part during the rhythmic interaction (Kawamichi et al., 2016; Sabu et al., 2019), which was potentially reflected in that many participants spontaneously gave high affectionate verbal responses after their experience of the task as well as rated high success for both leading and following. The communicative aspects of the task were probably also reflected in the activations of the lateral STG and insula. Especially the insula has been reported to be involved in interoceptive awareness, self-awareness and to detect salience and assess valence for acceptance or rejection (Blefari et al., 2017; Gogolla, 2017), with the anterior insula suggested to have a role in mediating empathy, the ability to understand and share the feelings of another individual (Blefari et al., 2017; Renier et al., 2009; Uddin et al., 2017). In the present study, insular reactivity was more pronounced during leading, which could indicate higher levels of both internal and external focus than in following (Menon & Uddin, 2010). This is also in line with the MFG activation for lead, as MFG is another proposed site for switching between internal attentional processes and attention toward external stimulus (Japee et al., 2015).

The used task with finger-tapping and hearing its sound naturally also requires recruitment of areas involved in auditory and sensory processing. The typical mean reaction time from hearing a sound to tapping a button is 0.16 s (Kosinski, 2010; Woods et al., 2015), while mean relative synchronicity between leaders and followers in this experiment was 0.0026 s, although with a standard deviation of 0.17 sec. Thus, during the experiment, the participants were generally tapping together without stopping to actively listen before each tap. However, in contrast to earlier studies using computer metronome, sometimes with built in variations, as a “leader” (M. T. Fairhurst et al., 2013; Sabu et al., 2019), the present design allowed for small perturbations in the rhythms, which required the followers to continuously adapt to the taps.

Regarding auditory and sensory processing, there was overall larger STG activity on the left side than on the right, possibly reflecting the left auditory cortex specialization on temporal coding such as rhythms (Liégeois-Chauvel et al., 1999). As the finger-tapping exercise was dependent on participants hearing the sound of their partner´s tapping, the primary auditory cortex, located in the STG, was activated for both lead and follow. The integration of multisensory input, here from touch and sound, is also likely reflected in the increased reactivity in the lateral STG (Beauchamp et al., 2008). Similar to this, the activation of IFG during leading may be linked to high-level capacities for processing of music and rhythms (Bashwiner & Bacon, 2019), with activity in the triangular part of the IFG representing feedback control (Tourville & Guenther, 2011). Studies involving unexpected changes of either auditory (Tourville et al., 2008; Toyomura et al., 2007) or somatosensory (Golfinopoulos et al., 2011) feedback during sound-based information also show activity in the right posterior IFG. For the lead contrast, this could implicate high-level processing of rhythms and adapting to changes in the follower's tapping.

During the following, there was activity in the left-somatosensory cortex, SMA and right cerebellum. This can represent the sensing of the button and the rhythm beats, such as part of the rhythm perception and tapping procedure (Bushara et al., 2001; Chen et al., 2008; Grahn & Brett, 2007; Ivry, 1996; Repp, 2005; Stoodley & Schmahmann, 2010), especially with the combined reactivity in the right cerebellum IV, V, the left thalamus VPL and the left precentral cortex, which indicate motor activity (Grodd et al., 2001; Stoodley & Schmahmann, 2010). However, the activation of the posterior cerebellum could also reflect pattern recognition and adaptation (Van Overwalle et al., 2020). Rolandic operculum and the cerebellum Crus I, activated for follow, as well as cerebellar Crus II, which was activated for lead, were also all reported to be active during pattern recognition and prediction as well as communication with and learning from other persons (Blefari et al., 2017; Van Overwalle et al., 2020). Crus I and Crus II have been observed to play a role in understanding other person's social actions, and in social mentalizing (Van Overwalle et al., 2020). The activity here could thus also be related to social adaptation for both leader and follower. Although this study is focusing on the basic neuronal reactivity, it may have applications for various situations of leader- and followership. However, beyond the scope for this setting, it would be highly interesting to assess this minimal model and levels of synchronicity in relation to success in a therapeutically setting most closely linked perhaps to aspects of music therapy (McFerran et al., 2020; Moumdjian et al., 2018).

Limitations

One important limitation in this study is the difficulty of finding a valid contrast especially for the following. Ideally, one would like to separate the act of following completely from performing the task, in this case from hearing and tapping the rhythm, but that this is difficult to achieve, has also been acknowledged by other authors (Chauvigné & Brown, 2018). Nevertheless, subtracting the act of listening to the other participant's rhythm from activity during following at least allows us to assess following without the auditory component. Another limitation is that in order to increase the drive for the follower to pay attention to the leaders' actions, the leader and the follower had different rhythms to present. This means that the motor patterns of leader and follower were similar, yet slightly different, which may impact the direct comparison of leading and following. However, the differences between rhythms were very small and not likely to affect the main results. It should also be acknowledged that the time frames for leading or following in other studies have usually been shorter, around 10 taps per rhythm (Konvalinka et al., 2014; M. Fairhurst et al., 2014). Here, we deliberately chose to give participants time to get to observe and adapt to each other's ways of tapping in order to minimize the effects of learning factors, and increase the assessments of continuous adaptation that characterizes a natural lead/follow situation such as mutual cooperation over a prolonged time. Another limitation is the small number of participants in the study, and the results should be interpreted with caution until replicated in a larger sample. One way to address the issue of different rhythms in a future study, could be to let the pairs of participants learn the same rhythm for leading the other, with the instruction to focus on achieving as close tapping synchronicity by the follower as possible. This would accomplish easier comparisons of leader- and follower contrasts because the tapping movements would be close to identical, and continuous synchronization would be in place.

Conclusion

Neural reactivity concerning both lead and follow was associated not only with sensory and motor activity but also with social cognition, interactivity and continuous adaptation, shown in the reactivity from STG, STS and TPJ. Lead contrasted with follow indicated empathy and sharing of feelings in the insular reactivity, whereas follow contrasted with lead indicated more focus on rhythmic processing. This study indicates that even a task with minimal interaction such as finger tapping could successfully, be used to study the concepts of leading and following.

Declaration of conflicts of interest

The authors declare no conflict of interest.

Disclosure statement

No potential conflict of interest was reported by the authors.

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