Following during physically-coupled joint action engages motion area MT+/V5

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Abstract. Interpersonal coordination during joint action depends on the perception of the partner's movements. In many such situations – for example, while moving furniture together or dancing a tango – there are kinesthetic interactions between the partners due to the forces shared between them that allow them to directly perceive one another's movements. Joint action of this type often involves a contrast between the roles of leader and follower, where the leader imparts forces onto the follower, and the follower has to be responsive to these force-cues during movement. We carried out a novel 2-person functional MRI study with trained couple dancers engaged in bimanual contact with an experimenter standing next to the bore of the magnet, where the two alternated between being the leader and follower of joint improvised movements, all with the eyes closed. One brain area that was unexpectedly more active during following than leading was the region of MT+/V5. While classically described as an area for processing visual motion, it has more recently been shown to be responsive to tactile motion as well. We suggest that MT+/V5 responds to motion based on *force*-cues during joint haptic interaction, most especially when a follower responds to force-cues coming from a leader's movements.

Keywords: Joint action, following, haptic motion, MT+/V5

1. Introduction

Humans, as a social species, spend a great deal of their time coordinating actions with others, doing so with remarkable seamlessness. Such coordination is often done in the service of cooperative goals that have mutual benefits for the actors [35,38]. Even a simple joint action, such as two people moving a piece of furniture together, requires that the participants achieve a high degree of both psychological and physical coordination [46]. Such coordination requires that the partners exchange information in an ongoing manner [42,52]. Although the most studied sensory cues for joint action are visual and auditory, haptic interaction is one of the most powerful means of coordinating people's actions [47], since the movement of one individual is directly perceived by partners as a pushing or pulling force [50]. Indeed, in contrast to coordination by visual or auditory information, joint actions in which there is mechanical coupling between the individuals lead to a bidirectional conveyance (and perception) of force-cues between the individuals. Kinesiological studies of joint action have explored the motor and proprioceptive mechanisms by which such force-cues form a haptic communication channel that allows partners to smoothly coordinate their actions and thereby support collective goals [50].

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Studies of joint action, whether of physical actions like moving furniture or of activities like reciprocal imitation [5,9,14,20,34], dyadic conversation [16,48], musical duetting [10,18,30,44] group decision making [28], or visual synchronisation tasks [6,36,40,42], have demonstrated that people play different roles in these joint actions and that these roles tend to be fluid. The most fundamental distinction is that between being a leader and a follower of a joint action. Leaders tend to be those individuals who make decisions and who actively transmit their ideas and intention to others, whereas followers receive this information and adapt their ideas or behaviors to the suggestions or commands of the leader. When joint actions include physical interactions, leading is often manifested as the conveyance of force-cues to the follower, whereas following is manifested as a perceptual awareness and behavioral responsiveness to the force-cues coming from the leader. As mentioned above, these roles can be quite fluid. When two people move a piece of furniture, each person might spend part of the time pushing (akin to leading) and part of the time being pushed along (akin to following), as determined adaptively by the moment-by-moment demands of the activity.

In some contexts, such as when two people move a piece of furniture, the physical contact between the two participants is not direct but is instead mediated by the object that they are jointly grasping. However, there are many situations in human life in which there is direct physical contact between the people producing a joint action. A common example of this is two people performing a couple dance, such as a tango, where the two partners form an embrace such that the forearm of each person contacts or wraps around the core of the partner (i.e., the classic ballroom dancer's embrace). Employing this embrace, the leader (often a man) is able to exert forces to the back of his partner so as to signal his movement intentions and carry out motor plans that navigate the couple through space, as well as initiate certain follower-specific movement patterns in his partner. The follower (often a woman) can return forces to the leader's hand on her back in order to create a haptic communication channel. In this way, the follower is better able to detect the force-cues coming from her partner and to synchronize her movements with his [50]. Although the flow of haptic information is bidirectional in a couple dance, there is a general asymmetry in the roles played by the partners due to the fact that only one partner knows the motor plan in advance [52]: the leader is responsible for creating the overall motor plan to move the couple through space and influence the particular movement patterns that the two partners carry out. Because of this, the follower is more engaged than the leader in detecting and interpreting the partner's force-cues.

In order to explore for the first time the neural basis of leading and following in a situation of haptic interaction with direct physical contact, we carried out a novel 2-person functional magnetic resonance imaging (fMRI) experiment with highly trained couple dancers (e.g., tango, salsa). In the experiment, the participants engaged in bimanual contact with an experimenter standing next to the bore of the magnet so that the two could generate joint motor actions. In different conditions, the participant acted as either the leader or the follower of the joint movements, all done with the eyes closed so as to limit communication to haptic interactions. The movement patterns were improvised, rather than pre-learned, in order to maintain an ongoing requirement for motor planning during leading and a heightened sense of responsiveness to force-cues during following. The major goal of the experiment was to identify the neural signatures of leading and following in a situation of joint action with physical contact. Two control conditions were carried out. In order to look at joint action in the absence of the leader/follower asymmetry, we created a "mutual" condition in which the participant and experimenter performed a pre-learned (rather than improvised) motor pattern with symmetrical roles, such that the conveyance and reception of forces were comparable between the two actors. Finally, as a control for the motor requirements of the three partnered conditions, we had participants perform a "solo" condition of improvised

bimanual movements but in the absence of physical contact with the experimenter. The analyses that assess the hypotheses for which we designed the study will be reported in another publication (in preparation), which will describe the main effect of partnering versus improvisation, as well as the differential effect of the partnering conditions. It is important to note that there is absolutely no overlap between the current analysis and those presented in the other publication. The current analysis presents a completely independent set of findings that are in no way dependent on the other publication.

We report here an unpredicted finding of the analysis of leading and following in our experiment that led us to a further exploration through a region-of-interest analysis. In particular, we observed that motion area MT+/V5 was significantly more active during following than leading. V5 has historically been described as an area for the perception of visual motion. It was initially discovered in the monkey brain [12] and later identified in the human brain through neuroimaging studies of visual motion [54]. In combination with surrounding motion-sensitive areas, it has been designated as the "MT+/V5 complex". More recently, studies have shown that this complex responds not only to visual motion but to tactile motion as well, such as occurs when the skin surface is passively stroked [3,4,21,51,53], as well as during the perception of self motion [13]. Hence, this led to the suggestion that MT+/V5 might be a supramodal area for the perception of motion. We provide here the first finding suggesting that MT+/V5 might also respond to motion perceived via *force* cues, and that it could be modulated by the degree to which individuals are receptive to these cues during joint haptic interaction. More specifically, we carried out a region-of-interest (ROI) analysis to show that a region that contains MT+/V5 is more strongly activated when a person haptically follows a leader's movements than when they themselves lead such movements.

2. Methods

Nineteen participants (9 males, mean age 40.4±13.2) took part in the study after giving their informed consent (Medical Research Ethics Board, St. Josephs Hospital). None of the participants had a history of neurological or psychiatric disease. All participants had at least two years of experience in one or more forms of couple dancing that involve leading and following (mean 7.11 years ± 5.58). These dances included Argentine tango, salsa, swing, and ballroom dancing. Data from one male participant was excluded due to excessive head movement, resulting in a final sample size of 18.

While a participant was lying supine in the MRI scanner, an experimenter (L.A.S.C.) was standing next to the bore of the scanner within reach of the participant's hands. The participant and experimenter were in physical contact at their hands, with the participant's palms facing upward and the experimenter's hands facing downwards. In other words, the participant's hands were always below the experimenter's hands such that participant's hands could not be passively moved. The principal contact between the participant's and experimenter's hands occurred at the inner surfaces of the fingers such that the two individuals were not holding hands (i.e., not creating an embrace with the hands). Based on this arrangement, participants had to actively move their hands in all conditions, including following.

The participant and experimenter together performed improvised bimanual movements of the wrist and metacarpophalangeal joints (not individual fingers) in a highly controlled manner. Such improvised movements were free in terms of direction of movement, although they were also highly constrained by the palm-surface contact between the participant and experimenter. In different conditions, the participant acted as either the leader (initiator) or follower (responder) of movements that were performed by the pair. A third joint-action condition, called "mutual", served as an intermediate condition between leading and following, whereby the participant and experimenter performed pre-learned (i.e.,

non-improvised) movements together and thus had a shared role in the joint movement, without the role asymmetry found in the leading and following conditions. Three different fixed patterns were taught to participants in advance of the scanning session, and were performed in separate epochs of the mutual task. Although the movement patterns were fixed and repetitive during the mutual condition, participants were specifically instructed that the speed and amplitude of the movement should emerge from an implicit mutual agreement between the two partners. As a motor control for these three partnered conditions, participants performed a "solo" condition in which they improvised bimanual movements on their own in the absence of physical contact with the experimenter. Finally, a rest condition served as the baseline. A sixth condition of no interest for the present report (pre-learned and unpartnered movement) was also performed during these scans. Participants' eyes were kept closed throughout the experiment. Although participants were informed about which task to perform during each task epoch by means of pre-recorded verbal cues delivered through MRI-compatible headphones, no auditory entrainment cues were presented during the movement tasks to mark tempo or rhythm.

Up to three days prior to the scan, participants were trained on the tasks outside of the scanner in order to ensure that the amount of motion (speed variation, space exploration, types of movement) was globally matched across all of the movement conditions. In the scanner, the participant's head was firmly secured using foam pillows, and their arms were fastened to the side of their body at the elbow/forearm such that only their wrists and hands were able to move, thereby ensuring highly controlled movement during scanning.

Participants performed the tasks in 28 s blocks interspersed with 8 s relaxation periods that were excluded from the analysis. During the relaxation period, a pre-recorded verbal auditory instruction cued participants for the next task. Auditory cues were presented using Presentation® software (version 14.4, Neurobehavioral Systems). Each of the five tasks (leading, following, mutual, solo, rest) was performed six times in a counter-balanced order equally distributed across three functional scans.

Acquisition of T2*-weighted axial gradient-echo echo-planar images (EPI) with blood-oxygen-level-dependent (BOLD) contrast was performed with a General Electric Achieva 3-Tesla MRI (2000 ms TR, 35 ms TE, 90° flip angle, 39 slices, 4 mm slice thickness, 0 mm gap, 3.75 mm × 3.75 mm in-plane resolution, 64 × 64 matrix, 240 mm field of view). Each functional scan consisted of 216 volumes and lasted 7′12″. An automatic shimming procedure was performed before each scan to minimize inhomogeneity of the static magnetic field. To avoid T1 saturation effects, the two first dummy volumes of each scan were discarded. Two magnetic-field mapping images (5 ms then 8 ms TE) with the same imaging parameters as the EPI were also acquired in order to unwarp the functional scans. High-resolution structural images were T1-weighted (TR/TI/TE/flip angle = 7752 ms/450 ms/2.44 ms/12°, FOV = 240 mm, resolution = 320 × 194, slice thickness = 2.0 mm, in-plane voxel size = 0.75 mm × 1.25 mm, 164 sagittal slices).

Images were processed using Brain Voyager QX 2.8. Functional images were spatially realigned, motion-corrected, unwarped, high-pass filtered (cut off frequency 0.0078 Hz), spatially smoothed (Gaussian filter with a 4 mm FWHM kernel size), and normalized to the Talairach template [49]. Three scans out of the 54 (18 participants × 3 scans) were excluded because head motion exceeded 3 mm of translation or 3° of rotation compared to the first volume of the first scan. The BOLD response for each task-block was modeled as the convolution of a 28 s boxcar with a synthetic hemodynamic response function composed of two gamma functions. In a first-level fixed-effects analysis, beta weights associated with the modeled hemodynamic responses were computed to fit the observed BOLD-signal time course in each voxel for each participant using the general linear model, with six regressors of interest modeling the experimental tasks. Six head-motion parameters plus one constant term were included as

nuisance regressors. In a second-level analysis, specific contrast images were brought forward into a random effects analysis.

Whole-brain analyses (unpublished) revealed an unexpected and intriguing difference between leading and following in MT+/V5 that we wanted to explore further with an ROI analysis. In particular, the whole-brain contrast of "following > rest" demonstrated activation in the vicinity of MT+/V5 in the middle temporal region (Talairach coordinates 48, −58, 4, $t = 7.16$; −48, −61, 4, $t = 9.48$, $p < 0.05$ Bonferroni corrected), among other activations. A similar activation was found in the contrast "mutual > rest" in the right hemisphere only (Talairach coordinates 45, -67, 7, $t = 7.23$, $p < 0.05$ Bonferroni corrected). No activation in this region was found in either "leading > rest" or "solo > rest" (Fig. 1).

We decided to follow-up on this interesting finding by performing an ROI analysis so as to compare the activity in MT+/V5 among the three partnered conditions. In order to avoid double dipping, we based the ROI analysis on a completely different contrast than those examined in the exploratory whole-brain analyses. In particular, the ROIs were localized with the whole-brain contrast "all partnered tasks > solo" (rather than "following > rest") in order to remove any bias that would favor any one of the partnered conditions over the others ($p < 0.005$ uncorrected). Bilateral ROIs were defined as spheres (5 mm radius) centered on the peak activation (see Table 1) in the middle temporal region (MT+/V5), and beta values were extracted. Our coordinates for MT+/V5 matched closely to those of previous studies on tactile motion [3,21,39,51,53]. An additional pair of ROI's was created from the peak voxels of same contrast in the primary somatosensory cortex (SI) bilaterally (Brodmann areas 3, 1, and 2). This was intended to serve as negative control, since the amount of tactile contact should have been, in principle, the same in all three partnered conditions. Beta values from each condition were subtracted
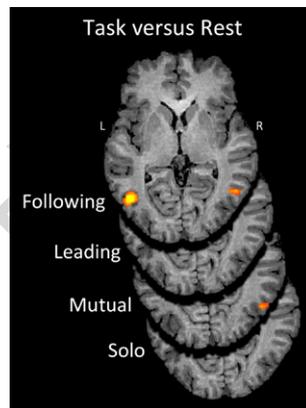

Fig. 1. Task versus Rest. The contrast "following > rest" showed bilateral activations in the vicinity of MT+/V5 in the middle temporal region. A similar activation was found in the contrast "mutual > rest" in the right hemisphere only. No activation in this region was found in either "leading > rest" or "solo > rest" ($p < 0.05$ Bonferroni corrected). The slices are at Talairach $z = 4$.

Table 1

Talairach coordinates for the peak activations in MT+/V5 and SI for the contrast "all partnered tasks > solo", which were used as the center of the ROIs for the ROI analyses

	Right				Left			
	x	y	z	t	x	y	z	t
MT+/V5	39	−61	7	5.07	−45	−61	4	3.32
SI	42	−31	55	9.41	−48	−31	52	10.13

from the baseline for each participant, and the effects in MT+/V5 and SI were tested using two 2×4 analyses of variance (2 hemispheres $\times$ 4 movement conditions) and pairwise t-test comparisons (FDR corrected).

Finally, the location of MT+/V5 observed in our study was compared to that found in previous studies of tactile motion [3,21,32,39,51,53], as well as to the localization of the extrastriate body area (EBA) compiled by Ferri et al. [15]. We examined the latter area due to the fact that its location has been reported to be very close to, if not overlapping with, MT+/V5 [15]. MNI coordinates were converted to Talairach coordinates using the icbm2tal transform. All peaks were displayed as spheres on a Talairach-normalized 3D template brain.

3. Results

Analyses of variance of beta values extracted from the two pairs of ROIs revealed a main effect of condition in both MT+/V5 ($F(3, 136) = 3.76$, $p = 0.013$) and the primary somatosensory cortex, SI ($F(3, 136) = 11.16$, $p < 0.001$). There was no effect of hemisphere and no condition $\times$ hemisphere interaction. Figure 2 shows the principal finding that MT+/V5 activity was significantly greater during following than both leading ($p = 0.028$) and solo ($p = 0.011$). No difference was found from mutual. In contrast to this profile for MT+/V5, there was no difference between following and either leading or mutual in S1. However, S1 activity was greater in each of the three partnered conditions than in the no-contact solo condition ($p < 0.001$; Fig. 2), as predicted by the presence of physical contact between partners in these three conditions. These results demonstrate that the enhanced activation of MT+/V5 in following compared to leading was due to a task-related difference in the perception of force-cues, rather than to a difference in tactile contact, since S1 activity did not differ between leading and following.

Figure 3 shows the neuroanatomical localization of our haptic MT+/V5 peaks (based on the whole-brain analysis of partnered versus solo, in red) compared to tactile MT+/V5 (in blue) and the EBA (in green) from previous studies. The peaks of MT+/V5 and EBA are separated antero-posteriorly in the left hemisphere and medio-laterally in the right hemisphere. Our peaks seem to belong more to the tactile MT+/V5 cluster than the EBA cluster. This effect was more striking in the left hemisphere, where our activation was the strongest and where the tactile MT+/V5 area is most commonly found [51,53].
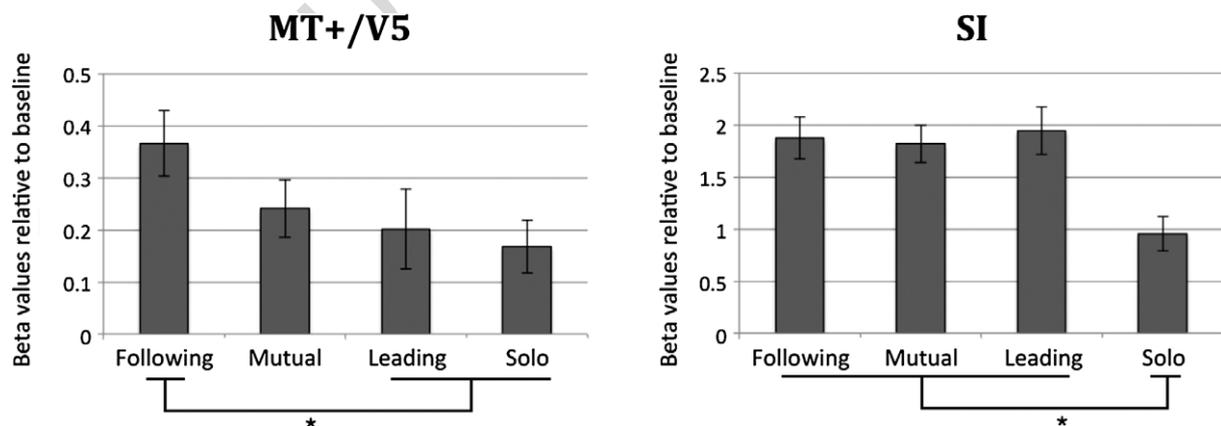

Fig. 2. ROI analysis. Mean beta values across participants and both hemispheres for the MT+/V5 and SI ROIs for each condition subtracted from baseline. Error bars show standard errors. $^* p < 0.05$ FDR corrected.
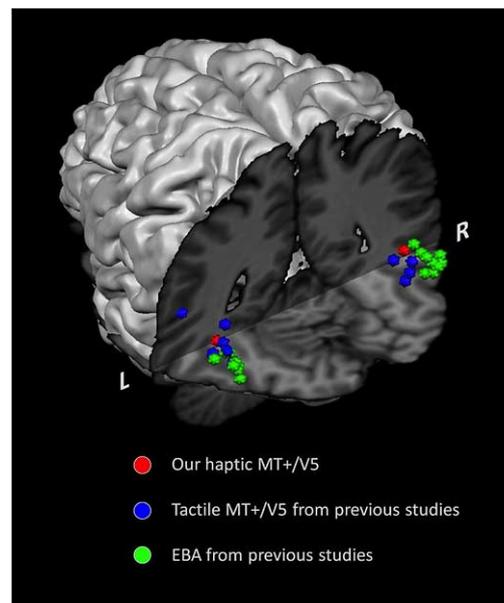
Fig. 3. Comparison of MT+/V5 and EBA. The group activation in MT+/V5 is shown for haptic motion (in red, partnered > solo, $p < 0.005$, uncorrected) compared to tactile MT+/V5 from previous studies (in blue, [3,21,32,39,51,53] and the EBA (in green, compiled by [15]). Peaks are displayed as spheres on a Talairach-normalized 3D template brain.

4. Discussion

The current fMRI study is the first to examine the neural correlates of leading and following in the context of joint action with physical contact, taking advantage of a novel 2-person interactive scanning arrangement in which an experimenter is engaged in partnered movements with the participant lying in the scanner. The results provide new insight into one critical facet of the asymmetry between leading and following in joint movement, namely that an area in the middle temporal region that is likely to be motion area MT+/V5 was significantly more active during following than leading. This might reflect the fact that, in order for individuals to coordinate their movements during joint actions, followers have a greater requirement than leaders to rely on the perception of motion-related force-cues coming from their partner. Our ROI analysis was motivated by the activation of MT+/V5 during following but not leading in an exploratory whole-brain analysis. To the best of our knowledge, this is the first evidence of MT+/V5 activation during an active and partnered task.

An increasing number of studies have suggested that MT+/V5 processes motion perception supramodally, rather than being restricted to visual motion. Indeed, this area has been shown to respond to visual [54], tactile [3,4,21,51,53], and possibly auditory [43,45] motion, as well as to the illusory perception of visual motion [22,41]. Our results may suggest for the first time that MT+/V5 also processes the perception of force-related motion cues coming from haptic coupling. This supports the emerging view of this area as a supramodal motion-processing module. Furthermore, we propose that MT+/V5 is one important component of the brain network responsible for coordinating movement with a partner during joint action.

While leading and following represent reciprocal forms of role asymmetry in joint action, the mutual condition is a situation of role symmetry, since the speed and amplitude of its joint movement emerge

from an implicit mutual agreement between the partners. The necessity to respond to haptic cues during the mutual condition was not as strong as during following, but was greater than during leading. In other words, the mutual condition is neither pure leading nor pure following, but something intermediate. Importantly, activity in MT+/V5 during the mutual condition reflected this intermediacy in haptic responsiveness to the partner's force-related motion cues, as compared to its activity during following and leading.

The greater activation of MT+/V5 during following than leading could not be attributed to a difference in visual motion since the participants' eyes were closed throughout the experiment, nor could it be attributed to differences in tactile motion per se since there was no difference in SI activity between following, leading, and mutual movement. SI has been previously shown to be sensitive to tactile motion and to be able to discriminate between moving and stationary tactile stimuli [53]. Additionally, we took great care to match the overall amount and variability of movement between leading and following. As there was no difference in either gross movement or tactile motion between leading and following, the increased MT+/V5 activity during following compared to leading can mainly be explained by the different roles taken by the participant in these conditions. Our main hypothesis is that this pattern of MT+/V5 activation reflects a change in the degree of reliance on haptic information and the degree of motor responsiveness to force-cues.

However, we are aware that our paradigm does not allow us to rule out some alternative interpretations that may also have contributed to the differential activation of MT+/V5 in our experiment. For example, the activity could have potentially been due to visual imagery [19] and/or the perception of self-motion [8,13]. We believe that a visual interpretation is unlikely since previous research has demonstrated that visual imagery cannot be the sole explanation for MT+/V5 activation during tactile motion, as this region is responsive to vibrotactile stimuli that are unlikely to induce imagery of visual motion [3]. In addition, this area is more activated during tactile motion than during visual imagery [4], and is even active during tactile motion perception in congenitally blind individuals [39]. While it is possible that following might have induced more visual imagery of the partner's movement than leading, one could equally argue that leading might have induced more imagery of the movement to be performed, since the leader is responsible for the creation of the movement plan. Further research is required to disentangle the potential involvement of visual imagery during haptically-based partnered movements.

Another alternative interpretation is that the increased response in MT+/V5 during following could be an attentional effect alone (i.e., enhanced somatotosensory attention), rather than reflecting a specific involvement of MT+/V5 in processing force-cues coming from the leader's movements. However, given that several studies have shown that attention to somatosensory stimuli enhances SI activity [17,26] and that we did not observe a difference in S1 between following and leading, this would suggest that attentional effects are probably not the major driving force for our findings. Another alternative is that an increased complexity of movement representation during following may also have contributed to our findings. While our design does not permit us to rule out such an interpretation, we would simply point out that this perspective does not conflict with our preferred interpretation that the engagement of MT+/V5 in our study is related to the need to process movement information (i.e., directional force-cues) from the partner. During an improvised dance like tango, only leaders have advance knowledge of the movement plans, and followers have to deal with the uncertainties inherent in improvised movements, which may lead to more-complex movement representations.

Finally, the results could also be interpreted in terms of sensory suppression of MT+/V5 during leading [25,27], rather than stimulation during following. Since the leader is the one who generates the motor plan, this can result in a suppression of associated tactile sensations during movement. The follower, by

contrast, should not be susceptible to such a suppression since s/he cannot predict the motor plan. In the present experiment, the mutual condition had a highly predictable motor pattern and yet still produced significant activation in MT+/V5. This suggests that the absence of MT+/V5 activation during leading is unlikely to be due to sensory suppression.

MT+/V5 is a complex with several divisions. Tactile motion has been proposed to be preferentially processed in the MST (medial superior temporal) division, but not in MT (middle temporal) proper [3], whereas the classic V5 area for visual motion is located primarily in MT. MT and MST are separated antero-posteriorly by the fundus of the ascending limb of the posterior inferior temporal sulcus (pITS), MST being the more anterior part [3,23]. In our data, MT+/V5 activation could not be attributed exclusively to either the MST or MT divisions, as the activation extended both anteriorly and posteriorly from the fundus of the ascending limb of the pITS in most participants. However, the properties of MST are more similar to those of the area localized in the present study, with its proposed role in haptic coupling. Indeed, MST is more involved than MT in tactile motion [3], self-motion perception [8], and non-visual pursuit [13]. Moreover, MST, but not MT, receives indirect somatosensory projections from SI via the parietal cortex [29] and is anatomically connected to the hand region of the primary motor cortex [31], suggesting that MST may be involved in haptic-motor coupling. Further research is needed to explore the functional differentiation between MST and MT during haptic interaction, most especially during the responsiveness to force-cues.

It is important to note that, within the middle temporal region, MT+/V5 is very close to the extrastriate body area (EBA; [11,15]). The most general response profile of the EBA is the visual perception of body parts, although the area is also involved in haptic exploration, visual imagery, and self-performed actions using a limb [7,24]. The EBA, rather than MT+/V5, could potentially be underlying our partnered movement effect. A very similar peak of activation has been observed in studies involving movement towards a stimulus, interpreted by some authors the EBA (pointing task, [2]) and others as MT+/V5 (pursuit task, [13]). Indeed, MT+/V5 has been shown to be involved in the pursuit of visual stimuli with both the eyes [13] and the hands [1,37], especially if the stimulus is complex [1]. Additionally, a comparison of our peak activations to both tactile MT+/V5 peaks and EBA peaks from the literature suggests that our activation is more likely to belong to an anterior division of MT+/V5 than to the EBA, although the partial overlap between these regions makes it difficult for us to rule out EBA involvement.

Dukelow et al. [13] and Antal et al. [1] suggested that MT+/V5 is involved in the transformation of visual motion perception into a motor action. The following condition in our study could be thought of as a type of *haptic pursuit* of a complex moving stimulus, since the leader's movements were improvised and thus had a fair degree of unpredictability. In order for someone to perform a pursuit task accurately, they have to estimate the speed and direction of the object's movement to predict the next position of the stimulus. Neurons in area MT+/V5 respond selectively to the speed, orientation and direction of visual stimuli [33], as well as to the direction of tactile stimuli [51]. Our results, combined with these previous findings, suggest that MT+/V5 can play a role in extracting the motion properties of a stimulus from any modality, especially if this information is necessary for guiding motor activity. This is especially relevant during joint action, since individuals have to coordinate their movements with one another through physical contact, and because perceiving a partner's movements is all the more challenging when we ourselves are in motion. Given the inherent asymmetries between leading and following during many forms of joint action, activity in MT+/V5 seems to preferentially reflect the behavioral requirements of the follower: in contrast to leaders, followers have to extract motion information from haptic coupling with their partner in order to perform a joint task.

In summary, the present study sheds light on one component of the brain network for coordinating joint action, namely an area that helps mediate a responsiveness to partner motion that is perceived via force-cues during physically-coupled movements, thereby helping in tracking the motion of the partner. Most forms of joint action require an ongoing alternation between leading and following by the participants involved. Our results suggest that the supramodal motion-perception complex MT+/V5, and most likely its MST subdivision, might contribute to the process of following during physically-coupled joint action. We hope that this finding will stimulate further research on the role of MT+/V5 during haptic following and interpersonal coordination of movement.

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Declaration of interest

The authors declare no competing financial interests or other conflicts of interest.

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