# NEURAL AND KINEMATIC ASSESSMENT OF HAPTIC MUTUAL ENTRAINMENT

# NEURAL AND KINEMATIC ASSESSMENT OF DANCE PARTNERING AS AN ECOLOGICAL MODEL OF HAPTIC MUTUAL ENTRAINMENT

BY

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# Lay Abstract

Entrainment is the rhythmic coordination of movement with a signal or other person. Most studies on entrainment have looked at synchronization with auditory or visual signals, whereas much less is known about how entrainment emerges mutually between individuals, especially when they are in physical contact with one another. I began my research by performing a statistical analysis of the literature examining the brain basis of synchronization with auditory signals, identifying a key brain area for entrainment. Next, using a group of participants trained at couple dancing, I explored the brain areas engaged when two individuals in physical contact improvised movement together, focusing on who is leading or following the interaction. Finally, I explored how folk dancers use multiple sensory signals (auditory, visual and tactile) to synchronize as a group. These studies advance our understanding of the neural and behavioural mechanisms by which people mutually entrain through physical interaction.

# Abstract

Entrainment is the rhythmic coordination of movement with a signal or other person. Most studies on entrainment have looked at synchronization with auditory or visual signals, whereas much less is known about how entrainment emerges mutually between individuals, especially when they are in physical contact with one another. In this dissertation, I empirically explored dance partnering as an ecological model for understanding interpersonal entrainment through haptic interaction. I began by performing a statistical meta-analysis of functional neuroimaging articles devoted to the most common experimental paradigm for entrainment, namely externally-paced finger tapping to an acoustic rhythmic stimulus (Chapter 2). The results showed that the cerebellar vermis was a strong neural marker of entrainment, as it was more activated by externally-paced tapping than by self-paced tapping, whereas the basal ganglia was activated by both types of rhythmic movements. Next, I used functional magnetic resonance imaging (fMRI) with a group of participants trained at couple dancing in order to explore the neural basis of haptic mutual entrainment, with a focus on the dynamics of leading and following (Chapter 3). While mutual interaction overall engaged brain networks involved in somatosensation, internal-body sensation and social cognition, leading showed enhanced activity principally in areas for motor control and self-initiated action, whereas following showed enhanced activity mainly in sensory and social-cognition areas. Finally, I used 3D motion capture to explore multisensory coupling for mutual entrainment at the group level during folk dancing (Chapter 4). The results showed that dancers relied most extensively on haptic coupling to synchronize as a group, whereas auditory and visual coupling were dependent on the spatiotemporal context. These studies advance our understanding of the neural and behavioural mechanisms underlying joint actions in which entrainment emerges mutually through haptic interaction.

# Acknowledgements

First of all, I am genuinely thankful to the members of my supervisory committee: Dr. Jim Lyons, whose advice was always valuable, Dr. Victoria Galea, who often gave me direct support as a researcher and as a woman, and most especially to my supervisor Steven Brown for giving me insightful guidance thorough my Ph.D. and for being deeply dedicated into all his students' work. I express my gratitude to all the dancers who took part in this journey and especially to the HIFDC dancers who became my true Canadian family, with a special thanks to Stefania Miller, without whom an entire chapter of this thesis would not have been possible. I thank all members of the NeuroArts lab: Blair Ellis, Ye Yuan, Mathew Berry Dr. Ivan Chow and Dr. Michel Belyk for their help and discussion in many domains and for their everyday care that made the lab such a friendly place. I am also thankful to: the researchers in the LIVElab and St Joseph's Imaging Research Center for their help in performing my studies; to my parents and siblings for always keeping me in their heart; to my friend Sarah Boucher for bringing enjoyment to the days in Hamilton. Finally and most of all, I am so thankful to my partner Arnaud Dubra who, with love and kindness, supported me in all senses of the word, and to my son Raphaël Dubra who turns my stress into joy in a single glance.

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# List of all Abbreviations

| | |
|---|---|
| ACC | anterior cingulate cortex |
| ACCd | dorsal part of the ACC |
| ACCv | ventral part of the ACC |
| aIPL | anterior inferior parietal lobule |
| ALE | activation likelihood estimation |
| Amyg. | amygdala |
| ANOVA | analysis of variance |
| BA | Brodmann area |
| BOLD (signal) | blood oxygen level dependent |
| CB | cerebellum |
| CMA | cingulate motor area |
| DLPFC | dorsolateral prefrontal cortex |
| EEG | electroencephalography |
| EMG | electromyography |
| FDR | false discovery rate |
| FG | fusiform gyrus |
| fMRI | functional magnetic resonance imaging |
| FWHM | full width at half maximum |
| IFG | inferior frontal gyrus |
| IPL | inferior parietal lobule |

| | |
|---|---|
| ITG | inferior temporal gyrus |
| k | number of voxels |
| L | left |
| LH | left hemisphere |
| M1 | primary motor cortex |
| Mb | midbrain |
| MCC | middle cingulate cortex |
| MFG | medial frontal gyrus |
| MNI | Montreal Neurological Institute |
| mPFC | medial prefrontal cortex |
| MT+ | motion area of the middle temporal region |
| MTG | middle temporal gyrus |
| NA | nucleus accumbens |
| PCC | posterior cingulate cortex |
| PET | positron emission tomography |
| PHC | parahippocampal gyrus |
| PMC | premotor cortex |
| PMCd | dorsal part of the PMC |
| PMCv | ventral part of the PMC |
| pSTG | posterior superior temporal gyrus |
| pSTS | posterior superior temporal sulcus |
| Put. | putamen |

| | |
|---|---|
| R | right |
| RH | right hemisphere |
| ROI | region of interest |
| S1 | primary somatosensory cortex |
| S2 | secondary somatosensory cortex |
| SMA | supplementary motor area |
| SMC | sensorimotor cortex |
| SPL | superior parietal lobule. |
| STG | superior temporal gyrus |
| TAL | Talairach |
| Th. | thalamus |
| TMS | transcranial magnetic stimulation |
| TPJ | temporo-parietal junction. |
| VPL thalamus | ventral posterolateral |

# Declaration of Academic Achievements

The following dissertation contains five chapters. Chapter 1 provides an overview of the theoretical background of the thesis regarding external entrainment, mutual entrainment, and haptic coupling in mutual interactions, and summarizes the relevant literatures. Chapter 2 is an article published in a peer-reviewed journal that has been reformatted to match the specifications of McMaster theses. Chapters 3 and 4 are, respectively, manuscripts under review and in preparation for submission. Chapter 5 links together the major findings of Chapters 2 to 4, and presents a theoretical discussion of the findings that opens up avenues for further empirical research.

## Chapter 1 - General introduction

*Author: Léa Chauvigné*

## Chapter 2 – The neural basis of audiomotor entrainment: an ALE meta-analysis.

*Authors: Léa Chauvigné, Kevin Gitau and Steven Brown*

Publication: Frontiers in Human Neuroscience, 2014, 8, 1-18.

Comments: SB conceived of the study. LC and KG collected the data. LC analyzed the data and wrote the first draft of the manuscript. LC and SB edited the manuscript.

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## Chapter 3 – Taking two to tango: fMRI analysis of improvised joint action with physical contact.

*Authors: Léa Chauvigné, Michel Belyk and Steven Brown*

Publication: Submitted to PLoS ONE.

Comments: SB and LC conceived of the study. LC and MB collected the data. LC analyzed the data and wrote the first draft of the manuscript. All authors edited the manuscript.

## Chapter 4 – Multi-person and multisensory synchronization among folk dancers

*Authors: Léa Chauvigné, Ashley Walton, Michael Richardson and Steven Brown*

Publication: Manuscript in preparation.

Comments: LC conceived of the study and collected the data. LC and AW analyzed the data. LC wrote the first draft of the manuscript. All authors edited the manuscript.

## Chapter 5 - General discussion

*Author: Léa Chauvigné*

# Chapter 1

# General introduction

*Léa Chauvigné*

All animal species have the need to coordinate their behaviours with their environment in order to survive. When this coordination involves a degree of rhythmicity, the phenomenon is called entrainment (Phillips-Silver et al. 2010). People can entrain with the natural environment, but they can also do so with each other people via reciprocal exchanges of information, also known as coupling. This exchange of information can be verbal or non-verbal, and can occur through the visual, auditory and haptic modalities, or some combination thereof. Auditory and visual couplings have been far more studied than haptic coupling (Repp and Su 2013), despite the powerful influence of haptic coupling on joint action and mutual entrainment (Sofianidis and Hatzitaki 2015). For example, when two individuals carry heavy furniture, or when a crew rows a boat (Cuijpers et al. 2015), they rely strongly on haptic communication in order to coordinate their actions. Perhaps the most magnificent example of this is dance partnering, where two or more individuals in physical contact coordinate their actions on a very short timescale, sometimes doing so while improvising their movements. This dissertation attempts to advance our understanding of the neural and kinematic bases of haptic mutual entrainment, using dance partnering as an ecological model of this interaction.

## 1.1 External entrainment

Entrainment is defined as the spatiotemporal coordination of rhythmic motor responses to a perceived rhythmic signal (Phillips-Silver et al. 2010). The animal kingdom is full of rhythmic motor behaviours, including locomotion, respiration, and the heartbeat, or, on a larger scale, the circadian rhythms that govern sleeping and eating behaviours. The natural environment also displays rhythmicity, such as the seasons and the day/night cycle, and most animal species are able to perceive and to coordinate their behaviour with such natural rhythms. However, on a shorter time-scale, isochronous (pulse-based) entrainment – where the rhythmic signal contains accents regularly spaced in time, such as in a musical beat – seems to be present only in humans and a small number of other taxa (Merker et al. 2009; Merchant and Honing 2014). This type of motor entrainment, also called sensorimotor synchronization, has been extensively studied experimentally using finger tapping to a computer-controlled acoustic pacing signal (Repp 2005; Repp and Su 2013). In this type of entrainment, the motor responses match the period and phase of the signal. In other words, the intervals between movements are similar to the intervals between pulses in the signal, and the movements occur close to the pulse onsets. In humans, adjustment to the period (or frequency) is thought to be consciously controlled by the individual and to be flexible to a large range of tempi. In contrast, adjustment to the phase of the signal is unconscious and is characterized by predictive, rather than reactive, control. Indeed, motor responses typically occur just before the pulses, resulting in a negative asynchrony with respect to the pulse (Repp 2005; Repp and Su 2013). Even in species of insects, frogs and crabs that are capable of pulse-based entrainment (through chorusing or signaling synchrony), they do not display phase correction, and are capable of period correction only over a limited range of tempi (Merker et al. 2009; Merchant and Honing 2014).

Only humans seem to be able to entrain to multiple sensory modalities. They can entrain not just to auditory signals, but to tactile (Giordano and Wanderley 2015; Ammirante et al. 2016), vestibular (Trainor et al. 2009), and visual (Kurgansky 2008) signals as well. Even though many studies suggest that motor entrainment to auditory signals is the most accurate form, followed by tactile-motor entrainment (Elliott et al. 2010), recent studies have shown that entrainment mainly depends on the nature of the stimuli (Hove and Keller 2010; Hove et al. 2013). Importantly, multimodal signals improve entrainment beyond what is possible with unimodal signals (Elliott et al. 2010; Wing et al. 2010). However, the opposite effect is found if the signals from different modalities are not aligned. In such a case, the auditory modality tends to dominate (Repp and Penel 2004; Elliott et al. 2010). This hierarchy of sensory modalities is influenced by individual experience. Musicians show much more precise synchronization with auditory stimuli than do non-musicians (Repp 2010), and deaf individuals entrain better to static visual stimuli than do hearing individuals (Iversen et al. 2015). Video gamers (visual experts) are more influenced by moving visual distractors than auditory distractors during multisensory synchronization tasks, even if they still show more accurate entrainment to unimodal auditory stimuli than visual stimuli (Hove et al. 2013).

Biologically speaking, pulse-based entrainment is based on the tight coupling between sensory and motor brain networks, where the ability to perceive and produce pulsed-based timing is supported by the basal ganglia (Teki et al. 2011; Merchant and Honing 2014). The entrainment brain network is more thoroughly reviewed in Chapter 2. Experimentally controlled studies in which individuals entrained to inanimate signals (i.e., external entrainment) have revealed the underlying mechanisms of pulsed-base entrainment. However, external isochronous stimuli that are inanimate are mostly the product of modern evolution (e.g., recorded music) and are quite rare in the natural environment (dripping water might be an example). The rhythmic signals necessary for entrainment are much more likely to be produced by other individuals (Merker et al. 2009; Phillips-Silver et al. 2010), who are neither as stable nor as unresponsive as inanimate signals (Konvalinka et al. 2010).

## 1.2 Mutual entrainment

Mutual entrainment (or social entrainment) refers to the coordination of the body and/or mind of two or more individuals who exchange information in such a manner that the motor response of one individual serves as a sensory signal for the other (Phillips-Silver et al. 2010). Such entrainment may be pulse-based but need not be. This "social coordination of motor movements" (Schmidt et al. 2011: 834) is also referred to as joint action. The reciprocal exchange of information can lead to complex feedback interactions, since the individuals can adapt to one another. Importantly, while individuals can coordinate their behaviour without information being exchanged between them if they are all entraining to the same external signal, this is not a case for mutual entrainment (Gallotti et al. 2017), unless the "external" signal can also adapt to those individuals (e.g., it is a person). The key for mutual entrainment is *adaptation*, or responsiveness, to the partners. Thus, it is not surprising that, at the neural level, mutual interactions rely on the social and mentalizing networks of the brain, which are involved in detecting and processing social stimuli and in inferring the mental states of others, respectively (Newman-Norlund et al. 2007; Yang et al. 2015). Much research has shown that shared goals and intentionality are important for joint actions (Reddish et al. 2013; Keller et al. 2014; Sacheli et al. 2015) and that interpersonal coordination is generally improved when there are shared intentions (Richardson et al. 2005, 2007; Nessler and Gilliland 2010; Ragert et al. 2013; although see Reddish et al. 2013). However, mutual entrainment can occur unconsciously (Richardson et al. 2005; Oullier et al. 2008; Demos et al. 2012) or it can be achieved without shared goals (Gallotti et al. 2017), and thus may not recruit mentalizing functions in such cases. The experiments presented in this thesis involved intentional entrainment, as the participants worked actively to coordinate with their environment, including others participants.

Mutual entrainment naturally triggers a differentiation of roles according to the degree to which each individual adapts to others (Fairhurst et al. 2014; Gallotti et al. 2017). A follower is someone who is attentive to the signals coming from their partner, and thus someone who adapts to this person, whereas a leader is someone who instead references their own internal states, and thus adapts less to other individuals. Gallotti et al. (2017) gave a good example of this regarding interpersonal synchronization tasks: one individual focuses on stabilizing the task, and thus becomes the leader, whereas the other individual focuses on stabilizing the mutual interaction, and thus becomes the follower. In this case, the leader reduces his own variability by stabilizing the period, whereas the follower reduces the phase variability between his movement and his partner's (Fairhurst et al. 2014; Konvalinka et al. 2014). The division between leader and follower can emerge by consensus or can develop spontaneously due to interpersonal differences in skill or personality, and can vary from moment to moment over the course of an interaction (Vesper et al. 2013; Fairhurst et al. 2014). Leaders more strongly engage brain networks involved in self-initiated action and motor control than do followers (Konvalinka et al. 2010; Sänger et al. 2012; Fairhurst et al. 2014), whereas followers rely more strongly on sensory networks (Guionnet et al.

2012; Zhou et al. 2016). These brain networks are more thoroughly described in Chapter 3.

It has been suggested that mutual interaction is a third category of interaction beyond strict leading and following (Konvalinka et al. 2010; Loehr and Palmer 2011). I prefer to see this in reverse: any case of mutual entrainment necessarily involves leading/following dynamics (Chauvigné et al. 2014). A leader would be purely self-paced if he could not receive any information from his partner (and thus not be mutually entrained). A follower would be purely externally-paced if he was completely unable to influence the leader. In general, most cases of asymmetric, or unidirectional, coupling (see Figure 1.1) involve a leader that is an inanimate signal (as described in the "External entrainment" section above), such as the recorded music to which dancers perform, although it can also be a person who is completely uncoupled from his partner (Goebl and Palmer 2009; Konvalinka et al. 2014; Gebauer et al. 2016). However, as soon as the least bit of information is exchanged bidirectionally, a situation of mutual adaptation can emerge (Gallotti et al. 2017). Indeed, people unconsciously adapt to information coming from others, and it does not seem possible to consciously prevent this from happening (Schmidt and O'Brien 1997; Issartel et al. 2007; Richardson et al. 2007). In between the two extremes of self pacing and external pacing, there is a wide range of mutually-adapted interactions, from impervious leadership to obedient followership, on the road to democratic cooperation. Thus, in most cases of mutual entrainment, each individual acts as both leader and follower, but to varying degrees. This involves an “anisotropic” coupling (de Poel 2016) between the members of the interaction, due to a partial asymmetry in the bidirectional information exchange, to the intentions of each partner, and/or to interpersonal differences (Figure 1.1). It is probably quite rate to have mutual entrainment with a perfectly symmetric interaction (i.e., an “isotropic” coupling) and a completely balanced leading/following relationship that is maintained over time. Importantly, the symmetry of coupling also depends on the sensory channel used to exchange information. While auditory and visual couplings between individuals can be unidirectional, tactile and haptic couplings are necessarily bidirectional.

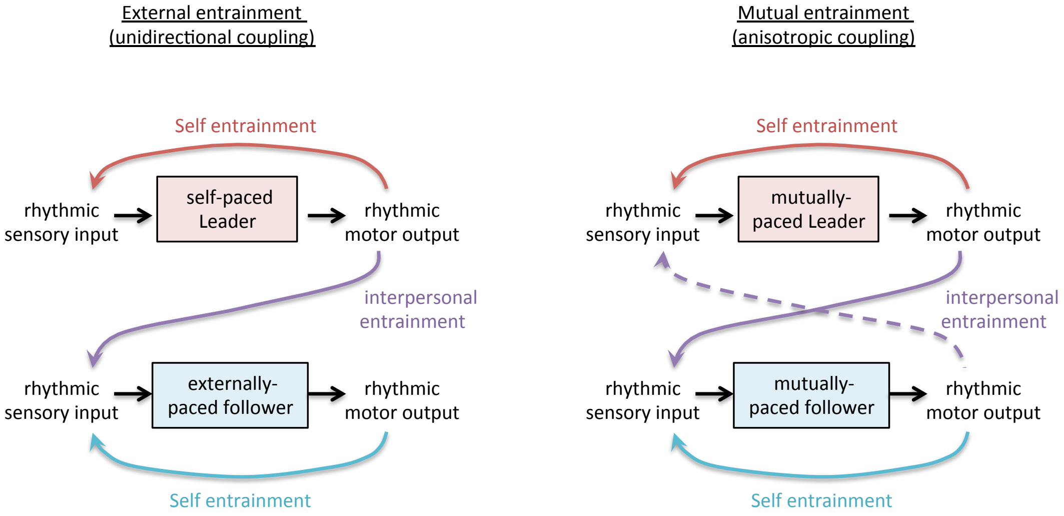

*Figure 1.1: Dynamics of leaders and followers in multi-person interaction.*

Unidirectional coupling from the motor output of a leader (in red) to the sensory input of a follower (in blue) is a case of external entrainment, where the leader is purely self-paced and the follower is purely externally-paced. Mutual entrainment necessitates bidirectional coupling, but this coupling is most often anisotropic (i.e., bidirectional and asymmetric) due to many contextual and/or individual factors. Even if one individual is more influential that the other (and is hence the leader), and the other individual adapts more to his partner (and is hence the follower), both individuals are mutually-paced by one another. Each individual uses self-generated output as an input signal, and these feedback loops foster self-entrainment. Adapted from Gallotti et al. (2017) and Phillips-Silver et al. (2010).

## 1.3 Haptic coupling in joint action

Although the most studied sensory cues for joint action are visual and auditory (Repp and Su 2013; Keller et al. 2014; Ellamil et al. 2016), haptic interaction is one of the most powerful means of coordinating people's actions (Zivotofsky and Hausdorff 2007; Nessler and Gilliland 2009; Sofianidis et al. 2012; Sofianidis and Hatzitaki 2015), since the movement of one individual is directly perceived by partners as a pushing or pulling force (van der Wel et al. 2011). Indeed, in contrast to coordination driven 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. Such force-cues form a haptic communication channel that allows partners to smoothly coordinate their actions and thereby support collective goals (van der Wel et al. 2011). For example, when walking side-by-side, people spontaneously fell into pace more often when they were holding hands than when they were only peripherally seeing each other or hearing each other's steps (Zivotofsky and Hausdorff 2007; Nessler and Gilliland 2009). Additionally, in a task where pairs of participants were swaying side-by side, mutual entrainment between participants was stronger when they shared light mutual contact through their fingertips than when they both heard the same metronome (Sofianidis et al. 2012; Sofianidis and Hatzitaki 2015). The multisensory integration of auditory and haptic coupling was shown to be modulated by dance expertise (Sofianidis and Hatzitaki 2015). Haptic coupling is present in many everyday mutual interactions, but it is optimally expressed during dance partnering, where haptic coupling is explicitly used to communicate detailed information that allows the partners to coordinate their movements at the micro-timing level.

A common example of this is two people performing a couple dance, such as an Argentine tango (Kimmel and Preuschl 2016), where the two partners form an embrace such that the forearm of each person contacts with 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 (van der Wel et al. 2011). 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 the dance is improvised and thus that only one partner knows the motor plan in advance (Vesper and Richardson 2014). The leader is responsible for creating the overall motor plan and influencing the particular movement patterns that the two partners carry out. At the same time, the couple entrains to the musical beat and must pay attention to other couples on the dance floor. Therefore, these individuals have to integrate haptic, auditory and visual couplings in order to succeed in their performance.

Another example of haptic interaction in joint action is folk dancing, where a group of dancers are haptically coupled through handholding in a chain. Like couple dancers, people who dance in a ring must integrate multisensory sources of information, such as the music, in addition to their two immediate neighbors and potentially other chains of dancers. In contrast to couple dancing, group dancing is generally not improvised. However, the dancers have to coordinate at the group level, instead of within a dyad. Dance partnering is therefore a perfect model to study the influence of haptic coupling on pulse-based mutual entrainment.

## 1.4 Research objectives

While there are many experiments investigating auditory, and even visual, entrainment, research regarding the haptic modality is rare, despite the known importance of haptic coupling during spontaneous mutual entrainment and the fact that haptic coupling is commonly used when people coordinate with one another. Little is known about how people intentionally entrain to each other via haptic coupling, such as during dance partnering. Kinematic studies on the topic are limited, and neuroimaging studies are non-existent. The goal of this dissertation is therefore to open the exploration of haptic mutual entrainment using an ecological model. To begin, I lay the groundwork by meta-analyzing neuroimaging studies of entrainment, and specifically audio-motor entrainment, which has thus far been the dominant paradigm of entrainment in the literature. Next, I describe the results of a novel two-person functional MRI study in which trained couple dancers engaged in bimanual contact with an experimenter standing next to the bore of the magnet, and in which the two alternated between being the leader and the follower of joint improvised movements. This allowed me to explore the neural basis of leading and following during haptically-driven interpersonal coordination of movement. I next describe one of the first kinematic studies to look at interpersonal coordination not at the dyadic level, but at the group level. Using 3D motion capture, I recorded a group of 13 folk dancers performing to the beat of music while holding hands in a ring configuration and watching their fellow dancers as well as a leader in the center of the ring. I explored coordination dynamics by examining the influence of auditory, visual and haptic couplings on this coordination. As a conclusion, I offer a discussion that attempts to link all of my findings into a general framework of interpersonal entrainment based on haptic interaction.

# Chapter 2

# The neural basis of audiomotor entrainment: an ALE meta-analysis

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## 2.1 Abstract

Synchronization of body movement to an acoustic rhythm is a major form of entrainment, such as occurs in dance. This is exemplified in experimental studies of finger tapping. Entrainment to a beat is contrasted with movement that is internally driven and is therefore self-paced. In order to examine brain areas important for entrainment to an acoustic beat, we meta-analyzed the functional neuroimaging literature on finger tapping (43 studies) using activation likelihood estimation (ALE) meta-analysis with a focus on the contrast between externally-paced and self-paced tapping. The results demonstrated a dissociation between two subcortical systems involved in timing, namely the cerebellum and the basal ganglia. Externally-paced tapping highlighted the importance of the spinocerebellum, most especially the vermis, which was not activated at all by self-paced tapping. In contrast, the basal ganglia, including the putamen and globus pallidus, were active during both types of tapping, but preferentially during self-paced tapping. These results suggest a central role for the spinocerebellum in audiomotor entrainment. We conclude with a theoretical discussion about the various forms of entrainment in humans and other animals.

## 2.2 Introduction

The capacity of humans to synchronize movements to an external metric rhythm has attracted much interest in both evolutionary psychology (Patel, 2014) and experimental psychology (Repp, 2005). Such synchronization to an external rhythm is considered as a form of "entrainment." However, the concept of entrainment is broader than that, as it applies not only to synchronization with external signals but also to interpersonal coordination (Knoblich and Sebanz, 2008; Schmidt et al., 2011; Phillips-Silver and Keller, 2012), such as when a rowing team rows in unison or when two people attempt to move a bulky sofa up a narrow staircase. Despite that, much recent discussion about entrainment has focused on the external type since it is phylogenetically rare, seen only in humans and a small number of other taxa (Merker et al., 2009; Patel et al., 2009; Schachner et al., 2009; Cook et al., 2013). For humans, this trait is expressed ubiquitously in dance across cultures, where people entrain their body movements to metric rhythms, such as drum beats (Jordania, 2006), where metric rhythms are temporal sequences in which accents appear regularly such that perception of predictable beats emerges (Kung et al., 2013). In addition, humans are quite prone to performing such synchronization in an unconscious manner (Repp and Keller, 2004), such as when they spontaneously tap body parts to the beat while listening to music. Given the fact that there is little compelling evidence that non-human primates can move to a beat (although see Zarco et al., 2009; Hattori et al., 2013), audiomotor entrainment—the ability of an animal to move in synchrony with an external beat—has been seen as a signature feature of human evolution, akin to bipedality (Larsson, 2014) and perhaps related to it through the evolution of dance. Hence, there has been a large interest in identifying the neural underpinnings of this sensorimotor trait in humans and in understanding what kind of brain changes may have underlain its evolutionary emergence.

Experimentally, the standard paradigm for looking at entrainment to an external beat is paced finger tapping (see Repp, 2005 and Repp and Su, 2013 for reviews), for which there is a substantial literature, both behavioral and neuroscientific. Given the fact that all rhythmic motor behaviors are driven by internal timekeeping mechanisms, the key question for external entrainment is how such motor-timing mechanisms—which are universal across animals and are thus generic—become synchronized with external oscillators like metronome beats to generate the highly specialized trait of audiomotor entrainment. Sensorimotor synchronization can be thought of in terms of the temporal coordination between internal motor-timing mechanisms and the timing of the perceived stimulus. One way that this can be examined is to compare acoustically-paced movements with self-paced movements having the same tempo, thereby comparing external and internal determinants of movement timing. A major objective of the present article is to perform a comparison between externally-paced and self-paced finger tapping studies in order to identify brain areas specifically associated with acoustic entrainment.

Neuroimaging studies of finger tapping have provided the major testing ground for neural models of both rhythmic motor production and sensorimotor entrainment in humans. While many components of the motor system are involved in rhythmic finger tapping (Witt et al., 2008), much of the discussion of motor timing has focused on two key subcortical networks, namely the cerebellum and basal ganglia. These two systems have both been proposed as the candidate timekeeper of the brain, where a timekeeper is an entity that keeps track of timing, either as a clock for duration-based timing or as a metronome for beat-based timing. While these two systems have been described in relation to general timing mechanisms (both perception and production), we will focus our attention here on studies of production, as related to the rhythmic finger tapping paradigm.

The cerebellum is considered as a central structure for the control of internal timing (Mayville et al., 2002; Ivry and Spencer, 2004; Jantzen et al., 2004; Bengtsson et al., 2005; Pecenka et al., 2013). The neocerebellum, which is the cerebellum's lateral division, is thought to process timing per se and to be one of the clock mechanisms of the brain (Kawashima et al., 2000; Schubotz et al., 2000; Mayville et al., 2002; Oullier et al., 2005; Thaut et al., 2008; Keren-Happuch et al., 2014). The spinocerebellum, its medial division, is considered to be more involved in sensorimotor processing, including motor timing (Jäncke et al., 2000; Brown et al., 2006; Kornysheva and Schubotz, 2011; De Guio et al., 2012). Ivry and Spencer (2004) proposed that the processing of time is distributed across the cerebellum and that different cerebellar regions are activated depending on the context in which the timing has to be processed.

The basal ganglia have received much attention as a brain network involved in timing, both perceptual and motor. Indeed, the basal ganglia have been proposed to act as an internal clock of the brain that generates internal timing representations, in part related to dopamine signaling from the substantia nigra (Mayville et al., 2002; Ivry and Spencer, 2004; Jantzen et al., 2004; Grahn and Brett, 2007; Coull and Nobre, 2008; Thaut et al., 2008; Teki et al., 2011; Hove et al., 2013; Kung et al., 2013). According to such a model, the putamen acts as a time accumulator, i.e., a coincidence detector between oscillatory firing and dopaminergic inputs (Mayville et al., 2002; Ivry and Spencer, 2004; Wiener et al., 2010; Teki et al., 2011; Hove et al., 2013). While some researchers believe that the basal ganglia are more involved in controlling motor behaviors, rather than being general timing structures (e.g., Boecker et al., 1998), others argue that they function as an internal clock that supports both perceptual timing and motor timing, thereby having the potential to function independent of motor processes (Mayville et al., 2002). As with the cerebellum, it is also possible that different basal ganglia structures have different timing-related functions.

Regarding rhythm, the basal ganglia are often considered as a beat-based timing system (Grahn and Brett, 2007; Teki et al., 2011; Hove et al., 2013; Kung et al., 2013), which encodes isochronous stimuli and supports the basic processing of regular and predictable timing (Thaut et al., 2008). The basal ganglia are involved both in generating an internal rhythm and in finding the beat of an external stimulus by detecting its temporal regularity (Teki et al., 2011; Kung et al., 2013). In contrast, the cerebellum performs more-complex timing processing, such as encoding polyrhythmic stimuli (Thaut et al., 2008), establishing the duration of discreet stimuli (Ivry and Spencer, 2004; Teki et al., 2011), or performing a correction of timing errors led by the basic processing in the basal ganglia (Teki et al., 2011; Kung et al., 2013). Therefore, according to some models, the basal ganglia perform basic timing processing and the cerebellum, through its reciprocal connections with the basal ganglia, performs subsequent timing adjustments or other complex timing processes (Rao et al., 2001; Thaut et al., 2008; Teki et al., 2011).

Given our interest in understanding not just timing per se but sensorimotor entrainment in particular, what is the activity of these networks in externally-paced vs. self-paced motor behaviors? The cerebellum and lateral premotor cortex (both ventral and dorsal parts) are the most common areas activated in externally-paced motor tasks. Indeed, the cerebellum plays a role in sensorimotor synchronization (Jahanshahi et al., 1995; Rao et al., 1997; Weeks et al., 2001), the lateral premotor cortex plays a role in movements guided by external sensory stimuli (Jahanshahi et al., 1995; Larsson et al., 1996; Rao et al., 1997; Jäncke et al., 2000; Kawashima et al., 2000; Weeks et al., 2001; Kornysheva and Schubotz, 2011; Pecenka et al., 2013), and the cerebellum and lateral premotor cortex are reciprocally connected (Jahanshahi et al., 1995; Rao et al., 1997). In addition, the caudal part of the supplementary motor area (SMA proper) is activated by the execution of externally-triggered sequences (Kawashima et al., 2000; Weeks et al., 2001; Lehéricy et al., 2006) and is thought to mediate a comparison between external rhythms and internal timing representations (Schubotz et al., 2000; Jantzen et al., 2007), On the other hand, a network from the putamen to the rostral part of the SMA (pre-SMA) is often highlighted in studies of self-paced tasks (Rao et al., 1997). Internally-guided movements and self-paced tasks often elicit activity in the basal ganglia, particularly the putamen (Jenkins et al., 2000; Cunnington et al., 2002; Garraux et al., 2005). Similarly, the SMA, and especially the pre-SMA, is often involved in monitoring motor timing and preparing for internally-guided sequences and self-triggered movements (Jahanshahi et al., 1995; Boecker et al., 1998; Jäncke et al., 2000; Jenkins et al., 2000; Kawashima et al., 2000; Cunnington et al., 2002; Mayville et al., 2002; De Guio et al., 2012).

However, the problem with any simple model of motor timing is that most of the abovementioned areas have been found in studies of bothself-paced and externally-paced production. For example, Jenkins et al. (2000) found that both externally-paced and self-paced tasks elicited activity in the putamen, but that the self-paced task led to greater activation (see also Boecker et al., 1998). Similarly, both types of tasks are shown to activate the dorsal premotor cortex, sometimes to a greater extent for externally-triggered tasks (Larsson et al., 1996; Kawashima et al., 2000). In addition, Jantzen et al. (2004) showed that the network activated by self-paced tasks was dependent on the context in which the pace was determined. Indeed, many of the abovementioned self-paced studies did not distinguish whether the pace was purely self-determined or if it was determined by prior tempo instructions in the experiment. According to Jahanshahi et al. (1995), movements where the pace is indicated by prior instructions should not be called self-paced, even if they are done in the absence of an external stimulus. We will return to this important point below.

Of interest to our analysis is the small number of studies that have performed direct contrasts between externally-paced and purely self-paced rhythmic tasks. Kornysheva and Schubotz (2011) had subjects perform finger tapping either to the beat of an auditory rhythm or at a freely determined rate while listening to sounds devoid of rhythm (thereby controlling for auditory stimulation). The contrast of externally-paced with self-paced tapping showed activations in several regions, including bilateral auditory areas and the left lateral premotor cortex. In a separate session, subjects received transcranial magnetic stimulation (TMS) over the left ventral premotor cortex. Doing so led to a disruption of externally-paced tapping but not self-paced movements. An functional magnetic resonance imaging (fMRI) scan several minutes following TMS showed that stimulation of the ventral premotor cortex led to activity in the cerebellar vermis (lobule V). Vermal activation in this post-TMS fMRI scan was inversely correlated with the external-pacing impairment caused by TMS and thus reliably predicted how well subjects preserved audio-motor synchronization. It could therefore be related to a process of audio-motor timing correction (Kornysheva and Schubotz, 2011).

Brown et al. (2006) had dancer subjects perform patterned leg movements that were either externally-paced to music or self-paced at the same general tempo (in the absence of music). The contrast of acoustically-paced movement vs. self-paced movement revealed not only expected activations in the auditory cortex (since the self-paced condition lacked music) but activity in the anterior vermis (lobule III) of the spinocerebellum. The cerebellar activation was not driven by music per se, since subtraction of passive music listening did not reduce the z score of the vermal activation. Hence, the spinocerebellar activation reflected sensorimotor entrainment rather than sensory or motor processing alone. This entrainment-contrast further revealed activity in the medial geniculate nucleus of the thalamus, leading the authors to propose a "low road" model of acoustic entrainment in the spinocerebellum in which the auditory information driving entrainment comes to the cerebellum principally from ascending (subcortical) rather than descending (cortical) auditory pathways.

In the present study, we employed activation likelihood estimation (ALE) meta-analysis to a broad corpus of neuroimaging studies of finger tapping in order to examine brain areas involved in entrained vs. self-paced finger tapping. A previous ALE meta-analysis of finger tapping carried by Witt et al. (2008) set the stage for several of the findings reported in the current study. The major limitation of that study, from our standpoint, is that the authors did not perform an entrainment contrast; in other words, they did not examine the direct contrast between acoustically-paced and self-paced tapping, although they analyzed each condition separately and used logical images to demonstrate overlap in the activation patterns between the two. Despite this limitation, the study reported a number of important findings. The authors characterized the basic brain network involved in rhythmic motor production, including the primary sensorimotor cortex (SMC), SMA, basal ganglia, cerebellum, premotor cortex, and parietal cortex. They also compared acoustically-paced, visually-paced, and self-paced finger tapping. The ventral premotor cortex was shown to have a preference for acoustically-paced tapping, while the SMA was shown to be primarily activated by self-paced tapping, which is concordant with the literature described above. The basal ganglia and the thalamus were shown to be activated by both acoustically-paced and self-paced tapping.

One problem with their analysis relates to how they classified some of the studies. In particular, we feel that certain tapping studies defy a simple categorization into externally-paced or self-paced types. For example, there are studies of “continuation tapping” in which subjects initially tap in synchrony with an external timekeeper but then continue tapping at the same tempo in the absence of the external signal. In addition, there are studies in which subjects learn to tap at a particular pace during a training phase of the study and then tap on their own during an experimental phase. We can think of these two types of paradigms as being examples of “memory pacing” driven by auditory imagery of a previously-heard metric rhythm. For Witt et al. (2008), both of these types of protocols were included as part of their “no stimulus” condition and thereby combined with studies of true self-paced tapping. We find this to be problematic since such paradigms are contaminated by an external pacing signal, even if it not present at the time of tapping (Jahanshahi et al., 1995). Hence, one of our key objectives was to restrict ourselves to studies of true self-paced tapping when examining the contrast with acoustically-entrained tapping. Memory pacing became a third category of pacing in our analysis.

The principal objective of the current study was to use voxel-based meta-analysis techniques to identify the major brain areas involved in acoustic entrainment in order to better understand the evolution of this trait in humans. Along these lines, we examined the finger tapping literature with the aim of comparing studies of acoustically-paced and self-paced tapping. We used the relevant literature employed in the Witt et al. (2008) meta-analysis as our starting point and updated the analysis to the present year. Acoustically-paced tapping in these studies was done to the beat of either an isochronous stimulus (the majority of studies) or to a more complex rhythm. The use of both was justified since isochronous stimuli represent the simplest form of rhythm, where the beat is equivalent to the stimulus (or a multiple of it). That is, in both cases, the perception of the regularity of the rhythm allows the generation of an internal model, which predicts the upcoming beat. In addition, since Witt et al. (2008) included studies of memory tapping in their self-paced category, we wanted to rectify this situation by only using studies of true self-paced tapping as the comparison group for acoustically-entrained tapping in order to create the purest entrainment contrast. We ran a conjunction analysis of studies of acoustically-paced and self-paced tapping in order to identify regions commonly activated by both types of pacing. We also ran contrast analyses to identify brain areas preferentially activated by each type of pacing. We were particularly interested in differentiating the role of the cerebellum and basal ganglia in the two types of pacing. Finally, we analyzed studies of memory tapping separately in order to determine how, given their implicit pacing signals, their activation pattern compared with both externally-paced and self-paced tapping. We discuss these results in the broader context of a general model of entrainment types.

## 2.3 Materials and Methods

### 2.3.1 Inclusion Criteria

Meta-analyses of published neuroimaging studies of acoustically-paced and self-paced finger-tapping tasks were performed using ALE meta-analysis (Turkeltaub et al., 2002) in order to compare brain activations across these two types of pacing. Articles were initially obtained from a previous meta-analysis of finger tapping (Witt et al., 2008). Additional articles, published through March 2014, were retrieved by searching the Medline database using the PubMed search engine with the search terms “finger tapping fMRI,” “finger tapping positron emission tomography (PET),” and “self-paced tasks.” In order to identify papers that might have been missed, we performed a more thorough search of the Medline database using the OVID engine with a Boolean search paradigm. Finally, the reference sections of the resultant articles were searched for additional studies. A full listing of the studies included in the meta-analyses is found in Table 2.1.

***Table 2.1.*** *Studies included in the meta-analyses.*

| Experiments | Subjects | Contrasts | Foci | Pacing type | Hand | Fingers |
|---|---|---|---|---|---|---|
| Albouy et al. (2012) | 30 | Tapping vs Rest, training | 12 | self-paced | left | sequence |
| Aoki et al. (2005) | 10 | Index finger vs Listen | 1 | externally-paced | right | index |
| | | Ring finger vs Listen | 7 | externally-paced | right | ring |
| | | double finger vs Listen | 12 | externally-paced | right | pairs |
| Aramaki et al. (2006) | 15 | Parallel vs Listen | 18 | externally-paced | bimanual | pair I-M |
| | | Miror vs Listen | 7 | externally-paced | bimanual | pair I-M |
| Bijsterbosch et al. (2011) | 16 | Regular vs Rest | 11 | externally-paced | right | index |
| | | Subliminal vs Rest | 16 | externally-paced | right | index |
| | | Supraliminal vs Rest | 10 | externally-paced | right | index |
| Blinkenberg et al. (1996) | 8 | Finger tapping vs Rest | 10 | externally-paced | right | index |
| Calautti et al. (2001), old group | 7 | RH tapping vs Listen | 4 | externally-paced | right | index to thumb |
| | | LH tapping vs Listen | 10 | externally-paced | left | index to thumb |
| Calautti et al. (2001), young group | 7 | RH tapping vs Listen | 10 | externally-paced | right | index to thumb |
| | | LH tapping vs Listen | 10 | externally-paced | left | index to thumb |
| Catalan et al. (1998 & 1999) | 13 | Sequence 12 vs Listen | 9 | externally-paced | right | sequence |
| | | Sequence 16 vs Listen, controls | 12 | externally-paced | right | sequence |
| Chen et al. (2006) | 11 | Finger tapping 0dB vs Silence | 7 | externally-paced | right | index |
| De Guio et al. (2012) | 10 | Unpaced tapping vs Rest, Children | 30 | memory paced | right | index |

***Table 2.1** (continued)*

| Experiments | Subjects | Contrasts | Foci | Pacing type | Hand | Fingers |
|---|---|---|---|---|---|---|
| Gerardin et al. (2000) | 8 | Motor execution vs Listen | 24 | externally-paced | right or left | index or pair I-L |
| Jantzen et al. (2005) | 12 | Auditory synchronise pacing vs Rest | 7 | externally-paced | right | index to thumb |
| Jantzen et al. (2005) | 12 | Auditory synchronise continuation vs Rest | 4 | memory paced | right | index to thumb |
| Joliot et al. (1998) | 5 | Finger tapping vs Rest, PET | 13 | self-paced | right | index |
| Joliot et al. (1999) | 8 | Finger tapping vs Rest, PET | 11 | self-paced | right | index |
| | | Finger tapping vs Rest, fMRI average | 16 | self-paced | right | index |
| | | Finger tapping vs Rest, fMRI correlation | 20 | self-paced | right | Index |
| Kadota et al. (2010) | 10 | Right hand tapping vs Rest | 6 | self-paced | right | sequence |
| | | Left hand tapping vs Rest | 8 | self-paced | left | sequence |
| | | Both hands tapping vs Rest | 13 | self-paced | bimanual | sequence |
| Kawashima et al. (2000) | 8 | Memory timed finger movement vs Rest | 10 | memory paced | right | index |
| Kuhtz-Buschbeck et al. (2003) | 12 | Motor execution simple RH vs Baseline | 4 | externally-paced | right | index to thumb |
| | | Motor execution simple LH vs Baseline | 9 | externally-paced | left | index to thumb |
| | | Motor execution complex RH vs Baseline | 8 | externally-paced | right | sequence |
| | | Motor execution complex LH vs Baseline | 12 | externally-paced | left | sequence |
| Kung et al. (2013) | 11 | Tap isochronous vs Silence | 15 | externally-paced | right | index |
| Larsson et al. (1996) | 8 | Self-paced movement vs Rest | 12 | memory paced | right | index |
| Lehericy et al. (2006) | 12 | Simple vs Rest | 8 | externally-paced | right | index |
| | | Scale vs Rest | 11 | externally-paced | right | sequence |
| | | Complex vs Rest | 27 | externally-paced | right | sequence |
| Lerner et al. (2004) | 10 | Tapping vs Listen, Controls | 9 | externally-paced | right | index |
| Lissek et al. (2007) | 33 | Simple non-DH vs Rest | 14 | self-paced | left | index |
| | | Simple DH vs Rest | 15 | self-paced | right | index |
| | | Complex non-DH vs Rest | 28 | self-paced | left | sequence |
| | | Complex DH vs Rest | 37 | self-paced | right | sequence |
| Matthys et al. (2009) | 18 | Finger tapping vs Baseline, No mirror | 13 | memory paced | right | index |
| Mayville et al. (2002) | 9 | Motor only vs Rest | 5 | memory paced | right | index to thumb |
| Mostofsky et al. (2006), control children | 11 | Right-handed finger sequencing vs Rest | 3 | self-paced | right | sequence |
| | | Left-handed finger sequencing | 5 | self-paced | left | sequence |
| Nyberg et al. (2006), group 1 | 8 | Before, trained sequence vs Rest | 4 | self-paced | left | sequence |
| | | Before, untrained sequence vs Rest | 4 | self-paced | left | sequence |
| | | After, trained sequence vs Rest | 2 | self-paced | left | sequence |
| | | After, untrained sequence vs Rest | 2 | self-paced | left | Sequence |
| Nyberg et al. (2006), group 2 | 8 | Before, trained sequence vs Rest | 4 | self-paced | left | sequence |

***Table 2.1*** *(continued)*

| Experiments | Subjects | Contrasts | Foci | Pacing type | Hand | Fingers |
|---|---|---|---|---|---|---|
| | | Before, untrained sequence vs Rest | 4 | self-paced | left | sequence |
| | | After, trained sequence vs Rest | 2 | self-paced | left | sequence |
| | | After, untrained sequence vs Rest | 2 | self-paced | left | sequence |
| Oullier et al. (2005) | 15 | Executed sychronization vs. Rest | 17 | externally-paced | right | index to thumb |
| Peres et al. (2011) | 15 | Finger tapping vs Rest | 19 | self-paced | right | Index |
| Rao et al. (1997) | 13 | Synchronization vs. Rest (interval 300ms) | 4 | externally-paced | right | index |
| | | Synchronization vs. Rest (interval 600ms) | 3 | externally-paced | right | index |
| Rao et al. (1997) | 13 | Continuation vs. Rest (interval 300ms) | 7 | memory paced | right | index |
| | | Continuation vs. Rest (interval 600ms) | 7 | memory paced | right | index |
| Riecker et al. (2006), young group | 10 | Movement vs Listen, Main effects | 6 | externally-paced | right | index |
| Riecker et al. (2006), old group | 10 | Movement vs Listen, Main effects | 8 | externally-paced | right | index |
| Roessner et al. (2012), control children | 16 | Finger tapping vs Rest | 27 | memory paced | right | index |
| Rounis et al. (2005) | 16 | Main effect of movement vs Listen | 17 | externally-paced | right | random finger |
| Sadato et al. (1997), experiment 1 | 12 | Mirror vs Listen | 13 | externally-paced | bimanual | sequence |
| | | Parallel vs Listen | 15 | externally-paced | bimanual | sequence |
| Sadato et al. (1997), experiment 2 | 9 | Right unimanual vs Listen | 3 | externally-paced | right | index |
| | | left unimanual vs Listen | 6 | externally-paced | left | index |
| | | bimanual mirror vs Listen | 12 | externally-paced | bimanual | index |
| | | bimanual parellvs Listen | 13 | externally-paced | bimanual | index |
| Thaut et al. (2008) | 12 | Polyrhythmic movements vs. Listen | 26 | externally-paced | right | index |
| | | Isorhythmic movements vs. Listen | 9 | externally-paced | right | index |
| Vuust et al. (2006) | 18 | Tap vs Listen | 8 | externally-paced | right | index |
| Weeks et al. (2001) | 22 | Internal move vs. Rest | 9 | memory paced | right or left | index or middle |
| Wylie et al. (2013) | 18 | Auditory-paced finger Tapping vs. Rest | 5 | externally-paced | right | index |
| Yoo et al. (2005) | 10 | group-level finger tapping activation vs Rest | 17 | externally-paced | right | sequence |

Experimental conditions in which subjects performed finger tapping to an auditory pacing cue were classified as “externally-paced.” Experiments in which subjects performed tapping without external pacing were divided into two sub-categories based on whether or not a prior entrainment/training phase of the experiment specified a tapping rate to the subjects. Only conditions that lacked both external pacing and any prior indication of a tapping rate were classified as "self-paced." Intermediate types of conditions, in which tapping occurred without acoustic pacing but was preceded by either a previous bout of entrainment (continuation tapping) or a training phase with a metronome, were classified as "memory-paced."

Our inclusion criteria for the studies were: (i) that brain scanning was performed using either fMRI or PET; (ii) that papers reported activation foci in the form of standardized stereotaxic coordinates in either Talairach or Montreal Neurological Institute (MNI) space; (iii) that subjects were healthy individuals, thereby excluding studies using clinical populations but including studies of healthy children; (iv) that the pacing stimulus for the externally-paced conditions was auditory, thereby excluding studies of visual pacing of tapping; (v) that the analyses included contrasts against rest or a suitable low-level control condition; and (vi) that results from the entire scanned volume were reported, thereby excluding studies scanning only a portion of the brain or that only reported region-of-interest analyses. Note that studies that did not include data from minor parts of the brain, such as the most inferior part of the cerebellum, were included. Wherever studies reported multiple experiments from the same group of subjects, the contrasts were included together as a single study. For studies that reported the results of more than one subject-group, each group was treated separately, in accordance with the approach of Turkeltaub et al. (2012).

As a result, 43 studies were included in our meta-analysis, including 25 externally-paced tapping experiments (295 subjects, 469 foci), nine self-paced tapping experiments (128 subjects, 244 foci), and nine memory-paced tapping experiments (116 subjects, 124 foci). During all the experiments, participants tapped at an isochronous rate (including four self-paced experiments where they tapped as fast as possible). Among the externally-paced studies, 23 experiments used an isochronous auditory stimulus, whereas two used musical rhythms. For 24 of the externally-paced experiments, subjects' tapping was supposed to occur on every beat of the stimulus, whereas one study used hemiola tapping to an isochronous stimulus.

### 2.3.2 Analysis

GingerALE 2.3 (www.brainmap.org/ale) was used for all analyses as well as for converting MNI coordinates into Talairach coordinates. The ALE results were registered onto a Talairach-normalized template brain using Mango 3.1 (ric.uthscsa.edu/mango). Separate meta-analyses were conducted for externally-paced (n = 25), self-paced (n = 9), and memory-paced (n = 9) tapping. All individual analyses were corrected for multiple comparisons using the false discovery rate (FDR) $p < 0.01$ with a cluster threshold of k = 120 mm3.

In addition to running individual analyses, we performed a conjunction analysis and direct statistical contrasts between the externally-paced and self-paced ALE maps (Nichols et al., 2005) in order to identify areas that were specific for acoustic entrainment. The conjunction was generated by taking the smallest

ALE value between the two individual ALE maps (FDR corrected $p < 0.01$ for individual maps). The contrast analyses were performed at $p < 0.05$ uncorrected on the previously-corrected individual ALE maps, with a cluster threshold of k = 120 mm3. Note that visual comparison between the individual meta-analyses might lead to misleading conclusions due to the difference in the number of studies in each analysis. However, such a difference is corrected for statistically in the conjunction and contrast analyses (Eickhoff et al., 2011). The one caveat to point out is that the low number of self-paced studies may have produced a bias toward more variance in its ALE analysis, thereby resulting in false increases in the number or size of clusters in the contrast of self-paced vs. externally-paced tapping.

## 2.4 Results

Figure 2.1 shows the conjunction of activations for externally-paced and self-paced tapping, demonstrating the common brain network underlying rhythmic finger tapping, irrespective of pacing type. Talairach coordinates for these ALE foci are presented in Table 2.2. Activations were seen in the bilateral SMC (somatotopic hand representation), caudal part of the SMA, left ventral and dorsal premotor cortex (BA 6), and bilateral inferior parietal lobule (IPL; BA 40). Regarding the two subcortical networks involved in timing, cerebellar activity was seen bilaterally in lobules V and VI, which is a region that includes the somatotopic finger representation of the lateral cerebellum (Grodd et al., 2001), itself linked to the bilateral activity seen in the SMC. Basal ganglia activity was seen in both the putamen and globus pallidus, but only in the left hemisphere. Activity was also seen in the nearby ventral lateral nucleus of the left thalamus, although this activity could not be unambiguously associated with either the cerebellum or basal ganglia alone.

***Table 2.2.*** *Conjunctions and contrasts between the externally-paced and self-paced ALE maps.*

| | | | **Conjunction** | | | | **External > Self** | | | | **Self > External** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Area | | BA | x | y | z | ALE | x | y | z | z score | x | y | z | z score |
| *Frontal Lobe* | | | | | | | | | | | | | | |
| M1 | L | 4 | -34 | -16 | 60 | 14.8 | | | | | | | | |
| | R | 4 | 36 | -24 | 56 | 18.5 | | | | | 30 | -22 | 60 | 2.8 |
| | | 4 | | | | | | | | | 38 | -22 | 58 | 2.7 |
| SMA | L | 6 | 0 | -4 | 54 | 21.7 | | | | | | | | |
| | | 6 | -2 | -10 | 58 | 17.8 | | | | | | | | |
| PMCd | L | 6 | | | | | | | | | -29 | -11 | 64 | 3.5 |
| PMCv | L | 6 | -56 | 0 | 30 | 15.9 | | | | | | | | |
| | | 6 | -54 | -4 | 36 | 14.4 | | | | | | | | |
| | | 6 | -50 | 4 | 8 | 13.6 | | | | | | | | |
| *Parietal Lobe* | | | | | | | | | | | | | | |
| S1 | L | 2 | -48 | -26 | 46 | 21.8 | | | | | | | | |
| | | 2 | -52 | -28 | 42 | 16.3 | | | | | | | | |
| | | 3 | -38 | -28 | 56 | 20.1 | | | | | | | | |
| | R | 2 | | | | | | | | | 36 | -38 | 60 | 2.3 |
| | | 2 | | | | | | | | | 56 | -24 | 36 | 2.3 |
| | | 2 | | | | | | | | | 54 | -24 | 32 | 2.1 |
| | | 2 | | | | | | | | | 50 | -20 | 26 | 2.1 |
| | | 3 | | | | | | | | | 36 | -34 | 60 | 2.3 |
| IPL | L | 40 | -54 | -24 | 20 | 15.5 | | | | | -52 | -32 | 48 | 2.8 |
| | | 40 | -46 | -26 | 18 | 15.4 | | | | | -50 | -24 | 26 | 1.9 |
| | | | | | | | | | | | -48 | -22 | 22 | 1.8 |
| | R | 40 | 58 | -22 | 20 | 14.2 | | | | | 44 | -22 | 24 | 2.0 |
| SPL | L | 7 | | | | | | | | | -26 | -57 | 57 | 2.1 |

***Table 2.2** (continued)*

| | | | Conjunction | | | | External > Self | | | | Self > External | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Area | | BA | x | y | z | ALE | x | y | z | z score | x | y | z | z score |
| *Temporal Lobe* | | | | | | | | | | | | | | |
| Posterior STG | R | 42 | | | | | 62 | -24 | 8 | 2.0 | | | | |
| | | 22 | | | | | 58 | -18 | 4 | 1.9 | | | | |
| *Subcortical* | | | | | | | | | | | | | | |
| Putamen | L | | -26 | -4 | 12 | 18.6 | | | | | | | | |
| Globus pallidus | L | | -18 | -8 | 2 | 24.4 | | | | | -14 | -4 | 4 | 2.2 |
| VL thalamus | L | | | | | | | | | | -12 | -10 | 4 | 2.3 |
| *Cerebellum* | | | | | | | | | | | | | | |
| Lateral (VI) | L | | -20 | -58 | -20 | 15.1 | | | | | -22 | -60 | -18 | 2.1 |
| | R | | 20 | -56 | -22 | 14.3 | | | | | | | | |
| Lateral (V) | R | | | | | | 14 | -52 | -18 | 1.9 | | | | |
| Vermis (V) | L | | | | | | 10 | -50 | -24 | 1.9 | | | | |
| | R | | | | | | 15 | -59 | -13 | 2.1 | | | | |
| | | | | | | | 10 | -62 | -16 | 2.1 | | | | |
| Vermis (VI/VII) | R | | | | | | 6 | -60 | -24 | 1.9 | | | | |

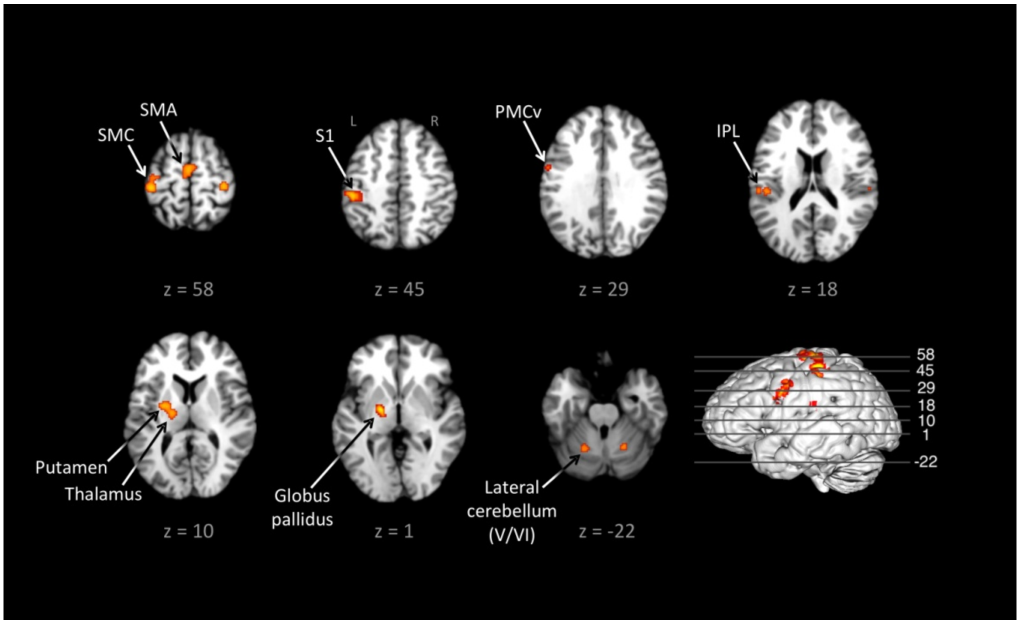


*Figure 2.1. Conjunction between the externally-paced and self-paced.*

ALE maps. The analysis is $p < 0.01$, FDR corrected. The 3D brain is shown to indicate the slice levels. The slices are shown in neurological convention.

Abbreviations: IPL, inferior parietal lobule; L, left; PMCv, ventral part of the premotor cortex; R, right; S1, primary somatosensory cortex; SMA, supplementary motor area; SMC, sensorimotor cortex.

Given this shared network, the next step was to perform reciprocal contrasts between the two types of pacing (Figure 2.2 and Table 2.2). The contrast of External > Self (red foci in Figure 2.2) revealed activity in only two regions. One was an expected activation in the auditory association cortex (posterior superior temporal gyrus, pSTG; BA 22), reflecting the exclusive presence of auditory stimulation in entrained tapping. The other area was the vermis of the cerebellum (lobules V and VI/VII) extending toward the right lateral cerebellum (lobule V). The reverse contrast of Self > External (blue foci) revealed a greater number of foci. Areas of activation included the right SMC, left dorsal premotor cortex (BA 6), left superior parietal lobule (BA 7), bilateral IPL (BA 40), and left lateral cerebellum (lobule VI). It is important to point out that the activity in the right SMC and left lateral cerebellum is mainly related to the larger number of left-handed studies in the self-paced analysis compared to the entrained analysis (see below), and may not be a reflection of neural differences between self-pacing and external pacing. Finally, activity was seen in the left basal ganglia, mainly in the globus pallidus and ventral lateral nucleus of the thalamus. Thus, these two subtractions revealed a double dissociation between the subcortical timing circuits: External > Self showed activity in the cerebellar vermis, while Self > External showed activity in the globus pallidus of the basal ganglia.

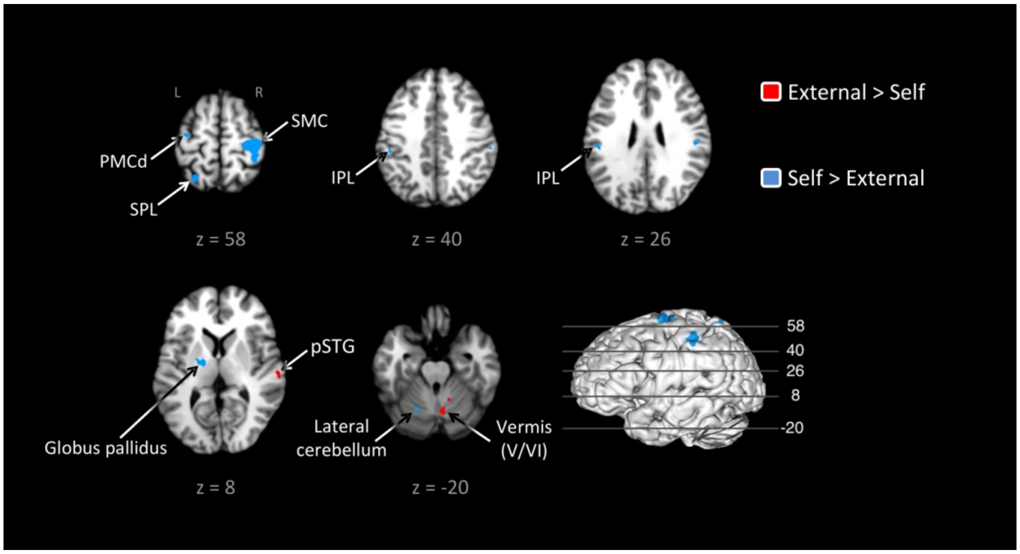


*Figure 2.2. Contrast between the externally-paced and self-paced ALE maps.*
The analyses are $p < 0.05$, uncorrected. The activations are color-coded according to the legend at the right. The 3D brain is shown to indicate the slice levels. The slices are shown in neurological convention. Note that the large activation in the right SMC and the corresponding activation in the left lateral cerebellum are simply a reflection of the larger number of left-handed studies for self-paced tapping (see text). Abbreviations: IPL, inferior parietal lobule; L, left; PMCd, dorsal part of the premotor cortex; R, right; SMC, sensorimotor cortex; SPL, superior parietal lobule.

Figure 2.3 and Table 2.3 present the individual ALE analyses, including that for memory pacing. As mentioned in the Introduction, memory pacing is an intermediate case between external and self-pacing, since the tapping occurs in the absence of a pacing cue but is driven by auditory imagery of a previously heard cue. Memory-paced finger tapping showed activity in the same basic network described above for the conjunction of external and self-pacing, but also included areas that were seen in externally-paced tapping but not self-paced tapping, namely the cerebellar vermis, inferior frontal gyrus (IFG; BA 44), and ventral posteromedial nucleus of the thalamus. This activation profile suggests that memory pacing is much closer to entrained tapping than it is to self-paced tapping. Finally, regarding the subcortical timing circuits, it is important to point out that the left putamen was present for both external pacing and self-pacing, while the vermis was only present for external pacing and memory pacing, but not self-pacing.

***Table 2.3.*** *The three types of pacing studied*

| | | | **Externally-paced** | | | | **Memory-paced** | | | | **Self-paced** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Area | | BA | x | y | z | ALE | x | y | z | ALE | x | y | z | ALE |
| *Frontal Lobe* | | | | | | | | | | | | | | |
| M1 | L | 4 | -38 | -22 | 54 | 53.7 | -36 | -24 | 56 | 21.3 | | | | |
| | R | 4 | 36 | -24 | 56 | 18.5 | | | | | 30 | -24 | 58 | 28.4 |
| SMA | L | 6 | -6 | -12 | 54 | 47.0 | -2 | -10 | 56 | 20.4 | 0 | -4 | 54 | 21.7 |
| | | 6 | -2 | -4 | 58 | 38.9 | -6 | -4 | 52 | 19.7 | -2 | -10 | 58 | 17.8 |
| PMCd | L | 6 | | | | | | | | | -32 | -12 | 62 | 18.2 |
| PMCv | L | 6 | -54 | 0 | 28 | 17.7 | | | | | -56 | 0 | 32 | 17.5 |
| | | 6 | -54 | -6 | 34 | 17.0 | | | | | -54 | -4 | 38 | 14.4 |
| | | 6 | | | | | | | | | -52 | 4 | 8 | 14.0 |
| IFG | R | 44 | 56 | 4 | 20 | 22.3 | 48 | 8 | 8 | 13.2 | | | | |
| *Parietal Lobe* | | | | | | | | | | | | | | |
| S1 | L | 3 | | | | | | | | | -38 | -28 | 56 | 20.1 |
| | R | 3 | 32 | -30 | 52 | 17.3 | | | | | 38 | -32 | 58 | 17.5 |
| | | 3 | | | | | | | | | 54 | -22 | 40 | 14.2 |
| | | 2 | | | | | | | | | 54 | -20 | 34 | 16.1 |
| | | 2 | | | | | | | | | 58 | -20 | 22 | 15.2 |
| IPL | L | 40 | -52 | -24 | 14 | 31.0 | -46 | -30 | 46 | 14.0 | -48 | -28 | 46 | 25.6 |
| | | 40 | -56 | -28 | 36 | 30.1 | -46 | -28 | 26 | 13.6 | -54 | -24 | 20 | 15.5 |
| | | 40 | -46 | -42 | 46 | 18.2 | | | | | -54 | -22 | 24 | 14.9 |
| | | 40 | | | | | | | | | -46 | -26 | 18 | 15.4 |
| | R | 40 | 36 | -40 | 42 | 22.3 | | | | | 46 | -24 | 22 | 15.6 |
| IPL | R | 40 | | | | | | | | | 56 | -34 | 40 | 15.1 |
| | | 40 | | | | | | | | | 36 | -38 | 56 | 14.8 |
| | | 40 | | | | | | | | | 52 | -20 | 24 | 14.1 |
| SPL | L | 7 | | | | | | | | | -26 | -56 | 58 | 16.1 |
| | R | 5 | | | | | | | | | 36 | -40 | 60 | 14.2 |

***Table 2.3** (continued)*

| | | | **Externally-paced** | | | | **Memory-paced** | | | | **Self-paced** | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Area | | BA | x | y | z | ALE | x | y | z | ALE | x | y | z | ALE |
| *Temporal Lobe* | | | | | | | | | | | | | | |
| Posterior STG | L | 42 | -44 | -4 | 8 | 22.4 | | | | | | | | |
| | R | 42 | 58 | -20 | 10 | 23.8 | | | | | | | | |
| *Subcortical* | | | | | | | | | | | | | | |
| Putamen | L | | -24 | -8 | 12 | 24.6 | | | | | -26 | -4 | 12 | 18.6 |
| | R | | 22 | -8 | 12 | 19.7 | 30 | 10 | 6 | 12.0 | | | | |
| Globus pallidus | L | | -20 | -8 | 2 | 29.0 | | | | | -18 | -8 | 2 | 24.4 |
| Claustrum | L | | -34 | -2 | 4 | 19.3 | | | | | | | | |
| VPM Thalamus | L | | -14 | -20 | 8 | 32.7 | -16 | -20 | 6 | 23.4 | | | | |
| | R | | 12 | -22 | 10 | 24.2 | | | | | | | | |
| *Cerebellum* | | | | | | | | | | | | | | |
| Lateral (V) | L | | -22 | -54 | -24 | 30.8 | 16 | -52 | -20 | 13.9 | | | | |
| Lateral (VI) | L | | -16 | -52 | -18 | 24.2 | | | | | -20 | -58 | -20 | 15.1 |
| | R | | 22 | -54 | -22 | 44.1 | | | | | 20 | -56 | -22 | 14.3 |
| Vermis (IV) | R | | | | | | 8 | -50 | -14 | 14.5 | | | | |
| | | | | | | | 2 | -54 | -12 | 13.7 | | | | |
| Vermis (V) | R | | 2 | -62 | -16 | 39.2 | | | | | | | | |
| Vermis (VI/VII) | R | | | | | | 2 | -60 | -22 | 13.0 | | | | |
| Dentate nucleus | R | | 16 | -52 | -20 | 47.7 | | | | | | | | |

In order to know if movement complexity had an influence on these results, we examined which fingers and hands were used across the different types of conditions. We found that 52% of the entrained experiments were done with only one finger (usually the index finger), compared to 33% of the self-paced experiments and 78% of the memory-paced experiments. We generated a "complexity" value for each experiment according to the number of fingers and hands used. The mean complexity value was 2.3, 4.0, and 1.4, respectively, for entrained, self-paced, and memory-paced tapping. A two-tailed unpaired t-test showed that the difference in complexity between entrained and self-paced tapping was not significant ($p > 0.01$).

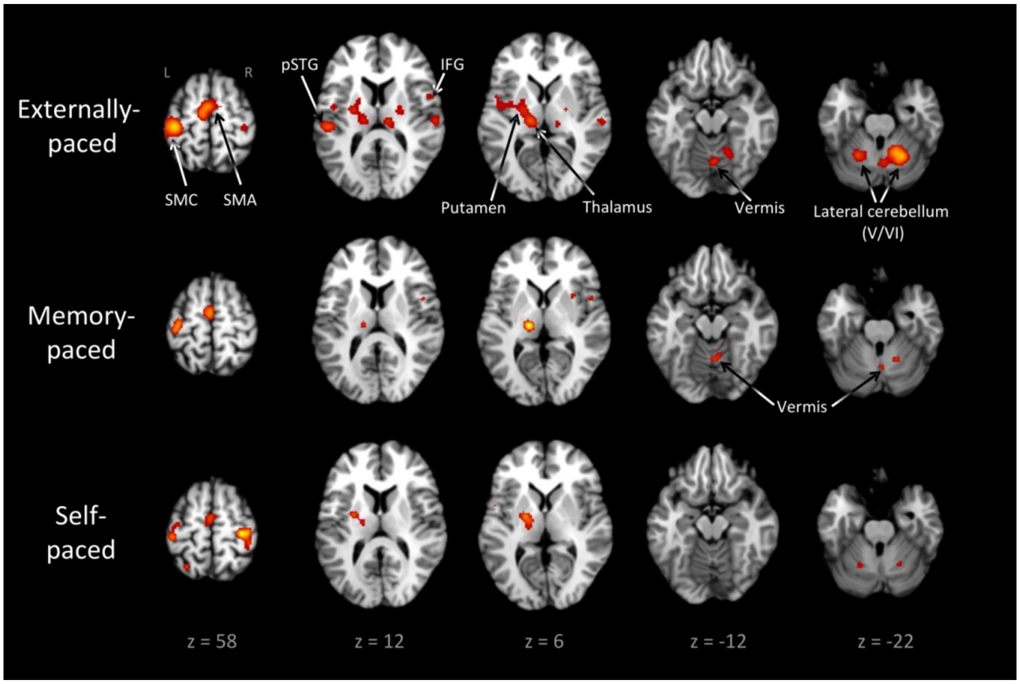


*Figure 2.3. Individual ALE maps for the three types of pacing studied.*

The analyses are $p < 0.01$, FDR corrected. The slices are shown in neurological convention. Abbreviations: IFG, inferior frontal gyrus; L, left; pSTG, posterior superior temporal gyrus; R, right; SMA, supplementary motor area; SMC, sensorimotor cortex.

Regarding the hand used in the tapping tasks, the left hand or both hands were used in 28, 66, and 11% of the experiments, respectively, for entrained, self-paced, and memory-paced tapping. These proportions explain the bilateral activations in the SMC and lateral cerebellum seen in the self-paced analysis, compared with the unilateral activations for both of these structures in the entrained and memory-paced analyses.

## 2.5 Discussion

In this study, we sought to examine the neural basis of the phylogenetically rare ability of humans to entrain movements to a metric rhythm. To do so, we meta-analyzed the neuroimaging literature devoted to rhythmic finger tapping in order to identify regions of the brain specifically activated by externally-paced finger tapping, as compared with self-paced tapping. The results demonstrated a dissociation between the two major subcortical systems implicated in timing control. Contrast analyses revealed the importance of the spinocerebellar vermis for acoustically-paced tapping. The basal ganglia were observed for both types of pacing but were preferentially activated by self-paced tapping. Overall, these results suggest that entrained movement to the underlying beat of an acoustic rhythm, which is a novel human ability, is more related to the cerebellum than the basal ganglia, while the latter might be more important for internally-regulated control of movement timing (as well as for finding the underlying beat, see Kung et al., 2013). These results raise important evolutionary questions about acoustic entrainment, not least since the cerebellar vermis is a highly conserved structure among vertebrates and has even been shown to have undergone an evolutionary reduction in humans compared to non-humans primates (see below).

The conjunction analysis of externally-paced and self-paced tapping (Figure 2.1) replicated the basic findings of Witt et al. (2008), demonstrating a brain network for rhythmic finger tapping irrespective of pacing type, including the SMC, lateral premotor cortex, SMA, IPL, putamen/globus pallidus, and lateral cerebellum. This is not surprising given the strong overlap in the literatures covered by these meta-analyses. The major difference between our analysis and theirs was the stronger bilaterality of their profile, with bilateral activations in the IPL and basal ganglia that were both left-lateralized in our analysis. In addition, they observed activity in the IFG and pSTG that we only saw for externally- and memory-paced tapping. Table 2.3 reveals that this same basic network was activated across all three types of pacing examined in this study. Hence, this seems to be a general circuit for rhythmic control of finger movement.

Our interest in revisiting the finger tapping literature was not to look at metric motion per se but to identify brain areas specifically associated with entrainment. For that, it was necessary to employ the comparison task of self-paced tapping. While Witt et al. (2008) performed a comparison between auditory pacing, visual pacing, and "no stimulus" pacing, they only did so using logical analyses and not statistical contrasts. In addition, as mentioned in the Introduction, they included studies of memory pacing in their "no stimulus" category, hence contaminating the self-paced category with studies having an implicit external pacing signal. Indeed, it is possible that the brain regions responsible for entrainment maintain their activity even after the external stimulus is removed. Therefore, we wanted to perform a statistical contrast between entrained and self-paced tapping, with the additional provision that the self-paced corpus be free of the confounding effect of memory pacing.

The contrast of entrained vs. self-paced tapping revealed activity in the vermis of the spinocerebellum in addition to an expected activation in the auditory association cortex (pSTG). Examination of the individual ALE analyses showed that the vermis was present in the externally-paced analysis but absent in the self-paced analysis. Given that entrainment is typically viewed as a form of prediction, our results are consistent with the general role of the cerebellum in mediating prediction and in reducing prediction error during motor tasks (Tseng et al., 2007; Taylor et al., 2010; Kornysheva and Schubotz, 2011). One could argue that the activation in the vermis only reflects error correction between the stimulus and the tap during audio-motor synchronization, rather than entrainment per se. However, additional evidence for the role of the vermis in acoustic entrainment, rather than error correction, comes from the observation that the vermis was active during memory pacing, where no auditory stimulus was present. This result argues that the entrainment circuit of the spinocerebellum does not require external auditory input to stimulate it but that it can be driven by auditory imagery of a pacing signal, as processed by cortical auditory areas (Halpern and Zatorre, 1999). The IFG too could mediate the storage and rehearsal of auditory timing information (Rao et al., 1997). It plays a role in timed motor tasks whenever an auditory stimulus is involved, whether the stimulus is currently present or was previously presented (Kawashima et al., 2000; Bengtsson et al., 2005; Witt et al., 2008). Activation of the vermis and IFG during memory pacing suggests that this type of pacing is actually a form of covert acoustic entrainment.

Overall, the vermis, probably through its interaction with other motor-timing areas, emerged in this study as the strongest candidate for a brain area that mediates audiomotor entrainment, such as occurs not just in finger tapping (Jäncke et al., 2000; Kornysheva and Schubotz, 2011; De Guio et al., 2012) but in dance as well (Brown et al., 2006). In fact, our entrainment contrast replicated the results of the only motor-timing study performed using dancers. Brown et al. (2006) had tango dancers execute patterned leg movements that were either externally-paced to tango music or self-paced at the same general tempo. The contrast of acoustically-paced vs. self-paced movement revealed, beyond expected activations in the auditory cortex, activity in the anterior vermis of the spinocerebellum. Interestingly, the difference in the location of the vermal activation in the dance study (lobule III) and the finger-tapping meta-analysis (lobule V/VI) might reflect differences in the somatotopic location of the legs and fingers in the spinocerebellum. The classic map of the medial cerebellum shows an inverted homunculus in the anterior lobe such that the lower extremity is most anterior and the upper extremity is more posterior (Grodd et al., 2001).

The entrainment-contrast of Brown et al. (2006) further revealed activity in the medial geniculate nucleus of the thalamus. Based on this, the authors proposed a “low road” model of acoustic entrainment in the spinocerebellum in which the auditory information driving entrainment comes to the cerebellum principally from ascending (subcortical) rather than descending (cortical) auditory pathways. They argued that the beat information that drives entrainment – not least the unconscious kind of entrainment that routinely occurs when people listen to music – is coarsely-processed sensory information that does not require the elaborate spectral analysis that the auditory cortex is specialized at carrying out. However, the results of the present meta-analysis with memory pacing indicate that descending input from cortical areas involved in auditory memory can drive vermal activation. Interestingly, Petacchi et al.'s (2005) ALE meta-analysis of cerebellar activations during passive listening to acoustic stimuli did not reveal ALE foci in the vermis but only in more-lateral hemispheric regions, with the exception of Crus II posteriorly. Hence, vermal activation might be explicitly linked to sensorimotorprocessing, rather than sensory processing alone, as would be expected for an area that mediates entrainment. The finding that the vermis receives strong input from the primary motor cortex (Coffman et al., 2011) suggests that the vermis might be ideally situated to compare motor commands with ascending inputs from the sensory pathways in order to facilitate sensorimotor synchronization by reducing prediction error (see Kornysheva and Schubotz, 2011).

It is worth pointing out that the vermis is not the only part of the cerebellum that is implicated in timing. The bilateral cluster in the lateral cerebellum (lobule VI) observed in the conjunction analysis is close to the somatotopic finger representation (Grodd et al., 2001) but is also considered a key structure for generating internal timing representations (Kawashima et al., 2000; Schubotz et al., 2000; Mayville et al., 2002; Oullier et al., 2005; Thaut et al., 2008; Keren-Happuch et al., 2014). Several studies have found that timing complexity is linked with the lateral cerebellum, even when motor activity is controlled for Kawashima et al. (2000), Mayville et al. (2002), Oullier et al. (2005), Thaut et al. (2008). Lobule VI of the lateral cerebellum is consistently found in both perceptual and motor tasks involving timing, as shown by a meta-analysis of cerebellar function (Keren-Happuch et al., 2014). Therefore, the timing circuit of the cerebellum includes not only the vermis but the hemispheres as well. In contrast to the vermis, the lateral cerebellum does not show specificity for entrainment, as it was activated comparably by all three types of pacing (Figure 2.3).

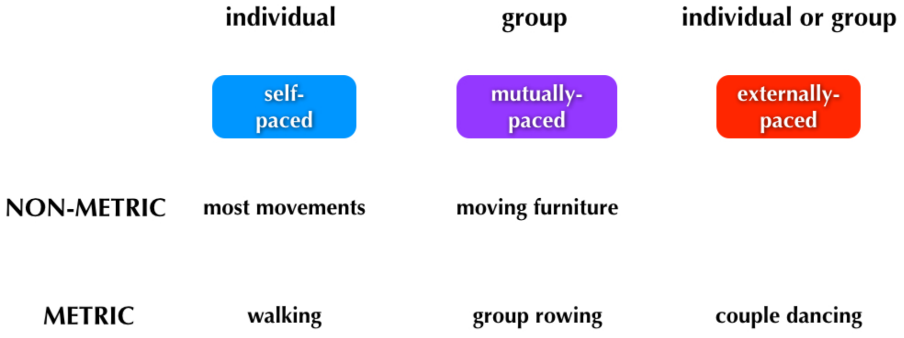
What about the basal ganglia, the other major subcortical circuit strongly implicated in timing? The individual meta-analyses showed the basal ganglia to be active during both externally-paced and self-paced tapping. However, contrast analysis revealed that the globus pallidus was more active during self-paced compared with externally-paced tapping. The common presence of the basal ganglia in the externally-paced and self-paced analyses is consistent with the fact that both types of pacing are isochronous and that the basal ganglia are reliably activated by tasks that involve regularity and predictability, whether during perceptual, motor, or sensorimotor tasks. The basal ganglia, and especially the putamen, are involved in the processing of metric stimuli (Brown et al., 2006; Grahn and Brett, 2007) as well as in the generation and maintenance of internal representations of time (Jantzen et al., 2007; Coull and Nobre, 2008; Kung et al., 2013). Such representations can be purely self-determined without external cues (Mayville et al., 2002; Ivry and Spencer, 2004; Jantzen et al., 2007; Coull and Nobre, 2008; Hove et al., 2013) or they can be generated according to external stimuli (Jantzen et al., 2007; Coull and Nobre, 2008; Kung et al., 2013). Indeed, externally-paced movements that are regular and predictable can establish representations of movement timing that can be internally guided (Jahanshahi et al., 1995; Jäncke et al., 2000; Jenkins et al., 2000). Thus, the regular and predictable nature of isochronous tapping tasks elicits basal ganglia activity, as seen during both externally-paced and self-paced tapping. The residual activation of the basal ganglia for self-paced compared with externally-paced tapping is consistent with the well-known function of the basal ganglia in goal-directed (as opposed to stimulus-directed) movement and with movement initiation (Redgrave et al., 2010). Hence, the basal ganglia might play a stronger role in self-initiated movements than in movements entrained to external signals. The absence of the basal ganglia in the memory-pacing analysis (Figure 2.3) was unexpected. The detection by fMRI of activity in small internal structures such as the basal ganglia is less reliable than the detection of activity in cortical structures (Kawashima et al., 2000; Weeks et al., 2001; Yoo et al., 2005). The low number of foci in the memory-paced dataset compared to the externally- and self-paced datasets could also explain the absence of putamen activation.

The overall finding of the meta-analyses was a shared network of brain areas that was activated regardless of the pacing type, a network broadly supported by the literature reviewed in the Introduction. It includes not only frontal and parietal cortical areas (SMC, SMA, PMC, IPL) but the lateral cerebellum and putamen/globus pallidus. It also includes the ventral region of the thalamus that acts as a relay for both the cerebellum and basal ganglia in conveying information back to motor regions of the cortex (Asanuma et al., 1983; Haber and Calzavara, 2009). While the pallidal part of this shared network was shown to be more activated for self-paced tapping than externally-paced tapping, the vermis of the cerebellum was shown to be active for externally-paced tapping but absent for self-paced tapping, hence being a neural signature of entrainment. The vermis might be able to coordinate internal motor timing to the timing of external stimuli.

But this latter point raises an evolutionary conundrum. While the human capacity to keep the beat is a rarity among mammals, the vermis of the cerebellum is a highly conserved structure in vertebrates (Shmuelof and Krakauer, 2011). Even more paradoxically, Matano and Hirasaki (1997), in performing volumetric analyses of the cerebellum across 26 species of anthropoids, found that the targets of the vermis, namely the fastigial and interpositus nuclei, were reduced in volume (when controlling for the volume of the medulla) in humans compared to non-human primates, whereas the lateral cerebellum showed the reverse trend. This is certainly not the expectation that one would have for a specialized brain area that mediates a novel species-specific function. While we do not currently have a finite explanation for this, a prominent role might be played by the connectivity between the timing circuits of the basal ganglia (which support beat-based timing) and the cerebellum, where interactions have been proposed to occur in regions such as the pontine nuclei, inferior olive, and substantia nigra (Onodera and Hicks, 1998; Bostan and Strick, 2010; Teki et al., 2011). As beat-based timing is needed for both metrical self- and external-pacing, the brain network responsible for this timing seems to be necessary but not sufficient for audiomotor entrainment. In addition, non-human primates, as well other most other animals, lack the ability to find the beat. (Zarco et al., 2009; see also Merchant and Honing, 2014; Patel and Iversen, 2014). Thus, the capacity for entrainment could emerge from the connectivity between the cerebellar vermis and beat-based timing areas. Another important avenue to consider is the interaction between the medial and lateral zones of the cerebellum, possibly through their joint innervation by the primary motor cortex and through their complementary auditory input from ascending (medial cerebellum) and descending (lateral cerebellum) projections. Indeed, Zarco et al. (2009) showed that monkeys lack beat-based timing partly due to an inability to phase-adapt, a process needed during entrainment and which is supported essentially by the lateral cerebellum (Bijsterbosch et al., 2011). We therefore suggest that the vermis could be a central area in the entrainment network, responsible for synchronizing internal and external timing, and that others areas of the network, and connectivity between them, might have evolved to make acoustic entrainment a specific feature of humans. Further comparative research is necessary to address this important phylogenetic question about synchronization mechanisms.

## 2.6 A classification of entrainment types

As mentioned in the Introduction, the concept of entrainment applies not only to synchronization with external signals but also to interpersonal coordination, such as when a rowing team rows in unison or when two people attempt to move a bulky sofa up a narrow staircase, situations where the tempo of movement is established mutually, not by some signal external to the group. As a conclusion to this article, we would like to present a framework for thinking about entrainment, one that covers all forms of human pacing (see Figure 2.4). In addition, we would like to highlight important differences between the pacing-types of music and dance (see Figure 2.6), since these two processes are often combined under the umbrella of "rhythmic" or "metric" behaviors.



| | individual | group | individual or group |
|---|---|---|---|
| | self-paced | mutually-paced | externally-paced |
| NON-METRIC | most movements | moving furniture | |
| METRIC | walking | group rowing | couple dancing |

*Figure 2.4. Major categories of human pacing.*

The figure summarizes the three major types of pacing. Examples of each type are shown below the boxes.

We can think about three categories of timing: (1) self-paced, done only by individuals; (2) mutually-paced, done only by groups, and (3) externally-paced, done by either individuals or groups. The critical distinction between the latter two categories is whether the pacing-cue is coming from outside of the performers (external pacing) or whether it is negotiated internally by the group (mutual pacing). Distinguishing mutual pacing from external pacing might seem contradictory at first, since multiple individuals are influencing one another and thus acting as cues "external" to one another. However, if we focus on the group as a unit, then we can think of the tempo of the group's movements as being determined internally to the group rather than by some external pulse. Finally, rhythm is a component of the scheme. Whereas external pacing of movement is almost always done in a metric manner, self-pacing, and mutual pacing can be done in either a non-metric or metric manner.

Typical examples of movements of each type are shown below the boxes in Figure 2.4. Looking first to self-pacing, we see that the vast majority of movements carried out by individuals are self-paced and non-metric. There are important examples of self-paced movements that are done metrically, including walking and repetitive forms of work movements. It is worth noting that any kind of rehearsal without the presence of an external stimulus may reasonably involve imagery, such as the auditory imagery that could occur when a dancer is rehearsing without music. In this case, the movements would be memory-paced and not self-paced. Jumping now to external pacing, this occurs almost invariably in a metric manner. Dancing is a key example, whether done by an individual or group. Finally, mutual pacing can occur in either a non-metric or metric manner. An example of the former would be two people moving a heavy piece of furniture up a narrow staircase; such movement would be jerky and non-metric, although there might be short bouts of meter during it. An example of mutual pacing that is metric would be the movements of a rowing team. (Should there be a coxswain calling out the pace, then this would become a form of external pacing as well). As will be described below, the most complex aspect of the scheme relates to phenomena like group dancing to music in which external pacing and mutual pacing operate simultaneously. For example, the two individuals dancing a tango have to entrain both to a musical beat (external) and to one another (mutual), and this involves different sensory modalities and effector systems (see Figure 2.6).

Figure 2.5 presents the same scheme but adds some new distinctions to it as well as a few more examples of each category of movement. The first is a distinction between movements that are designed to be sound-generating (sonorant movements) vs. those that are not (non-sonorant movements). Whereas the vast majority of movements are non-sonorant (at least at the level of conscious awareness), sonorant movements occur during activities like speaking, singing, playing of a musical instrument, or the dancing that occurs while using body percussion, such as in tap dancing. The reason why sonorance is important in thinking about entrainment is that the sound self-generated by the movement creates cues for external entrainment. While all sensory cues have the potential to mediate entrainment, acoustic cues are far more effective (Repp and Penel, 2002, 2004; Witt et al., 2008). Thus, self-generated acoustic cues have a strong potential to influence entrainment (Phillips-Silver et al., 2010). This is seen routinely in group musical performance, where the sonorance of the production blurs the distinction between mutual and external pacing of movement, a problem that does not occur for non-sonorant movements (or even for sonorant though non-metric movements like speech). The second new distinction shown in Figure 2.5 relates to the idea that external pacing can occur using multiple types of sensory cues, including auditory and visual cues. Hence, whereas a tango couple is paced by the acoustic cues coming from an orchestra, the members of that orchestra are paced

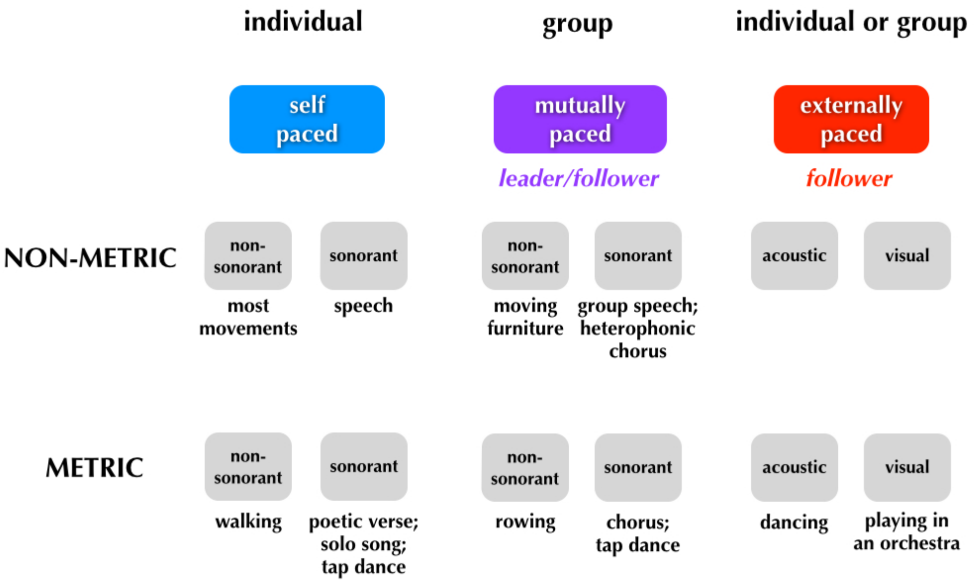


*Figure 2.5. Sonorant vs. non-sonorant movements.*

This figure is similar to Figure 2.4 but adds new distinctions related to sonorance, leading/following, and the sensory modalities for external entrainment.

by the visual cues coming from a conductor (see also Figure 2.6). Mutual pacing as well employs multiple types of sensory cues, not just visual and auditory but also kinesthetic cues when there is physical contact between the members, as occurs very often in dance, but only rarely in music. Overall, any person interacting with other people in a joint activity is influenced by multiple timing cues such that their internal timing is moderated by both external and mutual pacing mechanisms.

Finally, the scheme in Figure 2.5 adds information about one more important component of pacing during group production, namely the distinction between leading and following. We usually think about this in the everyday sense of a tango couple in which one member of the pair is the leader (often the man) and the other member is the follower (often the woman). While we do not typically apply this distinction to solo movements, it seems reasonable to argue that any individual who is being paced by an external signal, for example recorded music, is a follower, whether in a solo context (e.g., a solo dancer) or a group context (e.g., a group of dancers). So, in Figure 2.5, external pacing is labeled as being an example of following. When dancers move to music, they generally do not have any ability to influence the tempo of the music and therefore do not have the ability to "lead" the music the way that the music leads them. The external signal acts as a leader. The most interesting and complex situation relates to mutual pacing in a group. We would argue that any situation of mutual pacing by a group involves a leader-follower dynamic. Moreover, this dynamic is fluid such that the roles can switch back and forth between members during the course of the movement. For example, when two people move a piece of furniture up a staircase, there might be times when the front person (the puller) is pacing the overall movement of the pair and other times when the back person (the pusher) is doing so. This is no less true during a duet between two musicians (Goebl and Palmer, 2009; Loehr et al., 2013; Palmer et al., 2013). The major point is that any situation of mutual entrainment requires a specification of a leader-follower dynamic. The greater the number of people that make up the group, the more complex (and potentially chaotic) the dynamic can become. Moreover, when group movement of this kind is paced by an external beat, such when a group of folk dancers moves to the beat of music, mutual pacing and external pacing interact.

This overall arrangement is summarized by the cartoon in Figure 2.6, in which we see three couples of tango dancers moving to music produced by a small ensemble, which itself is led by a conductor. Movement is non-sonorant in the case of the dancers but sonorant in the case of the musicians. Mutual pacing is seen (1) between the two members of each couple; (2) among the multiple couples; and (3) among the multiple musicians of the ensemble. Likewise, while a leader/follower distinction is seen within each couple, we can further imagine that a “lead couple” (shown by the middle couple in the figure) is serving as the leader of the other two couples. So, for the dancers, we have to consider both a between-couple and within-couple leader/follower arrangement for mutual pacing. External pacing is seen in both the dancers/musicians and musicians/conductor arrangements. Regarding sensory modalities for external pacing of movement, the dancers are being led by acoustic cues from the music, while the musicians are being led by visual cues from the conductor.

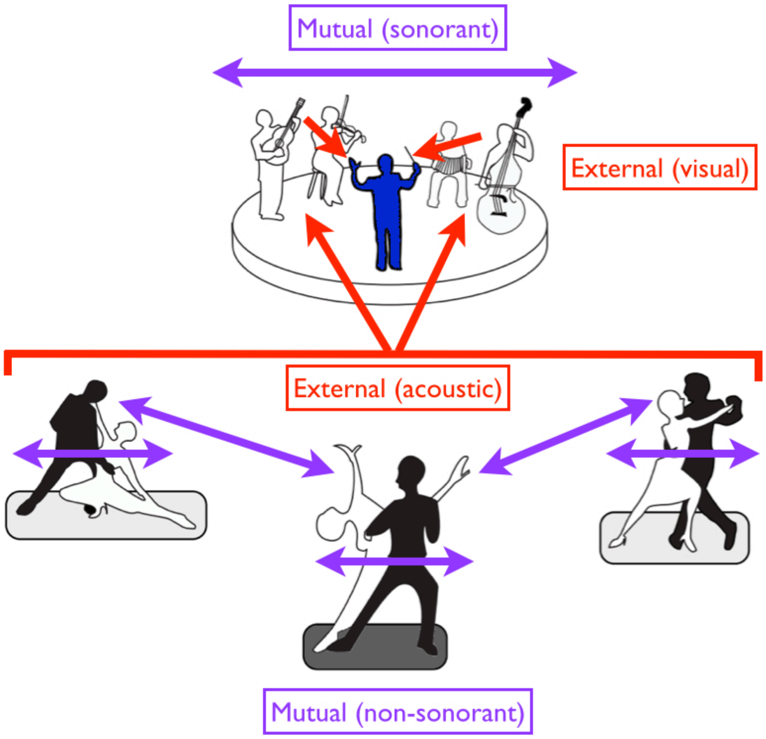


*Figure 2.6. A diversity of entrainment types in dancers and musicians.*

Red arrows suggest external pacing, while purple arrows suggest mutual pacing. Black figures are leaders while white figures are followers. Regarding external pacing, the dancers are acoustically paced by the music, while the musicians are visually paced by the conductor. Mutual pacing is seen at two levels for the dancers: (1) within each couple (through both kinesthetic and visual interactions), and (2) between the "lead" couple in the center and the two outer couples (through visual interactions alone). Such pacing is non-sonorant. Mutual pacing is also seen at top among the four musicians of the ensemble, but this pacing is sonorant. In the case of mutual pacing, each individual or group of individuals can serve as both a leader and a follower, with the role alternating in an adaptive fashion. However, when individuals or groups are externally paced, they are purely followers.

As mentioned above, when dancers move to the beat of music, they do not have any influence over the music and therefore do not have the ability to "lead" the music the way that it leads them. However, things are different when it comes to the mutual pacing between the two dance partners themselves. The hallmark feature of mutual pacing is adaptivity, the idea that members of the group can dynamically influence one another's movements and timing. Each member is both the sender and receiver of signals. Entrainment is emergent. Each member contributes to the generation of the pace, even if the leader has the more dominant role. This contrasts with external pacing, where producers are literally "following the beat"; in other words, they are pure followers. (It is important to keep in mind that during external pacing, the music that is serving as the "leader" for the dancers is itself produced by either a solo musician in a self-paced manner or a group of musicians in a mutually-paced manner through an interplay between leaders and followers). The literature on entrainment has focused almost exclusively on external pacing, most especially using the finger-tapping paradigm. Mutual pacing has been far less studied (though, see Phillips-Silver et al. (2010) for a theoretical model of mutual entrainment). A small number of finger tapping studies have looked at situations of "adaptive" tapping with virtual partners whose tempo varies over the course of a session (Repp and Keller, 2008; Fairhurst et al., 2013). What is strongly needed is a research program dealing with the nature of mutual pacing, including its leader/follower dynamic. Such a research program has to address the two problematic issues described above: (1) the relationship between mutual pacing and external pacing, such as when a dance couple moves to the beat of music or when a chorus performs with a conductor, and (2) the relationship between mutual pacing and external pacing when the movements are sonorant, such as when a chorus sings a cappella (Palmer et al., 2013).

Our final thought is about evolution. As mentioned in the Introduction, the human capacity for external entrainment has garnered much attention and has been analyzed by a large literature devoted to finger tapping. In reality, directed finger tapping of the type that occurs in a psychology experiment is one of the least naturalistic motor activities that people engage in; people are far more likely to tap their finger to music in an unconscious manner than they are to do so in a voluntary manner. The most naturalistic behavior that involves synchronization of movement to an acoustic beat is dance, either solo or in a group. So, the experimental finger-tapping paradigm is, in many respects, a model of dance, although it is never discussed as such. Likewise, the evolutionary analysis of the human capacity for acoustic entrainment is really an analysis of the evolution of dance. Finally, for all the discussion about external entrainment in animals (Patel et al., 2009; Schachner et al., 2009; Zarco et al., 2009; Cook et al., 2013; Hattori et al., 2013; Merchant and Honing, 2014), it needs to be pointed out that mutual entrainment is the dominant – and most ancient – form of entrainment in the animal world. Examples abound in the form of group locomotor behaviors (e.g., birds flying in formation, fish swimming in formation) and all forms of chorusing. This is especially expressed in non-metric forms. It is likely that the capacity for external entrainment is phylogenetically recent, having evolved from the capacity for mutual entrainment. While it might be the case that few animals are able to "follow the beat" when it comes to human-generated stimuli, we cannot allow this observation to obscure the fact that entrainment occurs on a massive scale in the animal world. Group locomotor and vocal behaviors are no less valid a topic for the analysis of entrainment than is a cockatoo bobbing its head to the beat of pop music. What is needed is an expansion of the research program on entrainment to include mutual pacing in humans and other animals.

## 2.7 Declarations

### 2.7.1 Conflict of Interest Statement

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

### 2.7.1 Acknowledgments

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# 2.8 References

Albouy, G., Sterpenich, V., Vandewalle, G., Darsaud, A., Gais, S., Rauchs, G., et al. (2012). Neural correlates of performance variability during motor sequence acquisition. Neuroimage 60, 324–331. doi: 10.1016/j.neuroimage.2011.12.049

Aoki, T., Tsuda, H., Takasawa, M., Osaki, Y., Oku, N., Hatazawa, J., et al. (2005). The effect of tapping finger and mode differences on cortical and subcortical activities: a PET study. Exp. Brain Res. 160, 375–383. doi: 10.1007/s00221-004-2008-9

Aramaki, Y., Honda, M., Okada, T., and Sadato, N. (2006). Neural correlates of the spontaneous phase transition during bimanual coordination. Cereb. Cortex 16, 1338–1348. doi: 10.1093/cercor/bhj075

Asanuma, C., Thach, W. T., and Jones, E. G. (1983). Distribution of cerebellar terminations and their relation to other afferent terminations in the ventral lateral thalamic region of the monkey. Brain Res. 286, 237–265. doi: 10.1016/0165-0173(83)90015-2

Bengtsson, S. L., Ehrsson, H. H., Forssberg, H., and Ullén, F. (2005). Effector-independent voluntary timing: behavioural and neuroimaging evidence. Eur. J. Neurosci. 22, 3255–3265. doi: 10.1111/j.1460-9568.2005.04517.x

Bijsterbosch, J. D., Lee, K.-H., Hunter, M. D., Tsoi, D. T., Lankappa, S., Wilkinson, I. D., et al. (2011). The role of the cerebellum in sub- and supraliminal error correction during sensorimotor synchronization: evidence from fMRI and TMS. J. Cogn. Neurosci. 23, 1100–1112. doi: 10.1162/jocn.2010.21506

Blinkenberg, M., Bonde, C., Holm, S., Svarer, C., Andersen, J., Paulson, O. B., et al. (1996). Rate dependence of regional cerebral activation during performance of a repetitive motor task: A PET study. J. Cereb. Blood Flow Metab. 16, 794–803. doi: 10.1097/00004647-199609000-00004

Boecker, H., Dagher, A., Ceballos-Baumann, A. O., Passingham, R. E., Samuel, M., Friston, K. J., et al. (1998). Role of the human rostral supplementary motor area and the basal ganglia in motor sequence control: Investigations with H2 15O PET. J. Neurophysiol. 79, 1070–1080.

Bostan, A., and Strick, P. (2010). The cerebellum and basal ganglia are interconnected. Neuropsychol. Rev. 20, 261–270. doi: 10.1007/s11065-010-9143-9

Brown, S., Martinez, M. J., and Parsons, L. M. (2006). The neural basis of human dance. Cereb. Cortex 16, 1157–1167. doi: 10.1093/cercor/bhj057

Calautti, C., Serrati, C., and Baron, J.-C. (2001). Effects of age on brain activation during auditory-cued thumb-to-index opposition: a positron emission tomography study. Stroke32, 139–146. doi: 10.1161/01.STR.32.1.139

Catalan, M., Ishii, K., Honda, M., Samii, A., and Hallett, M. (1999). A PET study of sequential finger movements of varying length in patients with Parkinson's disease. Brain 122, 483–495. doi: 10.1093/brain/122.3.483

Catalan, M. J., Honda, M., Weeks, R. A., Cohen, L. G., and Hallett, M. (1998). The functional neuroanatomy of simple and complex sequential finger movements: a PET study. Brain 121, 253–264. doi: 10.1093/brain/121.2.253

Chen, J. L., Zatorre, R. J., and Penhune, V. B. (2006). Interactions between auditory and dorsal premotor cortex during synchronization to musical rhythms. Neuroimage 32, 1771–1781. doi: 10.1016/j.neuroimage.2006.04.207

Coffman, K. E., Dum, R. P., and Strick, P. L. (2011). Cerebellar vermis is a target of projections from the motor areas in the cerebral cortex. Proc. Natl. Acad. Sci. U.S.A. 108, 16068–16073. doi: 10.1073/pnas.1107904108

Cook, P., Rouse, A., Wilson, M., and Reichmuth, C. (2013). A California sea lion (Zalophus californianus) can keep the beat: motor entrainment to rhythmic auditory stimuli in a non vocal mimic. J. Comp. Psychol. 127, 412–427. doi: 10.1037/a0032345

Coull, J., and Nobre, A. (2008). Dissociating explicit timing from temporal expectation with fMRI. Curr. Opin. Neurobiol. 18, 137–144. doi: 10.1016/j.conb.2008.07.011

Cunnington, R., Windischberger, C., Deecke, L., and Moser, E. (2002). The preparation and execution of self-initiated and externally-triggered movement: a study of event-related fMRI. Neuroimage 15, 373–385. doi: 10.1006/nimg.2001.0976

De Guio, F., Jacobson, S. W., Molteno, C. D., Jacobson, J. L., and Meintjes, E. M. (2012). Functional magnetic resonance imaging study comparing rhythmic finger tapping in children and adults. Pediatr. Neurol. 46, 94–100. doi: 10.1016/j.pediatrneurol.2011.11.019

Eickhoff, S. B., Bzdok, D., Laird, A. R., Roski, C., Caspers, S., Zilles, K., et al. (2011). Co-activation patterns distinguish cortical modules, their connectivity and functional differentiation. Neuroimage 57, 938–949. doi: 10.1016/j.neuroimage.2011.05.021

Fairhurst, M. T., Janata, P., and Keller, P. E. (2013). Being and feeling in sync with an adaptive virtual partner: brain mechanisms underlying dynamic cooperativity. Cereb. Cortex 3, 2592–2600. doi: 10.1093/cercor/bhs243

Garraux, G., McKinney, C., Wu, T., Kansaku, K., Nolte, G., and Hallett, M. (2005). Shared brain areas but not functional connections controlling movement timing and order. J. Neurosci. 25, 5290–5297. doi: 10.1523/JNEUROSCI.0340-05.2005

Gerardin, E., Sirigu, A., Lehéricy, S., Poline, J. B., Gaymard, B., Marsault, C., et al. (2000). Partially overlapping neural networks for real and imagined hand movements. Cereb. Cortex 10, 1093–1104. doi: 10.1093/cercor/10.11.1093

Goebl, W., and Palmer, C. (2009). Synchronization of timing and motion among performing musicians. Music Percept. 26, 427–438. doi: 10.1525/mp.2009.26.5.427

Grahn, J. A., and Brett, M. (2007). Rhythm and beat perception in motor areas of the brain. J. Cogn. Neurosci. 19, 893–906. doi: 10.1162/jocn.2007.19.5.893

Grodd, W., Hülsmann, E., Lotze, M., Wildgruber, D., and Erb, M. (2001). Sensorimotor mapping of the human cerebellum: fMRI evidence of somatotopic organization. Hum. Brain Mapp. 13, 55–73. doi: 10.1002/hbm.1025

Haber, S. N., and Calzavara, R. (2009). The cortico-basal ganglia integrative network: the role of the thalamus. Brain Res. Bull. 78, 69–74. doi: 10.1016/j.brainresbull.2008.09.013

Halpern, A. R., and Zatorre, R. J. (1999). When that tune runs through your head: A PET investigation of auditory imagery for familiar melodies. Cereb. Cortex 9, 697–704. doi: 10.1093/cercor/9.7.697

Hattori, Y., Tomonaga, M., and Matsuzawa, T. (2013). Spontaneous synchronized tapping to an auditory rhythm in a chimpanzee. Sci. Rep. 3:1566. doi: 10.1038/srep01566

Hove, M. J., Fairhurst, M. T., Kotz, S. A., and Keller, P. E. (2013). Synchronizing with auditory and visual rhythms: An fMRI assessment of modality differences and modality appropriateness. Neuroimage 67, 313–321. doi: 10.1016/j.neuroimage.2012.11.032

Ivry, R. B., and Spencer, R. M. C. (2004). The neural representation of time. Curr. Opin. Neurobiol. 14, 225–232. doi: 10.1016/j.conb.2004.03.013

Jahanshahi, M., Jenkins, I., and Brown, R. (1995). Self-initiated versus externally triggered movements. I. An investigation using measurement of regional cerebral blood flow with PET and movement-related potentials in normal and Parkinson's disease subjects. Brain 118, 913–933. doi: 10.1093/brain/118.4.913

Jäncke, L., Loose, R., Lutz, K., Specht, K., and Shah, N. J. (2000). Cortical activations during paced finger-tapping applying visual and auditory pacing stimuli. Cogn. Brain Res. 10, 51–66. doi: 10.1016/S0926-6410(00)00022-7

Jantzen, K. J., Oullier, O., Marshall, M., Steinberg, F. L., and Kelso, J. A. S. (2007). A parametric fMRI investigation of context effects in sensorimotor timing and coordination. Neuropsychologia 45, 673–684. doi: 10.1016/j.neuropsychologia.2006.07.020

Jantzen, K. J., Steinberg, F. L., and Kelso, J. A. S. (2005). Functional MRI reveals the existence of modality and coordination-dependent timing networks. Neuroimage 25, 1031–1042. doi: 10.1016/j.neuroimage.2004.12.029

Jantzen, K. J., Steinberg, F. L., and Kelso, J. A. (2004). Brain networks underlying human timing behavior are influenced by prior context. Proc. Natl. Acad. Sci. U.S.A. 101, 6815–6820. doi: 10.1073/pnas.0401300101

Jenkins, I. H., Jahanshahi, M., Jueptner, M., Passingham, R. E., and Brooks, D. J. (2000). Self-initiated versus externally triggered movements. II. The effect of movement predictability on regional cerebral blood flow. Brain 123,1216–1228. doi: 10.1093/brain/123.6.1216

Joliot, M., Crivello, F., Badier, J. M., Diallo, B., Tzourio, N., and Mazoyer, B. (1998). Anatomical congruence of metabolic and electromagnetic activation signals during a self-paced motor task: A combined PET-MEG study. Neuroimage 7, 337–351. doi: 10.1006/nimg.1998.0333

Joliot, M., Papathanassiou, D., Mellet, E., Quinton, O., Mazoyer, N., Courtheoux, P., et al. (1999). FMRI and PET of self-paced finger movement: comparison of intersubject stereotaxic averaged data. Neuroimage 10, 430–447. doi: 10.1006/nimg.1999.0483

Jordania, J. (2006). Who Asked the First Question? The Origins of Human Choral Singing, Intelligence, Language and Speech. Tbilisi: Logos.

Kadota, H., Nakajima, Y., Miyazaki, M., Sekiguchi, H., Kohno, Y., Amako, M., et al. (2010). An fMRI study of musicians with focal dystonia during tapping tasks. J. Neurol. 257, 1092–1098. doi: 10.1007/s00415-010-5468-9

Kawashima, R., Okuda, J., Umetsu, A., Sugiura, M., Inoue, K., Suzuki, K., et al. (2000). Human cerebellum plays an important role in memory-timed finger movement: an fMRI study. J. Neurophysiol. 83, 1079–1087.

Keren-Happuch, E., Chen, S.-H. A., Ho, M.-H. R., and Desmond, J. E. (2014). A meta-analysis of cerebellar contributions to higher cognition from PET and fMRI studies. Hum. Brain Mapp. 35, 593–615. doi: 10.1002/hbm.22194

Knoblich, G., and Sebanz, N. (2008). Evolving intentions for social interaction: from entrainment to joint action. Phil. Trans. R. Soc. B 363, 2021–2031. doi: 10.1098/rstb.2008.0006

Kornysheva, K., and Schubotz, R. I. (2011). Impairment of auditory-motor timing and compensatory reorganization after ventral premotor cortex stimulation. PLoS ONE6:e21421. doi: 10.1371/journal.pone.0021421

Kuhtz-Buschbeck, J., Mahnkopf, C., Holzknecht, C., Siebner, H., Ulmer, S., and Jansen, O. (2003). Effector-independent representations of simple and complex imagined finger movements: a combined fMRI and TMS study. Eur. J. Neurosci. 18, 3375–3387. doi: 10.1111/j.1460-9568.2003.03066.x

Kung, S.-J., Chen, J. L., Zatorre, R. J., and Penhune, V. B. (2013). Interacting cortical and basal ganglia networks underlying finding and tapping to the musical beat. J. Cogn. Neurosci. 25, 401–420. doi: 10.1162/jocn_a_00325

Larsson, J., Gulyás, B., and Roland, P. (1996). Cortical representation of self-paced finger movement. Neuroreport 7, 463–468. doi: 10.1097/00001756-199601310-00021

Larsson, M. (2014). Self-generated sounds of locomotion and ventilation and the evolution of human rhythmic abilities. Anim. Cogn. 17, 1–14. doi: 10.1007/s10071-013-0678-z

Lehéricy, S., Bardinet, E., Tremblay, L., Van de Moortele, P.-F., Pochon, J.-B., Dormont, D., et al. (2006). Motor control in basal ganglia circuits using fMRI and brain atlas approaches. Cereb. Cortex 16, 149–161. doi: 10.1093/cercor/bhi089

Lerner, A., Shill, H., Hanakawa, T., Bushara, K., Goldfine, A., and Hallett, M. (2004). Regional cerebral blood flow correlates of the severity of writer's cramp symptoms. Neuroimage 21, 904–913. doi: 10.1016/j.neuroimage.2003.10.019

Lissek, S., Hausmann, M., Knossalla, F., Peters, S., Nicolas, V., Güntürkün, O., et al. (2007). Sex differences in cortical and subcortical recruitment during simple and complex motor control: an fMRI study. Neuroimage 37, 912–926. doi: 10.1016/j.neuroimage.2007.05.037

Loehr, J. D., Koutis, D., Vesper, C., Sebanz, N., and Knoblich, G. (2013). Monitoring individual and joint action outcomes in duet music performance. J. Cogn. Neurosci., 25, 1049–1061. doi: 10.1162/jocn_a_00388

Matano, S., and Hirasaki, E. (1997). Volumetric comparisons in the cerebellar complex of anthropoids, with special reference to locomotor types. Am. J. Phys. Anthropol. 103, 173–183.

Matthys, K., Smits, M., Van der Geest, J. N., Van der Lugt, A., Seurinck, R., Stam, H. J., et al. (2009). Mirror-induced visual illusion of hand movements: a functional magnetic resonance imaging study. Arch. Phys. Med. Rehabil. 90, 675–681. doi: 10.1016/j.apmr.2008.09.571

Mayville, J. M., Jantzen, K. J., Fuchs, A., Steinberg, F. L., and Kelso, J. A. S. (2002). Cortical and subcortical networks underlying syncopated and synchronized coordination revealed using fMRI. Functional magnetic resonance imaging. Hum. Brain Mapp. 17, 214–229. doi: 10.1002/hbm.10065

Merchant, H., and Honing, H. (2014). Are non-human primates capable of rhythmic entrainment? Evidence for the gradual audiomotor evolution hypothesis. Front. Neurosci. 7:274. doi: 10.3389/fnins.2013.00274

Merker, B. H., Madison, G. S., and Eckerdal, P. (2009). On the role and origin of isochrony in human rhythmic entrainment. Cortex 45, 4–17. doi: 10.1016/j.cortex.2008.06.011

Mostofsky, S. H., Rimrodt, S. L., Schafer, J. G. B., Boyce, A., Goldberg, M. C., Pekar, J. J., et al. (2006). Atypical motor and sensory cortex activation in attention-deficit/hyperactivity disorder: a functional magnetic resonance imaging study of simple sequential finger tapping. Biol. Psychiatry 59, 48–56. doi: 10.1016/j.biopsych.2005.06.011

Nichols, T., Brett, M., Andersson, J., Wager, T., and Poline, J.-B. (2005). Valid conjunction inference with the minimum statistic. Neuroimage 25, 653–660. doi: 10.1016/j.neuroimage.2004.12.005

Nyberg, L., Eriksson, J., Larsson, A., and Marklund, P. (2006). Learning by doing versus learning by thinking: an fMRI study of motor and mental training. Neuropsychologia 44, 711–717. doi: 10.1016/j.neuropsychologia.2005.08.006

Onodera, S., and Hicks, T. P. (1998). Projections from substantia nigra and zona incerta to the cat's nucleus of Darkschewitsch. J. Comp. Neurol. 396, 461–482.

Oullier, O., Jantzen, K. J., Steinberg, F. L., and Kelso, J. S. (2005). Neural substrates of real and imagined sensorimotor coordination. Cereb. Cortex 15, 975–985. doi: 10.1093/cercor/bhh198

Palmer, C., Spidle, F., Koopmans, E., and Schubert, P. (2013). "Temporal coordination in vocal duet performances of musical rounds," in Proceedings of the Sound and Music Computing (SMC) Conference (Stockholm).

Patel, A. D. (2014). The evolutionary biology of musical rhythm: was darwin wrong? PLoS Biol. 12:e1001821. doi: 10.1371/journal.pbio.1001821

Patel, A., and Iversen, J. (2014). The evolutionary neuroscience of musical beat perception: the Action Simulation for Auditory Prediction (ASAP) hypothesis. Front. Syst. Neurosci. 8:57. doi: 10.3389/fnsys.2014.00057

Patel, A. D., Iversen, J. R., Bregman, M. R., and Schulz, I. (2009). Experimental evidence for synchronization to a musical beat in a nonhuman animal. Curr. Biol. 19, 827–830. doi: 10.1016/j.cub.2009.03.038

Pecenka, N., Engel, A., and Keller, P. E. (2013). Neural correlates of auditory temporal predictions during sensorimotor synchronization. Front. Hum. Neurosci. 7:380. doi: 10.3389/fnhum.2013.00380

Peres, I., Vetter, C., Blautzik, J., Reiser, M., Pöppel, E., Meindl, T., et al. (2011). Chronotype predicts activity patterns in the neural underpinnings of the motor system during the day. Chronobiol. Int. 28, 883–889. doi: 10.3109/07420528.2011.619084

Petacchi, A., Laird, A. R., Fox, P. T., and Bower, J. M. (2005). Cerebellum and auditory function: an ALE meta-analysis of functional neuroimaging studies. Hum. Brain Mapp. 25, 118–128. doi: 10.1002/hbm.20137

Phillips-Silver, J., Aktipis, C. A., and Bryant, G. A. (2010). The ecology of entrainment: foundations of coordinated rhythmic movement. Music Percept. 28, 3–14. doi: 10.1525/mp.2010.28.1.3

Phillips-Silver, J., and Keller, P. E. (2012). Searching for roots of entrainment and joint action in early musical interactions. Front. Hum. Neurosci. 6:26. doi: 10.3389/fnhum.2012.00026

Rao, S., Mayer, A., and Harrington, D. (2001). The evolution of brain activation during temporal processing. Nat. Neurosci. 4, 317–323. doi: 10.1038/85191

Rao, S. M., Harrington, D. L., Haaland, K. Y., Bobholz, J. A., Cox, R. W., and Binder, J. R. (1997). Distributed neural systems underlying the timing of movements. J. Neurosci. 17, 5528–5535.

Redgrave, P., Rodriguez, M., Smith, Y., Rodriguez-Oroz, M. C., Lehericy, S., Bergman, H., et al. (2010). Goal-directed and habitual control in the basal ganglia: implications for Parkinson's disease. Nat. Rev. Neurosci. 11, 760–772. doi: 10.1038/nrn2915

Repp, B. (2005). Sensorimotor synchronization: a review of the tapping literature. Psychon. Bull. Rev. 12, 969–992. doi: 10.3758/BF03206433

Repp, B. H., and Keller, P. E. (2004). Adaptation to tempo changes in sensorimotor synchronization: effects of intention, attention, and awareness. Q. J. Exp. Psychol. A 57A, 499–521. doi: 10.1080/02724980343000369

Repp, B. H., and Keller, P. E. (2008). Sensorimotor synchronization with adaptively timed sequences. Hum. Mov. Sci. 27, 423–456. doi: 10.1016/j.humov.2008.02.016

Repp, B. H., and Penel, A. (2002). Auditory dominance in temporal processing: new evidence from synchronization with simultaneous visual and auditory sequences. J. Exp. Psychol. Hum. Percept. Perform. 28, 1085–1099. doi: 10.1037/0096-1523.28.5.1085

Repp, B. H., and Penel, A. (2004). Rhythmic movement is attracted more strongly to auditory than to visual rhythms. Psychol. Res. 68, 252–270. doi: 10.1007/s00426-003-0143-8

Repp, B. H., and Su, Y.-H. (2013). Sensorimotor synchronization: a review of recent research (2006-2012). Psychon. Bull. Rev. 20, 403–452. doi: 10.3758/s13423-012-0371-2

Riecker, A., Gröschel, K., Ackermann, H., Steinbrink, C., Witte, O., and Kastrup, A. (2006). Functional significance of age-related differences in motor activation patterns. Neuroimage 32, 1345–1354. doi: 10.1016/j.neuroimage.2006.05.021

Roessner, V., Wittfoth, M., Schmidt-Samoa, C., Rothenberger, A., Dechent, P., and Baudewig, J. (2012). Altered motor network recruitment during finger tapping in boys with Tourette syndrome. Hum. Brain Mapp. 33, 666–675. doi: 10.1002/hbm.21240

Rounis, E., Lee, L., Siebner, H. R., Rowe, J. B., Friston, K. J., Rothwell, J. C., et al. (2005). Frequency specific changes in regional cerebral blood flow and motor system connectivity following rTMS to the primary motor cortex. Neuroimage 26, 164–176. doi: 10.1016/j.neuroimage.2005.01.037

Sadato, N., Yonekura, Y., Waki, A., Yamada, H., and Ishii, Y. (1997). Role of the supplementary motor area and the right premotor cortex in the coordination of bimanual finger movements. J. Neurosci. 17, 9667–9674.

Schachner, A., Brady, T. F., Pepperberg, I. M., and Hauser, M. D. (2009). Spontaneous motor entrainment to music in multiple vocal mimicking species. Curr. Biol. 19, 831–836. doi: 10.1016/j.cub.2009.03.061

Schmidt, R. C., Fitzpatrick, P., Caron, R., and Mergeche, J. (2011). Understanding social motor coordination. Hum. Mov. Sci. 30, 834–845. doi: 10.1016/j.humov.2010.05.014

Schubotz, R. I., Friederici, A. D., and von Cramon, D. Y. (2000). Time perception and motor timing: A common cortical and subcortical basis revealed by fMRI. Neuroimage 11, 1–12. doi: 10.1006/nimg.1999.0514

Shmuelof, L., and Krakauer, J. W. (2011). Are we ready for a natural history of motor learning? Neuron 72, 469–476. doi: 10.1016/j.neuron.2011.10.017

Taylor, J. A., Klemfuss, N. M., and Ivry, R. B. (2010). An explicit strategy prevails when the cerebellum fails to compute movement errors. Cerebellum 9, 580–586. doi: 10.1007/s12311-010-0201-x

Teki, S., Grube, M., and Griffiths, T. D. (2011). A unified model of time perception accounts for duration-based and beat-based timing mechanisms. Front. Integr. Neurosci. 5:90. doi: 10.3389/fnint.2011.00090

Thaut, M. H., Demartin, M., and Sanes, J. N. (2008). Brain networks for integrative rhythm formation. PLoS ONE 3:e2312. doi: 10.1371/journal.pone.0002312

Tseng, Y. W., Diedrichsen, J., Krakauer, J. W., Shadmehr, R., and Bastian, A. J. (2007). Sensory prediction errors drive cerebellum-dependent adaptation of reaching. J. Neurophysiol. 98, 54–62. doi: 10.1152/jn.00266.2007

Turkeltaub, P. E., Eden, G. F., Jones, K. M., and Zeffiro, T. A. (2002). Meta-analysis of the functional neuroanatomy of single-word reading: method and validation. Neuroimage16, 765–780. doi: 10.1006/nimg.2002.1131

Turkeltaub, P. E., Eickhoff, S. B., Laird, A. R., Fox, M., Wiener, M., and Fox, P. (2012). Minimizing within-experiment and within-group effects in Activation Likelihood Estimation meta-analyses. Hum. Brain Mapp. 33, 1–13. doi: 10.1002/hbm.21186

Vuust, P., Roepstorff, A., Wallentin, M., Mouridsen, K., and Østergaard, L. (2006). It don't mean a thing… Keeping the rhythm during polyrhythmic tension, activates language areas (BA47). Neuroimage 31, 832–41. doi: 10.1016/j.neuroimage.2005.12.037

Weeks, R. A., Honda, M., Catalan, M. J., and Hallett, M. (2001). Comparison of auditory, somatosensory, and visually instructed and internally generated finger movements: A PET study. Neuroimage 14, 219–230. doi: 10.1006/nimg.2001.0780

Wiener, M., Turkeltaub, P., and Coslett, H. B. (2010). The image of time: a voxel-wise meta-analysis. Neuroimage 49, 1728–1740. doi: 10.1016/j.neuroimage.2009.09.064

Witt, S. T., Laird, A. R., and Meyerand, M. E. (2008). Functional neuroimaging correlates of finger-tapping task variations: an ALE meta-analysis. Neuroimage 42, 343–356. doi: 10.1016/j.neuroimage.2008.04.025

Wylie, K. P., Tanabe, J., Martin, L. F., Wongngamnit, N., and Tregellas, J. R. (2013). Nicotine increases cerebellar activity during finger tapping. PLoS ONE 8:e84581. doi: 10.1371/journal.pone.0084581

Yoo, S.-S., Wei, X., Dickey, C. C., Guttmann, C. R. G., and Panych, L. P. (2005). Long-term reproducibility analysis of fMRI using hand motor task. Int. J. Neurosci. 115, 55–77. doi: 10.1080/00207450490512650

Zarco, W., Merchant, H., Prado, L., and Mendez, J. C. (2009). Subsecond timing in primates: comparison of interval production between human subjects and rhesus monkeys. J. Neurophysiol. 102, 3191–3202. doi: 10.1152/jn.00066.2009

# Chapter 3

# Taking two to tango: fMRI analysis of improvised joint action with physical contact

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## 3.1 Abstract

Many forms of joint action involve physical coupling between the participants, such as when moving a sofa together or dancing a tango. We report the results of a novel two-person functional MRI study in which trained couple dancers engaged in bimanual contact with an experimenter standing next to the bore of the magnet, and in which the two alternated between being the leader and the follower of joint improvised movements. Leading showed a general pattern of self-orientation, being associated with brain areas involved in motor planning, navigation, sequencing, action monitoring, and error correction. In contrast, following showed a far more sensory, externally-oriented pattern, revealing areas involved in somatosensation, proprioception, motion tracking, social cognition,

and outcome monitoring. We also had participants perform a "mutual" condition in which the movement patterns were pre-learned and the roles were symmetric, thereby minimizing any tendency toward either leading or following. The mutual condition showed greater activity in brain areas involved in mentalizing and social reward than did leading or following. Finally, the analysis of improvisation revealed the dual importance of motor-planning and working-memory areas. We discuss these results in terms of theories of both joint action and improvisation.

## 3.2 Introduction

Humans routinely engage in joint actions, where several individuals coordinate their behaviors around a common goal, generally for cooperative purposes, for example the members of a rowing team rowing in synchrony [1,2]. Joint actions can vary with regard to whether the individuals are all performing the same action (a bucket brigade) or complementary actions (tango dancers). For the purposes of the present study, our principal interest relates to the differential roles that partners can play during joint actions, with an emphasis on the contrast between leaders and followers. At one extreme are situations in which the role of each individual is explicitly defined and is maintained throughout the course of the action, for example during many couple dances or in ensemble musical performances. At the other extreme are situations where there may be no differences in the roles of the participants, for example during a bucket brigade, where each person's movement pattern is fixed and repetitive, and where every person performs the same movement. In between, are situations where leadership is fluid – rather than being either fixed or absent – as in the turn-taking that occurs during conversation or the complementary pushing and pulling actions that take place when moving a piece of furniture.

An important characteristic of these roles is the degree to which an individual adapts to one's partner(s) during the course of the interaction, in other words "who adapts to whom and to what degree" [3:688]. A person who adapts to others more than others adapt to him/her is considered a follower. A follower focuses on the external sensory cues that allow the person to align his/her behavior both spatially and temporally to the behavior of his/her partners. Because the actions of a follower are dependent on others' actions, following can be seen as an externally-driven behavior. Leading, in contrast to this, is far more internally-driven. A leader is less adaptive to others, and therefore mainly acts in accordance with his/her own intentions [3]. A leader is often the initiator of joint actions and is the major determinant of the spatio-temporal characteristics of the movements. As a result, leaders have to devise strategies to communicate their intentions to followers in order to accomplish the goals of the group [4,5]. Leading and following should not be seen as dichotomous roles, but instead as a continuum that depends on the degree to which each partner adapts to others [3]. Even for a pair of dancers or a group of musicians, where leadership roles are explicitly defined, partners nonetheless adapt to one another in an ongoing and mutual manner [6–8].

To the best of our knowledge, the only functional magnetic resonance imaging (fMRI) study to explicitly examine the dynamics of leading and following was that of Fairhurst et al. [3], in which participants performed an auditory finger-tapping task not with a human partner but with a computer program in the form of a virtual adaptive partner. The authors identified post-hoc those participants who tended to lead, compared to those who tended to follow, with leaders being defined as individuals who had a greater self-focus and who prioritized a stable tempo for the task, and followers as individuals who had a greater other-focus and who prioritized synchronization with their partner over stability of the task. Leaders showed greater activity in brain areas involved in self-initiated action, such as the pre-supplementary motor area (pre-SMA), dorsal anterior cingulate cortex (dACC), premotor cortex (PMC), right inferior frontal gyrus (IFG), and right inferior parietal lobule (IPL), as well as areas related to the integration of information coming from the self and other, such as the precuneus. However, Fairhurst et al. [3] did not report any activity specific for the followers.

A handful of electroencephalography (EEG) studies have looked at the neural basis of leading and following using hyperscanning methods. Sänger et al. [9], in a study of guitar duetting, showed that the pre-assigned leaders of these duets had an increased phase locking in the delta frequency range before playing onsets and a more distributed network of activity than did followers, which may reflect, respectively, the decision to initiate playing and a greater sense of effort. Konvalinka et al. [10] examined a situation of joint finger tapping between two people, and demonstrated that spontaneously-emerging leaders, who adapted less to their partner during the task, had frontal alpha suppression related to an increase in resources allocated for self-processing, indicating a strategy to focus on their own taps. Leading thus seems to rely on motor processing and the self-initiation of action.

Studies of interactive imitation of visually-presented hand movements, in which one participant performs a movement that should be imitated by another, explicitly assign participants the roles of leader or follower [11–13]. Performing an action to be imitated by another person engages a set of brain areas similar to the profile of a leader observed by Fairhurst et al. [3], whereas imitating someone else's actions enhances activity in occipito-parietal regions, which may reflect enhanced attention to visual information [12] and/or the integration of visual information in order to elaborate a motor plan and regulate movement [13]. One might expect that following through another sensory modality (e.g., auditory or tactile) would lead to an increased reliance on the modality-related sensory-processing areas. In addition, interactive tasks of all kinds engage social-cognitive processes and hence activate areas associated with the mentalizing network, including the posterior superior temporal sulcus (pSTS), temporo-parietal junction (TPJ), and medial prefrontal cortex (mPFC) [14–16].

The efficacy of leading and following depends on an exchange of information between partners, as related to both the conveyance and perception of leadership cues. While the above-mentioned studies focused on the use of auditory and visual cues for guiding coordination, far less is known about the exchange of haptic information, which is the focus of the present study. This is surprising considering the strong involvement of haptic cues in real-world joint action, such as when moving furniture together or dancing with a partner. In these settings, force-based cues (i.e., pushing and pulling forces), perceived either through direct body contact or through the intermediary of a jointly-handled object, create a haptic information channel that allows individuals to coordinate their actions [17]. For example, during a partnered dance, the leader uses his arms to exert forces on the follower's upper body in order to signal his movement intentions. The haptic channel may provide a particularly efficient mechanism for interpersonal coordination, since humans entrain more effectively with one another through tactile than auditory coupling [18], although other modalities may become more explicit with training [19]. This might be due to the faster response-time of haptic than auditory or visual stimulation [20] and to the higher coupling strength of haptic contact, which supports both informational (sensory) and mechanical (physical) coupling. Mechanical links exert a stronger coupling over a system, which enhances joint coordination [17,21–23]. Moreover, haptic stimulation is less affected by the degree of attentional engagement [24], and so it can be a spontaneous source of interpersonal coordination during joint action. In spite of the prominent role of haptic information transmission during everyday interactions, the neuroscience of joint action with haptic contact has been poorly studied.

Another important feature related to the differentiation of roles during joint action is the extent to which the actions of the individuals are fixed or are improvised. Situations where the action patterns are not pre-specified and must be created in the moment tend to foster a differentiation of roles into leaders and followers [5,25]. Motor improvisation involves the online generation of novel motor sequences, as guided by movement planning, often from pre-learned repertoires of movement sequences. It also includes the use of sensory feedback to modify ongoing production [26–28]. There have been a number of studies that have looked at motor improvisation at the individual-subject level, mainly work on musical improvisation, which tends to compare improvised performance of musical sequences with the execution of pre-learned sequences, for example comparing the improvisation of jazz sequences with the performance of musical scales [29]. Such studies have revealed the importance of two types of brain areas for improvisation, namely motor-planning areas (domain-specific) and working memory areas (domain-general). The former include the PMC, pre-SMA, IPL, and IFG, whereas the latter include the dorsolateral prefrontal cortex (DLPFC) and dACC [26–28,30–32] (see also the meta-analyses of [33,34]). Interestingly, studies of willed action and pseudorandom generation of responses have highlighted a network highly similar to the ones just mentioned [28,30,35]. In the present study, we were interested in seeing if the brain network that underlies solo improvisation during transitive tasks like piano performance would be recruited during a *joint* task involving direct body contact between two individuals, something similar to a dance improvisation. In addition, the present neuroimaging study is one of the first attempts to examine the joint improvisation of a motor task. Donnay et al. [31] demonstrated that interactive musical improvisation with a partner engaged more neural resources for action monitoring and working memory than performing a pre-learned interactive task. However, this study did not compare joint improvisation with solo improvisation.

In order to explore for the first time the neural basis of leading and following in a situation of joint improvisation with direct physical contact – akin to a couple dance – we carried out a novel 2-person fMRI experiment using highly trained couple dancers (e.g., tango, salsa) as participants. In the experiment, the participant 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 hand movements, all done with the eyes closed and without any type of acoustic timekeeper (e.g., music) so as to limit communication to haptic interactions. In these conditions, the movement patterns were improvised, rather than pre-learned, in order to maintain an ongoing requirement for motor planning during leading and a comparably 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. 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 roughly comparable between the two actors. This allowed us to compare complementary vs. symmetric interactions. Finally, as a control for the motor requirements of the partnered conditions, we had participants perform a "solo" condition of improvised bimanual movements, but in the absence of physical contact with the experimenter.

We hypothesized that 1) partnered movements, compared to solo movements, would activate brain circuits involved in somatosensory and proprioceptive functioning, as well as social-cognition areas associated with interpersonal interaction, 2) leading would be associated with a motor network, including brain areas involved in motor planning, navigation, and self-initiated action, 3) following would be associated with a haptic sensory network that would mediate responsivity to haptic cues, 4) the brain network for mutual interaction would be intermediate between leading and following, 5) dance-like movement improvisation would engage a network similar to that established from other domains of motor improvisation, and 6) improvising within the context of joint action, as compared with solo improvisation, would be associated with increased demands on working memory and motor planning.

# 3.3 Methods

## 3.3.1 Participants

Nineteen dancers participated in the study after giving their written informed consent. The data from one participant was excluded due to excessive head movement. Of the remaining eighteen participants (9 males, mean age 40.4 ± 13.2), two were left-handed (1 male, 1 female). All were experts in one or several types of couple dances involving leading and following (Argentine Tango, Salsa, Swing, Ballroom), with a mean experience of 8.7 ± 7.2 years for males and 5.6 ± 2.9 years for females. None of the participants had a history of neurological or psychiatric disease. Participants received monetary compensation for their time. The study was approved by the Medical Research Ethics Board of St. Josephs Hospital, Hamilton, Canada (approval number: R.P. #12-3777).

## 3.3.2 Procedure

While a participant was lying supine in the MRI scanner, an experimenter (female, with 8 years of couple dance experience, L.A.S.C.) stood next to the bore of the scanner so as to be able to engage in bimanual contact with the participant. The side of the experimenter was counterbalanced across scans and participants. Together, the participant and experimenter performed highly controlled bimanual movements of the wrist and metacarpophalyngeal joints in all three planes of motion, with principal contact occurring at the inner surfaces of the fingers (Figure 3.1a). The participant's hands (palms up) were always below the experimenter's hands (palms down) such that his/her hands could not be passively moved by the experimenter; the participant had to actively move his/her hands in all conditions.

There were five movement conditions (Figure 3.1b) and a baseline condition of Rest. The tasks of interest were the partnered conditions of Leading, Following, and Mutual. As a control for partnering, we had participants perform similar movement tasks on their own (Solo and Alone) without contact with the experimenter. The movement patterns during Leading, Following and Solo were improvised, whereas they were pre-learned in Mutual and Alone. During Leading, the participant improvised the movements, which the experimenter followed. During Following, the experimenter improvised the movements, which the participant followed. Thus, the Following condition did not tap into improvisational mechanisms of production on the part of the participant. During Solo, the participant improvised on their own, employing the same kind of movement patterns that they would during Leading. Care was taken during a training session (see below) to ensure that the movements were globally matched among the three improvised conditions. Next, there were two non-improvised conditions, called Mutual (partnered) and Alone (non-partnered). During these conditions, participants performed one of three *pre-learned* movement sequences that were taught to them during a training session on a day prior to their scan. These sequences were designed to use the same joints and to match the degree of movement variation of the improvised conditions. The three sequences were randomized across the scans, where only one pattern was done per task-epoch. Whereas the participant and experimenter performed the Mutual condition in a partnered manner, neither of them acted as the leader or follower of the movement. Instead, the speed and amplitude of these fixed patterns arose from implicit mutual agreement. We opted for the Mutual condition to be pre-learned, rather than improvised (as in [36]), because it would have been difficult for us to verify that an improvised condition was indeed done mutually, rather than involving closely alternating bouts of leading and following between the two partners. Mutuality was more likely to emerge during pre-learned patterns where the participant and experimenter shared knowledge and goals. Finally, during Rest, participants were instructed to keep still and relax. All conditions were performed with they eyes closed and without music or auditory-entrainment cues in order to keep the focus on interpersonal entrainment through haptic cues, rather than on external entrainment to a musical beat. It should be pointed out that our paradigm has ecological relevance to dance, since many forms of contemporary dance and contact improvisation rely far more on haptic cues than on musical beats for coordination.

All participants underwent a one-hour training session on a day prior to the scanning session while lying supine on a table. They were specifically instructed to 1) not move their neck, shoulders or elbows; 2) not move any of their fingers individually, but only do so together as a hand-unit (only the

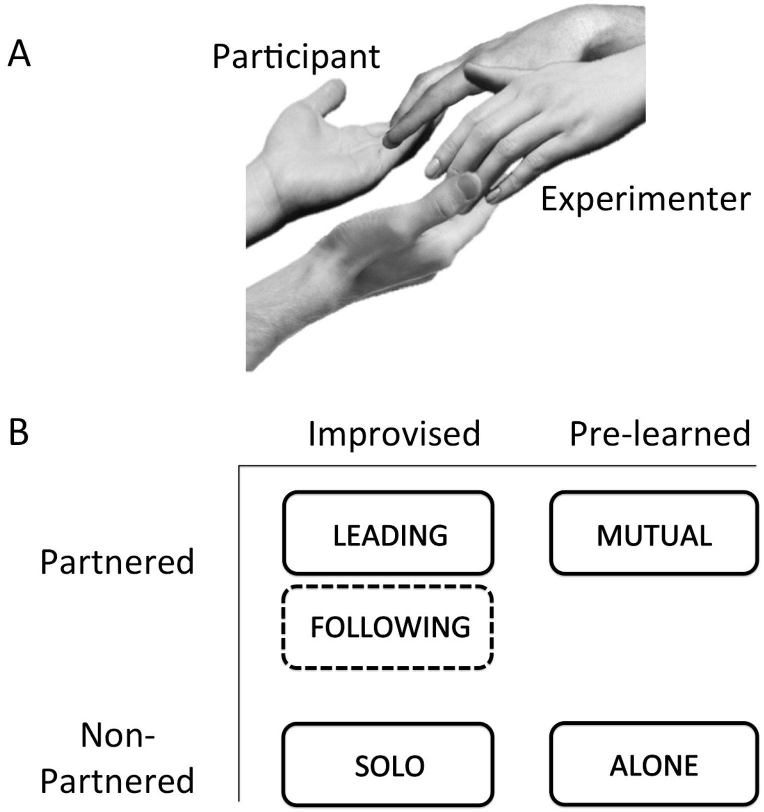

*Figure 3.1. Experimental design.*

(A) This figure shows the contact between the participant and experimenter during the partnered conditions. They performed bimanual movements of the wrist and fingers in all three planes of motion, with principal contact occurring at the inner surfaces of the fingers. The participant's hands were always palm-up below the experimenter's hands.

(B) The tasks were organized according to a 2 x 2 scheme, where one variable was partnership (partnered vs. solo tasks) and the other was improvisation (improvised vs. pre-learned movement patterns). There were five movement conditions and a baseline condition of Rest (not shown in the figure). The tasks of interest were the partnered conditions of Leading, Following, and Mutual. As a control for partnering, we had participants perform similar motor tasks, but on their own (Solo and Alone). Regarding the improvisation variable, the movements during Leading, Following and Solo were improvised. During the two non-improvised conditions, namely Mutual (partnered) and Alone (non-partnered), participants performed pre-learned movement sequences. Note that the Following condition did not tap into improvisational mechanisms of production on the part of the participant, as indicated by the jagged line for Following in the figure. Hence, the Following condition was excluded in the analysis of the main effect of improvisation.

metacarpophalyngeal joints); 3) match the speed and movement variation across all conditions; and 4) be as creative as possible when improvising. The training session ended when participants were able to perform highly controlled movements that respected the above restrictions and when they had memorized the three movement sequences for the non-improvised conditions. During the actual scanning session, the experimenter (who saw every movement in parallel to the timing progression) took detailed notes between each scan to ensure that those conditions were always fulfilled.

During scanning, the participant's head was firmly secured using foam pillows, and their forearms were fastened to the side of their body such that only their wrists, hands and fingers were able to move. Earplugs were used to help block out scanner noise. The participants and experimenter each wore MRI-compatible headphones and received verbal instructions through them. Participants were instructed to keep their eyes closed at all times. The tasks were performed according to a block design, alternating between 28s of task and 8s of a relaxation period that was excluded from the analysis. Toward the end of the relaxation period, a verbal auditory cue was delivered through the headphones informing the participant and experimenter of the next task to perform. Each task-epoch started with a high tone and ended with a low tone. All stimuli were presented using Presentation® software (version 14.4, www.neurobs.com). Each of the six tasks (five movement tasks and Rest) was performed six times in random order across three functional scans.

After scanning, participants were debriefed. They answered questions on a 5-point scale about the perceived difficulty of each task, an evaluation of their performance, the extent to which they had the feeling that they were dancing, and the extent to which they experienced auditory imagery of music while moving. These data were analysed using four one-way ANOVA's, with five levels corresponding to each of the movement conditions, respectively.

One limitation of the present study is that we were unable to collect behavioral data on task performance in the scanner. This would have required technologies such as either MRI-compatible motion capture or electromyography that we did not have access to at our imaging facility. As mentioned above, the first author participated in all of the scanning sessions and was able to verify that task performance was done properly.

### 3.3.4 Image acquisition

Axial T2*-weighted gradient-echo echo-planar images (EPI) with blood-oxygen-level-dependent (BOLD) contrast were acquired with a General Electric Achieva 3-Tesla MRI at the Imaging Research Centre at St. Joseph's Hospital in Hamilton, Ontario. The imaging parameters were 2000 ms TR, 35 ms TE, 90º flip angle, 39 axial slices, 4 mm slice thickness, 0 mm gap, 3.75 mm × 3.75 mm in-plane resolution, 64 × 64 matrix, and 240 mm field of view effectively covering the whole brain and the cerebellum. An automatic shimming procedure was performed before each scan to minimize inhomogeneities in the static magnetic field. In order to avoid T1 saturation effects, we discarded the first four dummy volumes of each scan. For each of the three functional scans, 216 volumes – corresponding to 12 epochs of 28s task + 8s relaxation – were collected over 7'12", leading to a total of 648 volumes. Intensive piloting and magnetic field (B0) testing showed no B0 distortion and very little susceptibility-by-movement distortion of the BOLD signal during this paradigm. Two magnetic field maps (5ms then 8ms TE) with the same imaging parameters as the EPI were also acquired in order to unwarp the EPI data. Structural images were acquired before the EPI sequences. The 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).

### 3.3.5 Image analysis

Functional and structural images were processed using BrainVoyager QX 2.8. Functional images were first spatially realigned and motion-corrected to the first volume of the first scan. Motion-correction analysis revealed that participants displayed very little head movement. For most participants (14 out of 18), translational and rotational corrections never exceeded 2 mm and 2º, respectively, across the three functional scans. Only three out of 54 scans (where total scans = 18 participants x 3 scans) were excluded because of motion that exceeded either 3 mm of translation or 3º of rotation. Following rigid motion correction, unwarping was performed with the relaxation method of "anatabacus", a plugin in BrainVoyager [37] in order to correct for non-rigid deformations. A temporal high-pass filter was applied at a cut-off frequency of 0.0078 Hz, or 1/128 cycles. Three-dimensional spatial smoothing was performed using a Gaussian filter with a FWHM kernel size of 4 mm. Each functional scan was then normalized to the Talairach template [38]. The BOLD response for each task-block was modeled as the convolution of a 28s 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. Six head-motion parameters, describing translation and rotation of the head, 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. The resulting statistical parametric maps were interpolated to facilitate comparison between conditions. Talairach coordinates were extracted using NeuroElf (neuroelf.net).

### 3.3.6 Definition of statistical contrasts

We performed three sets of analyses on the images. The first one tested the main effect of partnering and the difference between the three partnered conditions (Leading, Following, and Mutual). The second one assessed the main effect and specificity of improvisation. The third set assessed the specific effect of improvising during partnered movements. Direct contrasts between conditions were performed at $p < 0.05$ corrected with the False Discovery Rate (FDR) and a cluster threshold of $k = 20$ voxels. Because they were more stringent, the conjunctions of contrasts and the contrasts between conjunctions (see next section) were performed at $p < 0.005$ uncorrected. For such contrasts, we applied the same cluster threshold of $k=20$ voxels, which was above the cluster threshold estimated by Alphasim in NeuroElf (family-wise error correction $p<0.05$). All contrasts were balanced.

#### 3.3.6.1 Effects of partnering

To identify brain regions associated with partnered movement, we computed the conjunction of partnered versus non-partnered contrasts: [Leading > Non-Partnered] ∩ [Following > Non-Partnered] ∩ [Mutual > Non-Partnered], where the non-partnered conditions were Solo and Alone. We tested for the specificity of Leading, Following and Mutual among themselves after removing both basic motor effects (i.e., the non-partnered conditions) and partnering effects that all three conditions shared (i.e., the conjunction of the partnered conditions) using the following contrasts: 1) Leading: [Leading > Non-Partnered] > [Partnership Conjunction], 2) Following: [Following > Non-Partnered] > [Partnership Conjunction], and 3) Mutual: [Mutual > Non-Partnered] > [Partnership Conjunction].

#### 3.3.6.2 Effects of improvisation

We tested the main effect of improvisation irrespective of partnership by examining the contrast [Leading + Solo] > [Mutual + Alone]. However, these pairs of conditions actually varied in two manners. One was with regard to improvisation, while the other was with respect to movement variability. The improvised conditions tended to have more variability in motion compared to the sequences used in the non-improvised tasks, which were fixed and repetitive. We therefore used the Following condition to disentangle this situation, since 1) movement variability in Following was similar to that during Leading and Solo, but 2) Following did not require improvisation on the part of the participant, as with Mutual and Alone. We conducted region-of-interest (ROI) analyses, in which ROI's were defined as spheres of 5 mm radius centered on the peaks of the activations found in the improvisation contrast [Leading + Solo] > [Mutual + Alone]. Beta values were extracted from these ROI's, and t-tests were conducted to determine if the betas for Following were significantly different from the mean betas for the improvised conditions, on the one hand, and the non-improvised conditions, on the other. We defined purely improvisation-related areas as those whose activity was significantly higher when participants *generated* novel motor sequences (i.e., Leading and Solo) compared with when they *executed* similar sequences without generating them (Following). In contrast, we defined areas related to movement variability as those whose activity was significantly higher when participants executed *variable* sequences (Following) compared with when they executed *repetitive* sequences (Mutual and Alone).

Next, we looked at brain areas that were involved in self-initiation of movement (Leading, Mutual, Solo, Alone) versus Following as the one externally-driven condition. We did this with the contrast [Leading + Solo + Mutual + Alone] > Following.

### 3.3.6.3 Effects of improvising with a partner

Finally, we wanted to explore if there was an effect of improvising with a partner compared to improvising solo, beyond the mere presence of skin-to-skin contact. Such an effect might reflect an interpersonal signalling strategy in leaders during joint action. First, we directly contrasted Leading and Solo. Next, to search for activity for Leading that was not attributable to either improvisational production (as in Solo) or physical contact with a partner (as in Following and Mutual), we performed the contrast [Leading > Mutual] > [Solo > Alone], and the conjunction [Leading > Solo] ∩ [Leading > Following].

## 3.4 Results

### 3.4.1 Behavioural data

Post-scanning questionnaires revealed a main effect of condition for all four questions, as follows: perceived difficulty (D): $F(4,85) = 5.62$, $p < 0.001$; performance quality (P): $F(4,85) = 3.31$, $p= 0.014$; impression of dancing: $F(4,85) = 9.83$, $p < 0.001$; and musical imagery: $F(4,85) = 9.76$, $p= 0.001$. The first two effects were due to an increased perception of difficulty and a decreased perception of performance quality for Leading (D 2.1, P 4.1) and Following (D 2.0, P 4.1) compared to the Alone condition (D 1.1, P 4.7), with Solo (D 1.6, P 4.5) and Mutual (D 1.5, P 4.5) sitting in between. In general, perceived difficulty was low and perceived performance quality was high for all tasks. Interestingly, conditions with more-variable motor sequences were perceived as more dance-like (Leading: 3.9, Following: 3.7, and Solo: 4.0) than conditions with repetitive motor sequences (Mutual: 2.5, Alone: 2.4). The improvised conditions elicited more musical imagery (Leading: 3.9 and Solo: 4.0) than the non-improvised conditions (Following: 2.4, Mutual: 2.1, Alone: 2.7).

## 3.4.2 fMRI data

### 3.4.2.1 Partnering

We examined the main effect of partnering by contrasting the three partnered conditions with the two non-partnered conditions (Figure 3.2, with Talairach coordinates in Table 3.1). As expected, we found strong activations in brain regions involved in tactile perception and proprioception, including the primary somatosensory cortex (S1), secondary somatosensory cortex (S2), and ventral thalamus. In addition, we found activity in limbic areas such as the midcingulate cortex (MCC) and anterior insula that are involved in orienting the body to cutaneous stimuli and in processing internal sensation. Finally, we observed activity in areas involved in the perception of dynamic social stimuli (pSTS) and mentalizing (mPFC and TPJ).

Having looked at what the three partnered conditions shared, we next explored role-related effects by examining neural specificity for Leading, Following, and Mutual among themselves (Figure 3.3 and Table 3.2). Relative to the other two partnered conditions, Leading showed a clear profile indicative of motor planning and self-initiation of motor production. This included a series of brain areas involved in motor execution (primary motor cortex [M1]), motor planning (premotor cortex [PMC] and cingulate motor area [CMA]), bimanual coordination and internal initiation (supplementary motor area [SMA]), spatial navigation of the limbs (superior parietal lobule [SPL]), motor sequencing (inferior frontal gyrus [IFG]), error correction (lateral cerebellum), and the transformation of sensory information into temporally-organized motor actions (superior temporal gyrus [STG]), this latter of which overlapped with activations for Following.

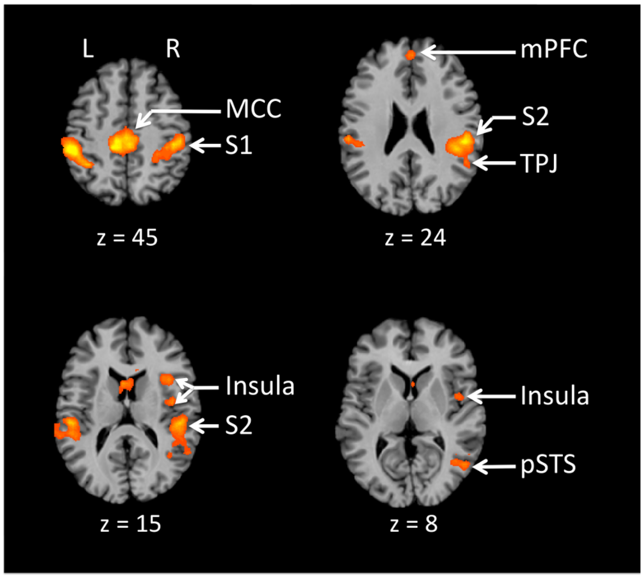

*Figure 3.2. Main effect of partnering*

Partnering was examined by contrasting the partnered conditions with the non-partnered conditions (Leading + Following + Mutual > Solo + Alone), with results reported at $p < 0.05$, FDR corrected, with a cluster threshold $k = 20$. The results in Figures 3.2-3.4 are registered onto a Talairach-normalized anatomical template MRI (the Colin brain). The Talairach z coordinate is shown below each slice. The left side of the slice is the left side of the brain. Abbreviations: MCC: middle cingulate cortex; mPFC: medial prefrontal cortex; pSTS: posterior superior temporal sulcus; S1: primary somatosensory cortex; S2: secondary somatosensory cortex; TPJ: temporo-parietal junction.

***Table 3.1.*** *Partnering*

Talairach coordinates for the peak activations for the contrast "partnered versus non-partnered" (i.e., Leading + Following + Mutual > Solo + Alone), p < 0.05 with FDR correction.

| | | | **TAL coordinates** | | | | |
|---|---|---|---|---|---|---|---|
| **Areas** | **Hemisphere** | **BA** | x | y | z | **t (peak)** | **k** |
| *Frontal* | | | | | | | |
| mPFC | RH | 9 | 3 | 47 | 28 | 7.08 | 53 |
| Insula | RH | 13, 45 | 39 | 14 | 16 | 5.58 | 57 |
| Insula | RH | 13, 44 | 42 | -7 | 16 | 5.47 | 55 |
| mPFC | LH | 10 | -9 | 47 | -5 | 5.43 | 22 |
| IFG | RH | 47 | 39 | 17 | -11 | 5.15 | 29 |
| *Parietal* | | | | | | | |
| S1 | LH | 2, 3, 7, 40 | -48 | -34 | 49 | 11.02 | 462 |
| S1 | RH | 2, 3, 7, 40 | 45 | -28 | 52 | 10.65 | 617 |
| S2/aIPL | RH | 40, 13 | 45 | -28 | 19 | 10.07 | 293 |
| MCC | LH | 5, 31 | -12 | -31 | 46 | 9.37 | 338 |
| S2/aIPL | LH | 40, 13, 22 | -51 | -25 | 16 | 7.19 | 174 |
| *Temporal* | | | | | | | |
| MT+ | RH | 37, 39 | 51 | -61 | 7 | 5.57 | 100 |
| Fusiform | RH | 37 | 48 | -61 | -8 | 5.50 | 36 |
| TPJ ant | RH | 40 | 51 | -46 | 25 | 4.91 | 43 |
| STS | RH | 39, 22 | 39 | -55 | 16 | 4.57 | 42 |
| *Subcortical* | | | | | | | |
| Caudate | LH | | -3 | 11 | 16 | 5.83 | 69 |
| Thalamus | RH | | 12 | -16 | 1 | 4.94 | 95 |
| Claustrum | RH | | 33 | -7 | -5 | 4.40 | 31 |
| *Cerebellum* | | | | | | | |
| Declive | RH | | 42 | -67 | -20 | 4.85 | 27 |
| Culmen | RH | | 15 | -52 | -17 | 4.46 | 29 |

Abbreviation: BA = Brodmann area, k = number of voxels, t = maximum t value, RH = right hemisphere, LH = left hemisphere. Abbreviations: aIPL, anterior inferior parietal lobule; FG, fusiform gyrus; IFG, inferior frontal gyrus; MCC, middle cingulate cortex; mPFC, medial prefrontal cortex; MT+/V5, motion area of the middle temporal region; S1, primary somatosensory cortex; S2, secondary somatosensory cortex; pSTS, posterior superior temporal sulcus; TPJ = temporo-parietal junction.

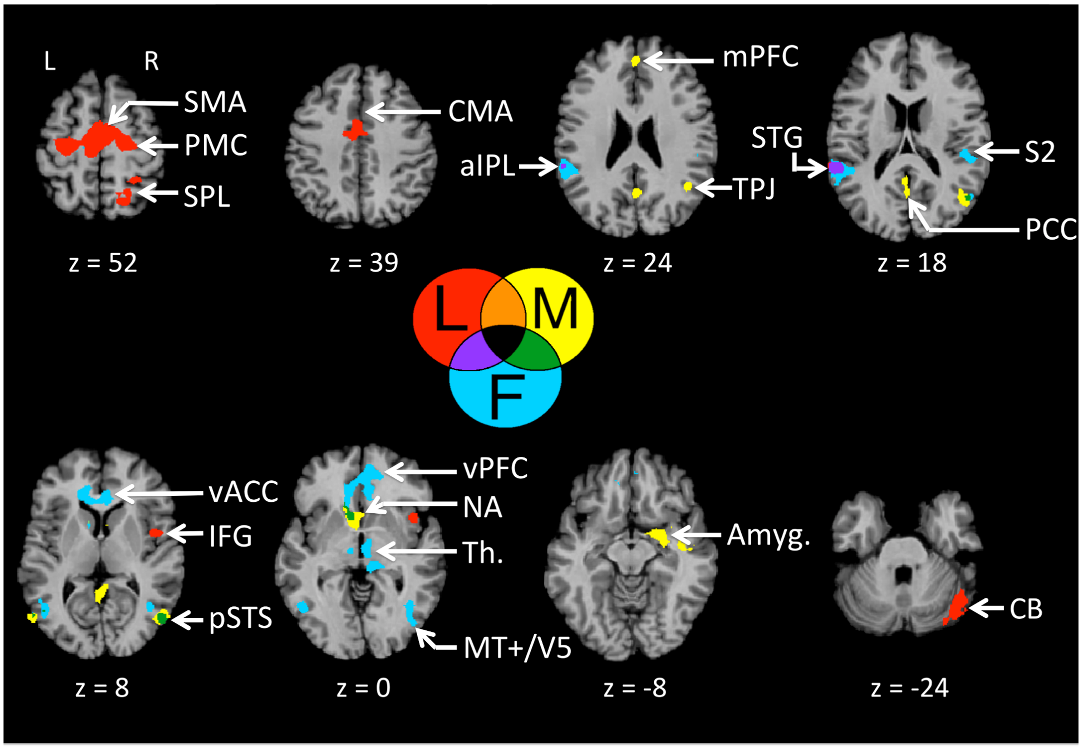

*Figure 3.3. Specificity for Leading, Following, and Mutual.*

Neural specificity for Leading, Following and Mutual is shown, after removing both basic motoric effects (through subtraction of the non-partnered conditions Solo + Alone) and partnering effects, as seen in a conjunction of the three partnership contrasts: [Leading > non-partnered conditions] ∩ [Following > non-partnered conditions] ∩ [Mutual> non-partnered conditions]. The role-specific activations are color-coded as follows: Leading (red): [Leading > Non-partnered conditions] > [Partnership Conjunction]; Following (blue): [Following > Non-partnered conditions] > [Partnership Conjunction]; and Mutual (yellow): [Mutual> Non-partnered conditions] > [Partnership Conjunction]. The results are $p < 0.005$ uncorrected, with a cluster threshold $k = 20$. Abbreviations: aIPL: anterior inferior parietal lobule; MCC: middle cingulate cortex; MT+/V5, motion area of the middle temporal region; mPFC: medial prefrontal cortex; NA: nucleus accumbens; pSTS: posterior superior temporal sulcus; S1: primary somatosensory cortex; S2: secondary somatosensory cortex; TPJ: temporo-parietal junction.

In contrast to the heavily motoric profile for Leading, Following showed a far more sensory profile, indicative of a responsiveness to external signals coming from the leader, where these signals serve as cues to guide movement. This included areas involved in tactile perception and proprioception (S2 and the sensory thalamus), motion tracking and social motion perception (MT+/V5 and pSTS), sensorimotor mapping of self and other's actions (anterior inferior parietal lobule [aIPL]), and the monitoring of external outcomes in relation to reward (ventral anterior cingulate cortex [vACC], extending into the ventral mPFC, as well as the caudate nucleus and nucleus accumbens). It is clear from these results that leading and following represent reciprocal specializations in the brain, with leading highlighting self-initiation of movement and following an external orientation toward sensory signals coming from the partner's actions.

The profile for the Mutual condition was distinguished from both Leading and Following by the presence of enhanced activity in the mentalizing network, including the mPFC, posterior cingulate cortex (PCC), and TPJ. This network was also part of the partnering network shared between Mutual, Leading and Following (Figure 3.2), but was more strongly recruited during Mutual, as if mutual interaction required a higher degree of awareness of the thoughts and intentions of the partner. The Mutual condition also recruited limbic areas involved in emotion and reward, including the amygdala and the nucleus accumbens. Unexpectedly, there was no overlap between Mutual and Leading in the three-way comparison (i.e., no area that was more activated for both Mutual and Leading than Following). However Mutual activity overlapped with Following activity in several regions, such as the pSTS and the nucleus accumbens. Overall, this suggests that mutual interaction might be more of a form of mutual following than mutual leading.

***Table 3.2.*** *Specific activations for Leading, Following, and Mutual.*

Talairach coordinates for the peak activations for the contrasts "one partnered condition versus the conjunction of the three partnered conditions" (see Methods for details), $p < 0.005$ uncorrected.

| | | | **TAL coordinates** | | | | |
|---|---|---|---|---|---|---|---|
| **Areas** | **Hemisphere** | **BA** | **x** | **y** | **z** | **t (peak)** | **k** |
| **Leading > Conjunction** | | | | | | | |
| *Frontal* | | | | | | | |
| M1/PMC | LH | 4, 6 | -21 | -16 | 58 | 10.36 | 159 |
| SMA | RH/LH | 6 | 0 | -13 | 52 | 8.42 | 370 |
| M1/PMC | RH | 4, 6 | 15 | -16 | 55 | 7.42 | 147 |
| IFG | RH | 44, 13 | 45 | 2 | 7 | 5.93 | 37 |
| CMA | RH/LH | 24 | 0 | -1 | 43 | 5.61 | 68 |
| *Parietal* | | | | | | | |
| SPL | RH | 40, 7 | 30 | -43 | 55 | 5.35 | 76 |
| *Temporal* | | | | | | | |
| STG | LH | 13,22 | -54 | -37 | 19 | 6.21 | 31 |
| *Cerebellum* | | | | | | | |
| Tuber | RH | | 45 | -64 | -23 | 6.41 | 86 |
| **Following > Conjunction** | | | | | | | |
| *Frontal* | | | | | | | |
| mPFC | RH/LH | 10 | -9 | 38 | -5 | 5.45 | 45 |
| ACC | RH/LH | 24,32,33 | -3 | 26 | 7 | 4.86 | 199 |
| MFG | LH | 6 | -9 | -22 | 58 | 4.11 | 52 |
| MFG | RH | 6 | 9 | -19 | 61 | 3.54 | 20 |
| *Parietal* | | | | | | | |
| aIPL/STG | LH | 40 | -54 | -37 | 25 | 6.75 | 101 |
| S2 | RH | 41 | 48 | -28 | 19 | 4.67 | 20 |
| aIPL/STG | RH | 13 | 51 | -43 | 22 | 4.33 | 20 |

***Table 3.2** (continued)*

| | | | TAL coordinates | | | | |
|---|---|---|---|---|---|---|---|
| **Areas** | **Hemisphere** | **BA** | **x** | **y** | **z** | **t (peak)** | **k** |
| *Temporal* | | | | | | | |
| MT+/V5 | LH | 37 | -45 | -61 | 4 | 5.60 | 34 |
| MT+/V5 | RH | 37,19 | 39 | -58 | 1 | 4.96 | 27 |
| STS | RH | 39,19 | 51 | -67 | 10 | 4.46 | 42 |
| STS | LH | 39 | -48 | -52 | 10 | 3.22 | 20 |
| *Subcortical* | | | | | | | |
| Thalamus | RH/LH | | 3 | -13 | 1 | 4.93 | 45 |
| Thalamus | RH | | 9 | -28 | 1 | 4.40 | 27 |
| Accumbens | LH | | -9 | 11 | 13 | 4.26 | 20 |
| Accumbens | RH | | 3 | 2 | 10 | 3.59 | 22 |
| **Mutual > Conjunction** | | | | | | | |
| *Frontal* | | | | | | | |
| mPFC | RH/LH | 9 | 3 | 44 | 31 | 5.05 | 20 |
| *Parietal* | | | | | | | |
| PCC | RH/LH | 30, 23 | 0 | -49 | 13 | 4.58 | 73 |
| TPJ ant | RH | 39 | 42 | -52 | 25 | 4.31 | 27 |
| *Temporal* | | | | | | | |
| STS | RH | 39, 19 | 48 | -67 | 16 | 6.33 | 64 |
| STS | LH | 39, 19 | -45 | -61 | 16 | 3.87 | 29 |
| *Subcortical* | | | | | | | |
| Put./Amyg. | RH | | 21 | -1 | -8 | 5.82 | 99 |
| Accumbens | RH/LH | | -6 | 14 | 4 | 4.89 | 69 |

Abbreviations: BA = Brodmann area, k = number of voxels, t = maximum t value, RH = right hemisphere, LH = left hemisphere. Abbreviations: ACC, anterior cingulate cortex; aIPL, anterior inferior parietal lobule; Amyg., amygdala; CMA, cingulate motor area; IFG, inferior frontal gyrus; M1, primary motor cortex; MFG, medial frontal gyrus; mPFC, medial prefrontal cortex; MT+/V5, motion area of the middle temporal region; PMC, premotor cortex; pSTS, posterior superior temporal sulcus; Put., putamen; S2, secondary somatosensory cortex; SMA, supplementary motor area; SPL, superior parietal lobule; STG, superior temporal gyrus; TPJ, temporo-parietal junction.

### 3.4.2.2 Improvisation

We examined the main effect of improvisation independent of partnership by contrasting the improvised generative conditions (Leading and Solo) with their fixed-pattern counterparts (Mutual and Alone). For reasons explained in the Methods section, Following was excluded from this analysis. Improvisation activated a network of brain areas similar to that for Leading, including M1, PMC, SMA, CMA, IFG, STG and SPL (Figure 3.4a and Table 3.3). Additional improvisation areas not found in Leading included the left dorsolateral prefrontal cortex (DLPFC) and bilateral putamen.

The improvised conditions differed from the non-improvised conditions not just in creative generation but in movement variability as well (see the Methods section). We therefore used the Following condition as a means of disentangling these two effects, since its movement variability was similar to that of the improvised conditions, but it did not require the participant to improvise at the generative level. Brain regions that were engaged more during improvised movements than during Following are likely associated with movement generation. Brain regions that were engaged more during Following than the non-improvised conditions are likely associated with movement variability.

Those areas that were most strongly associated with improvisational movement generation (Figure 3.4b, red box) were the SMA, SPL, CMA DLPFC, and lateral cerebellum. These were areas in which the improvised conditions

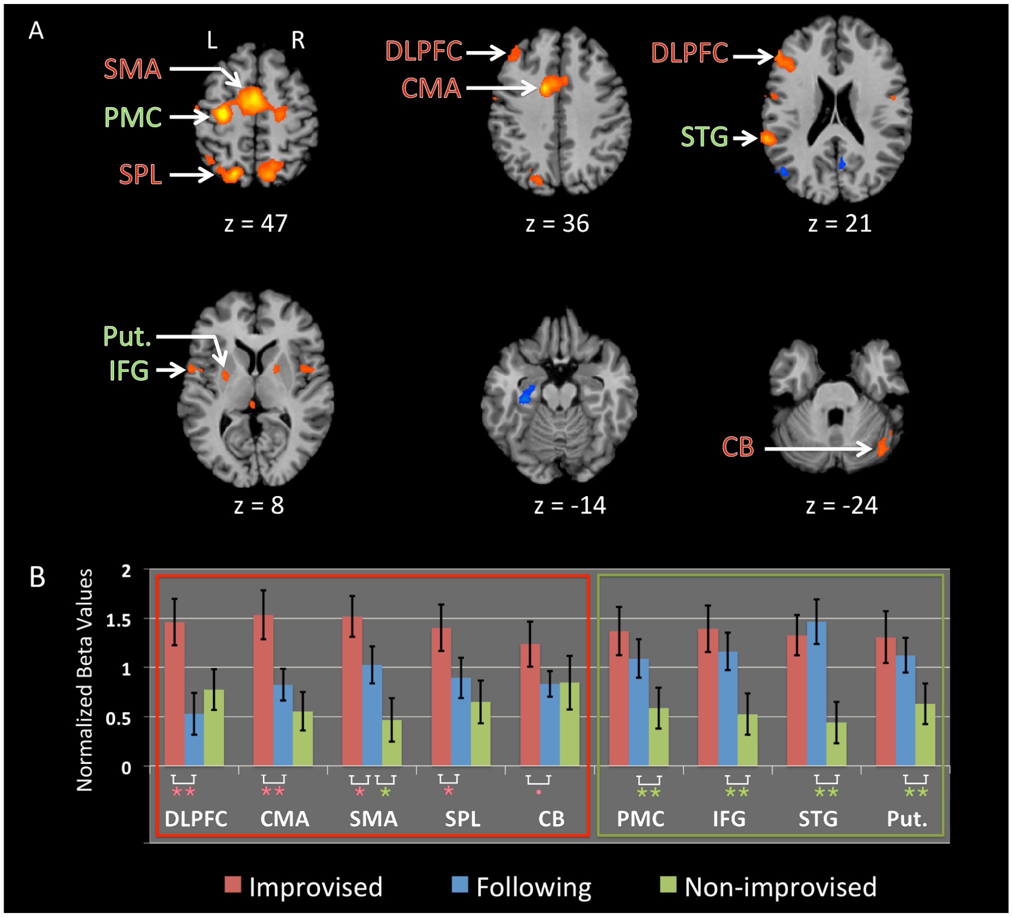

*Figure 3.4. Effect of improvisation.*

(A) Whole-brain analysis of improvisation: Leading + Solo > Mutual + Alone. $p < 0.05$ FDR corrected with a cluster threshold $k = 20$. Orange = activation, and blue = deactivation. Based on the results of the ROI analysis presented in panel B, areas with red labels in this panel (and that are surrounded with a red box in panel B) are those that are more likely to be involved in improvisational generation of movement, whereas those areas with green labels (and that are surrounded with a green box in panel B) are more likely to be associated with movement variability, rather than improvisation. Abbreviations: CMA: cingulate motor area; DLPFC: dorsolateral prefrontal cortex; IFG: inferior frontal gyrus; PMC: premotor cortex; SMA: supplementary motor area; SPL: superior parietal lobule; STG: superior temporal gyrus.

(B) ROI analysis of the improvisation areas in comparison with the Following condition. ** = $p < 0.005$, * = $p < 0.05$, • = trend ($p = 0.057$). Error bars are standard errors of the mean. Beta weights extracted from spheres of 5 mm radius are centered on the peak of the areas defined in the improvisation contrast in panel A (Leading + Solo > Mutual + Alone). Improvised (red): mean across Leading + Solo. Non-improvised (green): mean across Mutual + Alone. The means are averaged across both hemispheres for the bilateral areas (see Table 3.3).

***Table 3.3.*** *Improvisation and self-initiation.*

Talairach coordinates for the peak activations and deactivations for the contrast “improvised versus non-improvised” (i.e., Leading + Solo > Mutual + Alone), $p < 0.05$ with FDR correction. Also included are the coordinates for the peak activations for the contrast “self-initiated versus externally-triggered” ([Leading + Solo + Mutual + Alone] > Following), $p < 0.05$ with FDR correction.

| | | | **TAL coordinates** | | | | |
|---|---|---|---|---|---|---|---|
| **Areas** | **Hemisphere** | **BA** | **x** | **y** | **z** | **t (peak)** | **k** |
| **Improvisation** | | | | | | | |
| *Frontal* | | | | | | | |
| M1/PMC | LH | 4, 6 | -27 | -16 | 52 | 13.13 | 168 |
| SMA | RH/LH | 6 | 0 | -4 | 52 | 8.58 | 513 |
| CMA | LH | 24, 32 | -12 | 5 | 37 | 8.19 | 211 |
| M1/PMC | RH | 4, 6 | 18 | -22 | 55 | 6.71 | 114 |
| DLPFC | LH | 8, 9, 46 | -48 | 32 | 31 | 6.01 | 105 |
| PMC | LH | 6, 22 | -48 | -1 | 28 | 5.71 | 41 |
| IFG | RH | 44, 22, 6 | 45 | 2 | 7 | 5.59 | 49 |
| IFG | LH | 22, 6 | -54 | 5 | 4 | 5.25 | 49 |
| *Parietal* | | | | | | | |
| SPL | LH | 7 | -18 | -70 | 49 | 9.05 | 121 |
| SPL | RH | 7 | 15 | -64 | 55 | 7.63 | 127 |
| SPL | LH | 7, 40 | -39 | -55 | 52 | 4.38 | 23 |
| *Temporal* | | | | | | | |
| STG | LH | 22 | -60 | -40 | 19 | 7.41 | 67 |
| *Subcortical* | | | | | | | |
| Thalamus | RH/LH | | 0 | -16 | 16 | 5.64 | 33 |
| Putamen | RH | | 18 | 2 | 10 | 4.90 | 20 |
| Putamen | LH | | -24 | -7 | 10 | 4.63 | 22 |
| *Cerebellum* | | | | | | | |
| Declive | RH | | 39 | -70 | -20 | 5.20 | 40 |
| **Self-initiation** | | | | | | | |
| *Frontal* | | | | | | | |
| DLPFC | LH | 9 | -42 | 32 | 37 | 8.44 | 60 |

***Table 3.3** (continued)*

| Areas | Hemisphere | BA | TAL coordinates x | y | z | t (peak) | k |
|---|---|---|---|---|---|---|---|
| *Parietal* | | | | | | | |
| SPL | RH | 7, 19 | 6 | -82 | 49 | 5.87 | 77 |
| SPL | LH | 7, 19 | -12 | -82 | 46 | 6.65 | 198 |

Abbreviations: BA = Brodmann area, k = number of voxels, t = maximum t value, RH = right hemisphere, LH = left hemisphere. Abbreviations: CMA, cingulate motor area; DLPFC, dorsolateral prefrontal cortex; IFG, inferior frontal gyrus; M1, primary motor cortex; PHC, parahippocampal gyrus: PMC, premotor cortex; SMA, supplementary motor area; SPL, superior parietal lobule; STG, superior temportal gyrus; TPJ = temporo-parietal junction.

showed significantly greater activity than Following (marginally significant for the cerebellum). In contrast, areas more strongly associated with movement variability than creative generation per se (Figure 3.4b, green box) were the PMC, IFG, putamen, and STG, where Following showed significantly greater activity than the non-improvised conditions, but did not differ from the improvised conditions. Finally, the whole-brain analysis contrasting self-initiated movements that are either improvised (Leading and Solo) or performed by memory (Mutual and Alone) to externally-initiated movement (Following) gave rise to activity in the SPL and the left DLPFC (the coordinates are presented in Table 3.3 under "self-initiated activation").

### 3.4.2.3 Improvising with a partner

We sought brain areas associated with signalling movement intentions to a partner by comparing the Leading and Solo conditions, since both are improvised and only differ in partnership. The Leading > Solo contrast showed the same set of brain areas that came up in the partnership contrast, with no additional areas showing up (see Table 3.4; the insula and mPFC were present only at a more liberal threshold). To further explore whether there was activity that was specific to leading within these partnership areas or if the areas were fully shared with the other partnered conditions, we performed the contrast [Leading > Mutual] > [Solo > Alone] as well as the conjunction [Leading > Solo] ∩ [Leading > Following]. No areas were present in either analysis, even at a more liberal threshold. Overall, this indicates that, at least within the context of the present experiment, Leading is simply the additive combination of solo improvisation and partnering, with no indication of an interaction effect.

***Table 3.4.*** *Joint improvisation.*

Talairach coordinates for the peak activations and deactivations for the contrast “Leading > Solo”, $p < 0.05$ with FDR correction.

| | | | **TAL coordinates** | | | | |
|---|---|---|---|---|---|---|---|
| **Areas** | **Hemisphere** | **BA** | **x** | **y** | **z** | **t (peak)** | **k** |
| S1 | RH | 2,3,4,5,40 | 42 | -34 | 58 | 9.17 | 283 |
| S1 | LH | 3,40 | -48 | -34 | 46 | 8.73 | 210 |
| MCC | LH | 31 | 0 | -22 | 46 | 7.75 | 79 |
| S2 | RH | 13,40 | 45 | -34 | 22 | 6.08 | 69 |

Abbreviations: BA = Brodmann area, k = number of voxels, t = maximum t value, RH = right hemisphere, LH = left hemisphere. Abbreviations: MCC, middle cingulate cortex; S1, primary somatosensory cortex; S2, secondary somatosensory cortex.

# 3.5 Discussion

The capacity for joint action is a critical part of the social phenotype that permits humans to engage in cooperative actions. The majority of such joint interactions involve a balance between the more dominant pattern of leading and the more receptive pattern of following. In addition, one class of such interactions involves direct physical contact between the participants, spanning from sexual intercourse to group dancing. We have reported the results of the first experiment to examine the neural basis of leading and following during a situation of joint improvisation with direct haptic contact, employing a novel two-person scanning arrangement. Consistent with our predictions, leading was characterized by a motoric profile that reflected the role of leaders in motor planning, navigation, and the conveyance of forces to a partner. Following, by contrast, was associated with a far more sensory profile that reflected the role of followers in responding to the directional cues of a leader and in tracking the leader's movements. The mutual condition – in which we attempted to eliminate the role asymmetry present in the leading and following conditions by employing pre-learned movement patterns within the context of a symmetric interaction – had an activation profile similar to following, suggesting that both partners may have mutually followed one another. Finally, the analysis of improvisation revealed the importance of both premotor and working-memory areas for improvised movements compared to fixed movement patterns. It also permitted a disambiguation of which improvisation areas were associated with movement generation, compared to movement variability per se. Overall, these results present a first look at the brain systems important for leading and following in a situation of joint action with direct haptic contact.

### 3.5.1 Partnering

Joint action is characterized by a continuous interaction between partners. As expected given the haptic interaction occurring between partners in our paradigm, the analysis of partnering revealed activity in cortical areas that respond to somatosensory and proprioceptive stimulation, including the primary and secondary somatosensory cortices. Other areas included the pSTS, MCC, anterior and posterior insula, TPJ, and mPFC. The pSTS is a multimodal area [39] that processes dynamic social stimuli, including biological motion [40], implied human motion [41], facial expression [42], vocal prosody [43], eye movement, social gaze [44,45], and even animacy detection [46]. It is also involved in haptic identification of facial expression [47]. We found the pSTS to be more active during partnered than non-partnered movement, but most especially during the mutual and following conditions, where participants relied more heavily on haptic cues coming from their partner's movements. Haptic coupling with a partner can be seen as a form of dynamic social communication in which haptic cues are used to convey a partner's intentions.

The posterior MCC is commonly activated in studies that use tactile stimuli (e.g., [48,49]). It mediates response selection and body orientation toward somatic stimuli, and is functionally connected with the posterior insula [50,51]. The posterior MCC could therefore have played a role in the orientation of the hands in response to tactile cues coming from one's partner. For this reason, we predict that it would be involved in skeletomotor orientation during whole-body dance partnering. Related to the MCC, the posterior insula is stimulated by muscle activation during exercise [52], and is associated with interoception, the perception of emotional salience, and self-body consciousness. Hence, the involvement of the posterior insula in partnering might relate to increase reliance on internally-salient sensation and self-body awareness. The anterior insula, another area activated in the partnering contrast, is associated by subjective feeling and also trust with a partner [52,53]. It is thought to mediate interaction between brain regions that are externally salient and those that are internally salient [54,55], and so it could play a key role during social interactions.

Finally, all of the partnered tasks elicited activity in the TPJ and mPFC. These areas are core components of the mentalizing network, which is responsible for the ability to understand the mental states of others, to predict their intentions, and to think about social attributes of the self and others [56–59]. This network is activated both when observing and engaging in social interactions [16,60]. Its presence in our partnership contrast might reflect the mentalizing about a partner's intentions that occurs during a socially-interactive task, as compared to an action done on one's own.

### 3.5.2 Leading and Following

Having established the basic network involved in haptic interaction between partners in a situation of joint action, we wanted to explore brain areas that were specific for either leading or following during partnered movement. As predicted, leading showed a motoric profile related to movement planning, self-initiation, and spatial navigation, whereas following showed a sensory profile related to haptic awareness, motion tracking, and social perception. Leading's emphasis on motor activations is consistent with behavioral studies showing that leading, compared to following, involves a greater degree of movement control and a reduced degree of movement variability, both of which aim to achieve stable partnering of movement [4,61].

The brain network for leading was highly similar to that revealed for leading in studies of auditory finger tapping [3] and musical duetting [9,10], as well as that of the initiator in studies of reciprocal imitation of people's actions [12,14]. This network is associated with self-initiated action, decision making, self-prioritization, multi-limb coordination, and motor control. It includes the PMC, SMA, CMA, and cerebellum. In addition, our improvisational task required that the leader generate novel movement sequences throughout the task. Activation of the right IFG (BA 44) has been associated with the production of novel movement sequences, while controlling for rules maintenance, as seen in studies of improvisation during piano performance [27,28]. Moreover, activity in the IFG has been shown to be correlated with the perceived influence of the self on a virtual partner in a joint task [3], which is consistent with a role in leading. Finally, leading showed activity in the SPL, an area involved in spatially-oriented motor planning and attention that integrates visual, proprioceptive, somatosensory, and auditory information [62–64]. Lesions to the SPL have been shown to lead to impairments in tactile search [65]. A medial part of the SPL, located in the precuneus, has been shown to be activated by spatial navigation of the lower limbs in a non-partnered dance-like experiment [66], and so likely plays a similar role for the upper-limb movement in the present experiment. The SPL is likewise engaged in studies of gestural imitation and pantomime using the upper limbs [67,68]. Leading requires an exploration and representation of movement patterns in space in order to create a coordinated "dance" between the partners. However, a similar area within the SPL was shown to be engaged during a leading task without a spatial component [3], which was attributed to the integration of self and other information.

There is little literature regarding the neural basis of following. In fact, previous studies examining leading and following reported no activation for following compared to leading [3] or activations that were due to deactivations during leading [12]. The brain network that was engaged during our following task had a strong sensory orientation. This included areas involved in the processing of somatosensory and proprioceptive stimuli (the sensory thalamus and S2, [69–72]), motion perception (MT+/V5, [73,74]), and the perception of dynamic social stimuli (pSTS, [75]). Such areas support a follower's enhanced receptivity to haptic motion-cues coming from the leader. This is consistent with the enhanced receptivity to visual cues that occurs during visual imitation of a partner's movement [12,76]. Other areas associated with following included the ventral ACC and mPFC. These areas have been implicated in reward and punishment, as well as in assigning value to the outcome of an action [56]. More specifically, the ventral mPFC plays a role in monitoring the performance of one's own actions that are initiated by someone else [77]. This should thus be an important system for monitoring performance during following, in other words when one is not deciding on the action to be performed. It is notable that patients with damage to the ventral mPFC are less likely to emerge as followers when asked to respond to a leader's offer [25].

The contrastive networks engaged by leading vs. following highlight the complementary nature of these roles during joint action. While leading requires an internal orientation to movement execution, as related to self-initiation of movement (PMC and SMA), following requires an external orientation to movement execution, as related to responsiveness to the movement cues coming from a partner. While leading requires the planning and generation of movement sequences (IFG) occurring in a spatially-patterned manner (SPL), following requires a heightened awareness of sensory cues coming from leader (sensory thalamus and S2) and a system to track motion-cues from the leader (MT+/V5 and pSTS). Finally, the CMA (dACC), which was activated during leading, plays a role in monitoring performance during self-initiated actions, whereas the ventral ACC and mPFC, which were activated during following, play a role in monitoring performance during externally-triggered actions.

As mentioned in the Introduction, we acknowledge that during true social interactions, both leading and following are tasks that require individuals to adapt to one another in a bilateral fashion, and that neither activity involves unilateral conveyance (leading) or receipt (following) of forces [6–8]. However, due to the simplicity of our task, it is unlikely that the follower needed to improvise a motor plan, or that the leader needed to adapt his motor plan to the follower's behavior. This was not observed by the experimenter while interacting with the participants.

### 3.5.3 Mutual partnering

Although our overarching goal in the present study was to identify the brain areas that differentiated leading from following, we also wanted to explore a related facet of joint action in which the partners' roles were symmetric. An important question that we wanted to address was whether an egalitarian action – in which partners share symmetrical roles – is more similar to a process of mutual leading or one of mutual following. While the brain activity for the mutual condition was, in fact, different from both leading and following, it showed a profile much closer to following than leading, suggesting that mutual interaction might be a form of reciprocal following. This was seen particularly with reference to the overlapping activity between mutual and following in the pSTS. It should be pointed out, however, that this profile of mutual following might be dependant on the pre-learned nature of our task. We would speculate that a condition in which the partners' movements were jointly improvised might in fact be closer to a situation of mutual leading than mutual following. However, even in such a situation, there might be bouts in which the jointly improvising partners would achieve a state of "togetherness" (as described in [36]), so that both leading and following would come equally into play, as related to both self-focused motor planning and other-focused sensory receptiveness. We would additionally hypothesize that the core network for mutual interaction outlined here (i.e., areas for mentalizing and social processing) would be present, regardless of the type of mutual interaction.

While the mentalizing network was associated with partnering in general, it was preferentially engaged during mutual interaction. This suggests that our interpretation of this condition as reciprocal following might be underlain by ongoing mentalizing about the intentions of the partner as a strategy for achieving this reciprocity. The TPJ, mPFC and PCC were more activated during the mutual condition than both leading and following. The mPFC, in particular, has been shown to be involved in reasoning about others and the self in social contexts [78]. It is activated, for example, when our own actions have consequence for others in joint-action settings [79]. The fact that both self- and other-strategies have to be taken into account during the mutual condition may explain the greater involvement of the mPFC in mutual compared to leading and following. The TPJ was shown previously to be activated in a joint-action paradigm in which both individuals shared the same role [16], where the authors attributed TPJ activity to the perception of agency in an ambiguous situation. In our mutual task, participants were instructed that the speed and amplitude of the motion should arise by mutual agreement, whereas during the leading and following conditions these parameters were determined by the leader only. For this reason, agency would be more ambiguous during the mutual task, which might explain the additional engagement of mentalizing areas such as the TPJ, PCC and mPFC during this condition compared to the other two partnered conditions. The PCC plays a role in self-related processing [75], and is believed to balance internal and external foci of attention [80], which could be a key facet of the mutual task, since individuals have to focus on themselves but at the same time pay attention to their partner. In addition, there is a lesser need to predict and integrate another’s actions into our own motor plan during symmetric, as compared to complementary, interactions [60,80], as suggested by the reduced activation in the anterior IPL during mutual interaction, compared to leading and following. This area supports action coordination during interpersonal interactions, playing a role in the prediction of self and other sensory experiences and the integration of such predicted experiences with motor programs [80]. Overall, the differential involvement of mentalizing areas in the mutual condition, compared to leading and following, is consistent with previous research on the activity of this network in joint-action settings, such as when one’s own behavior affects joint performance or when partners’ roles are shared versus complementary.

The final class of brain areas specific for mutual interaction comprised areas involved in emotion and reward, including the amygdala and nucleus accumbens. The amygdala is an area important for emotional and motivational functions that is also thought to play a role in social interaction. It is involved in making the decision to cooperate with others [83,84], as would occur in our mutual task, with its bidirectional interactions. The activation in a reward center like the nucleus accumbens in our mutual task is perhaps the most interesting aspect of the results, which might suggest that "keeping together in time" with other people [85] is associated with a rewarding feeling of pleasure [86]. The nucleus accumbens is one of the key reward centers of the brain [87], playing a general role in cognition and action [88]. Its activity has been shown to be greater for social rewards than for non-social rewards, such as drugs [89,90]. Overall, the most cooperative, reciprocal and egalitarian of our joint-action conditions was associated with a neural signature of pleasure, suggesting that this form of mutuality is perceived as socially rewarding by its participants. This is in line with numerous studies showing that interpersonal interactions and mutual contingency between individuals engage reward centers, and do so more during cooperative than competitive interactions [91,92,93]. It is thus not surprising that activation in the social, mentalizing and reward networks would increase in parallel in our three partnered tasks, being lowest in the most self-focused condition (leading) and the highest in the most reciprocal one (mutual), with following being intermediate.

### 3.5.4 Improvisation

Our study involved patterned movement of the limbs that occurred in an improvised manner, and thus might serve as a neuroimaging model of dance improvisation. Improvisational movement of the hands, when contrasted with performing fixed and pre-learned movement patterns, led to activation in two general types of areas, namely premotor areas that may be specific to the domain of bimanual movement and working-memory areas that may generalize across movement domains. The network of areas seen for improvisation in our study was highly similar to that found in previous studies of musical improvisation [26–28,30–32] and random sequence generation [28,30,35], which includes the dorsal PMC, SMA, CMA, IFG, DLPFC, SPL, STG and putamen.

A more detailed analysis of the results allowed us to disentangle the function of these areas in improvisation compared with the production of sequence complexity/variability per se. We defined improvisation-related areas as those whose activity was significantly higher when participants *generated* novel motor sequences (i.e., leading and solo) compared with when they *executed* similar sequences without generating them (following). This network comprised three groups of areas. First, the CMA and cerebellum seemed not to be related to movement complexity, as there was no difference in their activity between following and the non-improvised conditions. Instead, the CMA is involved in decision making, willed action, voluntary selection, and sequence generation

[12,27]. Second, the SMA seems to play a role in both processes, as its activation during following was significantly higher than during the non-improvised conditions, but still less than during leading and solo. The SMA has been involved in many different processes, including self-triggered actions that are guided by an internal model or external cues [94], and the simulation/prediction of actions or events [95]. Thus, it could be more important for coordinating complex motor sequences than simple ones, and even more so if these sequences are internally generated online.

The third group of improvisation-related areas includes the DLPFC and SPL, where following was significantly lower than the non-improvised conditions. These areas were more activated during self-initiated movement than externally-triggered movement, regardless of whether the movement was improvised or performed from memory, but were still more active during improvisation. The DLPFC is activated when at least one parameter of the action is self-initiated [96–98]. It plays a role in the monitoring of information in working memory [99], attention during selection of action [12,28], suppression of unwanted responses, and the maintenance of the global motor plans [30]. It is more activated during complex than simple improvisation [30], as seen in our results. Regarding the SPL, whose role was discussed above, we suggest that, in our study, it was responsible for the voluntary exploration and control of the limbs in space during self-initiated actions. The more that there was a need for spatial exploration (improvisation), the more the SPL was activated. Most of brain areas associated with improvisation comprised premotor areas, consistent with a general finding in the literature that improvisation is mediated in large part by augmented activity in domain-specific motor-planning areas. Likewise, the association of the DLPFC with improvisation (rather than sequence complexity) is consistent with much published work on improvisation [28,30], where this area is thought to allocate domain-general resources for working memory.

Another set of regions that was more activated during improvised compared to non-improvised movement showed no difference in activity from following, therefore suggesting that they were associated with sequence complexity, rather than the generative component of improvisation. This included the IFG, dorsal PMC, putamen, and STG. While all of these areas have been shown to be involved in improvisation in previous studies [27,28,31], those studies only contrasted improvisation with the performance of pre-learned sequences, whereas we were able to control for both improvisation and movement variability in our analysis. The IFG is involved in sequencing, particularly with respect to the integration of rules or goals stored in working memory [16,27]. Our results support the involvement of the IFG in the execution of novel sequences, but not necessarily in the internal generation of those sequences.

A similar account can be given for the dorsal PMC and STG, which were more activated during the production (but not necessarily the generation) of richer and more-variable sequences. The PMC plays a role in the selection of movements, either spatially or temporally [30,32]. It is involved in the complexity of movement that emerges from coordination between multiple effectors [100], such as bimanual coordination [101,102]. In addition, it shows greater activity with increasing motor difficulty [101,103]. The dorsal PMC receives information from a dorsal portion of the STG [104] (also called area Spt, [105]). This multisensory area [106] deals with the transformation of sensory information into temporally organized motor actions [104], and has previously been implicated in musical improvisation [30,31]. Finally, the putamen is involved in sequence production, not least in sequence learning [107], such as that which underlies the imitative learning of song sequences in songbirds [108]. Not only is the putamen involved in internally-guided movement [109,110] and the generation of internal representations on external stimuli [94,111], but it is known to be modulated by movement complexity [112,113] and action selection [114,115]. Overall, the association of movement complexity in our improvised tasks with the IFG, PMC, STG and putamen fits well with the known function of these areas in rich movement sequencing.

We acknowledge that the improvisations in our study were very simple and that they might be closer to random generation than genuine improvisation. Even though studies of pseudorandom generation of responses have highlighted a network similar to the one used during true improvisation [28,30,35], further research is needed to explore more dance-like improvisations than the ones that were examined in the present study.

### 3.5.5 Improvising during joint action

We sought brain areas associated with signalling movement intentions to a partner by comparing the Leading to Solo. The results suggest that leading may be reducible to solo improvisation done with a partner. The direct contrast between the leading and solo conditions revealed nothing more than those exact areas that appeared in the partnership contrast (i.e., S1, S2, and MCC, as well as insula and mPFC at a slightly more liberal threshold), suggesting that leading in our experimental paradigm was nothing more than the additive combination of improvisation and partnering. This conclusion was supported by the fact that the contrast [Leading > Mutual] > [Solo > Alone] and the conjunction between [Leading > Solo] with [Leading > Following] failed to demonstrate activity, even at a more liberal threshold. Therefore, we were not able to identify any brain area that would be indicative of the leader signalling intentions to his/her partner, as has been shown in behavioral studies of leading during joint-action tasks [4,5]. A possible explanation for this paradoxical finding is that our relatively simple task did not place sufficiently strong demands on the leader. Additional studies using more-complex interactions will be required to address this issue.

### 3.5.6 Limitations

We were limited in our ability to measure behavioral performance during task production in the scanner due to an absence of MRI-compatible technologies like motion capture and electromyography. In spite of training the participants very thoroughly to match movement variation across conditions and despite the experimenter verifying in real time that this was indeed the case, we have no quantitative indicator of task performance. However, the motoric brain profile that we observed for leading – compared to following and mutual – would suggest that a difference in muscle force or motion between leading and following or mutual might not represent an artifactual difference between conditions but instead an indicator of the mechanistic nature of leading. We also note that our results of the leading task are concordant with previous paradigms that used more-restricted motor performance and interaction ([3] had no results for following). Further research combining fMRI with MRI-compatible versions of EMG or motion capture will be needed to further explore these effects.

### 3.5.7 Conclusions

Using a novel two-person fMRI scanning arrangement, we elucidated for the first time neural differences between the motor-driven task of being a leader and the sensory-driven task of being a follower during a situation of joint improvisation with direct haptic contact. The results shed light not only on the complementary features of leading and following, but on the neural basis of improvisation as well. We found that performing partnered hand movements activated somatosensory as well as social networks. Leading such movements principally activated a motor network involved in motor planning, spatial navigation, and monitoring self-initiated action. In a complementary fashion, haptically following partnered movements engaged areas that monitor externally-triggered action as well as sensory-oriented areas that process somatosensation, motion perception, and the perception of dynamic social stimuli. In contrast to the asymmetry of leading and following, engagement in a more symmetric and mutual interaction increased activity in mentalizing areas and regions involved in social reward. We observed that dance-like improvisation engaged a similar network to musical improvisation or random sequence generation. Moreover, we were able to dissociate a network devoted to improvisation – such as would be engaged in internal sequence generation, decision making, and willed action – from a network involved in sequence variability and movement complexity.

Haptic contact has been a neglected topic in the neuroscience of social interaction. Our study unites haptic contact with the topic of joint action, and by doing so highlights the importance not only of social touch but of the reciprocal exchange of forces necessary for joint cooperative actions of all types.

## 3.6 References

1. Sacheli LM, Aglioti SM, Candidi M. Social cues to joint actions: The role of shared goals. Front Psychol. 2015;6: 1–7.

2. Sebanz N, Bekkering H, Knoblich G. Joint action: Bodies and minds moving together. Trends Cogn Sci. 2006;10: 70–76.

3. Fairhurst MT, Janata P, Keller PE. Leading the follower: An fMRI investigation of dynamic cooperativity and leader-follower strategies in synchronization with an adaptive virtual partner. Neuroimage. 2014;84: 688–697.

4. Sacheli LM, Tidoni E, Pavone EF, Aglioti SM, Candidi M. Kinematics fingerprints of leader and follower role-taking during cooperative joint actions. Exp Brain Res. 2013;226: 473–486.

5. Vesper C, Richardson MJ. Strategic communication and behavioral coupling in asymmetric joint action. Exp Brain Res. 2014;232: 2945–2956.

6. Chauvigné LAS, Gitau KM, Brown S. The neural basis of audiomotor entrainment: An ALE meta-analysis. Front Hum Neurosci. 2014;8: 1–18.

7. Goebl W, Palmer C. Synchronization of timing and motion among performing musicians. Music Percept. 2009;26: 427–438.

8. Wing AM, Endo S, Bradbury A, Vorberg D. Optimal feedback correction in string quartet synchronization. J R Soc Interface. 2014;11: 20131125.

9. Sänger J, Müller V, Lindenberger U. Intra- and interbrain synchronization and network properties when playing guitar in duets. Front Hum Neurosci. 2012;6: 312.

10. Konvalinka I, Bauer M, Stahlhut C, Hansen LK, Roepstorff A, Frith CD. Frontal alpha oscillations distinguish leaders from followers: Multivariate decoding of mutually interacting brains. Neuroimage. 2014;94: 79–88.

11. Dumas G, Nadel J, Soussignan R, Martinerie J, Garnero L. Inter-brain synchronization during social interaction. PLoS One. 2010;5: e12166.

12. Guionnet S, Nadel J, Bertasi E, Sperduti M, Delaveau P, Fossati P. Reciprocal imitation: Toward a neural basis of social interaction. Cereb Cortex. 2012;22: 971–978.

13. Zhou G, Bourguignon M, Parkkonen L, Hari R. Neural signatures of hand kinematics in leaders vs. followers: A dual-MEG study. Neuroimage. 2016;125: 731–738.

14. Decety J, Chaminade T, Grèzes J, Meltzoff AN. A PET exploration of the neural mechanisms involved in reciprocal imitation. Neuroimage. 2002;15: 265–272.

15. Kokal I, Gazzola V, Keysers C. Acting together in and beyond the mirror neuron system. Neuroimage. 2009;47: 2046–2056.

16. Newman-Norlund RD, Bosga J, Meulenbroek RGJ, Bekkering H. Anatomical substrates of cooperative joint-action in a continuous motor task: Virtual lifting and balancing. Neuroimage. 2008;41: 169–177.

17. van der Wel RPRD, Knoblich G, Sebanz N. Let the force be with us: Dyads exploit haptic coupling for coordination. J Exp Psychol Hum Percept Perform. 2011;37: 1420–1431.

18. Sofianidis G, Hatzitaki V. Interpersonal entrainment in dancers: Contrasting timing and haptic cues. Posture, Balanc Brain Int Work Proc. 2015; 34–44.

19. Giordano M, Wanderley MM. Follow the tactile metronome: Vibrotactile stimulation for tempo synchronization in music performance. Proceedings of the Sound and Music Computing Conference. Maynooth, Ireland; 2015.

20. Ng AWY, Chan AHS. Finger response times to visual, auditory and tactile modality stimuli. Proc Int MultiConference Eng Comput Sci. 2012;II: 1449–1454.

21. Harrison SJ, Richardson MJ. Horsing around: Spontaneous four-legged coordination. J Mot Behav. 2009;41: 519–524.

22. Richardson MJ, Marsh KL, Isenhower RW, Goodman JRL, Schmidt RC. Rocking together: Dynamics of intentional and unintentional interpersonal coordination. Hum Mov Sci. 2007;26: 867–891.

23. Richardson MJ, Lopresti-Goodman S, Mancini M, Kay B, Schmidt RC. Comparing the attractor strength of intra- and interpersonal interlimb coordination using cross-recurrence analysis. Neurosci Lett. 2008;438: 340–345.

24. Hanson JVM, Whitaker D, Heron J. Preferential processing of tactile events under conditions of divided attention. Neuroreport. 2009;20: 1392–1396.

25. Price ME, Van Vugt M. The evolution of leader-follower reciprocity: The theory of service-for-prestige. Front Hum Neurosci. 2014;8: 363.

26. Beaty RE. The neuroscience of musical improvisation. Neurosci Biobehav Rev. 2015;51: 108–117.

27. Berkowitz AL, Ansari D. Generation of novel motor sequences: The neural correlates of musical improvisation. Neuroimage. 2008;41: 535–543.

28. de Manzano Ö, Ullén F. Goal-independent mechanisms for free response generation: Creative and pseudo-random performance share neural substrates. Neuroimage. 2012;59: 772–780.

29. Limb CJ, Braun AR. Neural substrates of spontaneous musical performance: An fMRI study of jazz improvisation. PLoS One. 2008;3.

30. Bengtsson SL, Csíkszentmihályi M, Ullén F. Cortical regions involved in the generation of musical structures during improvisation in pianists. J Cogn Neurosci. 2007;19: 830–842.

31. Donnay GF, Rankin SK, Lopez-Gonzalez M, Jiradejvong P, Limb CJ. Neural substrates of interactive musical improvisation: An fMRI study of "trading fours" in Jazz. PLoS ONE. 2014;9: e88665.

32. de Manzano Ö, Ullén F. Activation and connectivity patterns of the presupplementary and dorsal premotor areas during free improvisation of melodies and rhythms. Neuroimage. 2012;63: 272–280.

33. Gonen-Yaacovi G, de Souza LC, Levy R, Urbanski M, Josse G, Volle E. Rostral and caudal prefrontal contribution to creativity: A meta-analysis of functional imaging data. Front Hum Neurosci. 2013;7: 465.

34. Boccia M, Piccardi L, Palermo L, Nori R, Palmiero M. Where do bright ideas occur in our brain? Meta-analytic evidence from neuroimaging studies of domain-specific creativity. Front Psychol. 2015;6: 1–12.

35. Lau HC, Rogers RD, Ramnani N, Passingham RE. Willed action and attention to the selection of action. Neuroimage. 2004;21: 1407–1415.

36 Noy L, Dekel E, Alon, U. The mirror game as a paradigm for studying the dynamics of two people improvising motion together. Proceedings of the National Academy of Sciences. 2011;108: 20947–20952.

37. Breman H, Peters J, Weiskopf N, Ashburner J, Goebel R. Fast fieldmap-based EPI distortion correction with anatabacus: A plugin for BrainVoyager. Neuroimage. 2009;47.

38. Talairach J, Tournoux P. Co-planar stereotaxic atlas of the human brain. Stuttgart, New York. 1988.

39. Beauchamp MS, Yasar NE, Frye RE, Ro T. Touch, sound and vision in human superior temporal sulcus. Neuroimage. 2008;41: 1011–1020.

40. Grossman ED, Battelli L, Pascual-Leone A. Repetitive TMS over posterior STS disrupts perception of biological motion. Vision Res. 2005;45: 2847–2853.

41. Bernstein M, Yovel G. Two neural pathways of face processing: A critical evaluation of current models. Neurosci Biobehav Rev. 2015;55: 536–546.

42. Haxby J V., Hoffman EA, Gobbini MI. The distributed human neural system for face perception. Trends Cogn Sci. 2000;4: 223–233.

43. Campanella S, Belin P. Integrating face and voice in person perception. Trends Cogn Sci. 2007;11: 535–543.

44. Ethofer T, Gschwind M, Vuilleumier P. Processing social aspects of human gaze: A combined fMRI-DTI study. Neuroimage. 2011;55: 411–419.

45. Pelphrey KA, Morris JP, Michelich CR, Allision T, McCarthy G. Functional anatomy of biological motion perception in posterior temporal cortex: An fMRI study of eye, mouth and hand movements. Cereb Cortex. 2005;15: 1866–1876.

46. Hillebrandt H, Friston KJ, Blakemore S-J. Effective connectivity during animacy perception: Dynamic causal modelling of Human Connectome Project data. Sci Rep. 2014;4: 6240.

47. Kitada R, Johnsrude IS, Kochiyama T, Lederman SJ. Brain networks involved in haptic and visual identification of facial expressions of emotion: An fMRI study. Neuroimage. 2010;49: 1677–1689.

48. Ebisch SJH, Ferri F, Salone A, Perrucci MG, D'Amico L, Ferro FM, et al. Differential involvement of somatosensory and interoceptive cortices during the observation of affective touch. J Cogn Neurosci. 2011;23: 1808–1822.

49. Malinen S, Renvall V, Hari R. Functional parcellation of the human primary somatosensory cortex to natural touch. Eur J Neurosci. 2014;39: 738–743.

50. Taylor KS, Seminowicz D a., Davis KD. Two systems of resting state connectivity between the insula and cingulate cortex. Hum Brain Mapp. 2009;30: 2731–2745.

51. Vogt BA. Pain and emotion interactions in subregions of the cingulate gyrus. Nat Rev Neurosci. 2005;6: 533–544.

52. Craig AD. How do you feel? Interoception: The sense of the physiological condition of the body. Nat Rev Neurosci. 2002;3: 655–666.

53. Haas BW, Ishak A, Anderson IW, Filkowski MM. The tendency to trust is reflected in human brain structure. Neuroimage. 2015;107C: 175–181.

54. Menon V, Uddin LQ. Saliency, switching, attention and control: A network model of insula function. Brain Struct Funct. 2010;214: 655–667.

55. Brown S, Gao X, Tisdelle L, Eickhoff SB, Liotti M. Naturalizing aesthetics: Brain areas for aesthetic appraisal across sensory modalities. Neuroimage. 2011;58: 250–258.

56. Amodio DM, Frith CD. Meeting of minds: The medial frontal cortex and social cognition. Nat Rev Neurosci. 2006;7: 268–277.

57. Carter RM, Huettel SA. A nexus model of the temporal-parietal junction. Trends Cogn Sci. 2013;17: 328–336.

58. Isoda M, Noritake A. What makes the dorsomedial frontal cortex active during reading the mental states of others? Front Neurosci. 2013;7: 1–14.

59. Krall SC, Rottschy C, Oberwelland E, Bzdok D, Fox PT, Eickhoff SB, et al. The role of the right temporoparietal junction in attention and social interaction as revealed by ALE meta-analysis. Brain Struct Funct. 2015;220: 587–604.

60. Sartori L, Betti S. Complementary actions. Front Psychol. 2015;6: 1–6.

61. Masumoto J, Inui N. A leader-follower relationship in joint action on a discrete force production task. Exp Brain Res. 2014; 3525–3533.

62. Glover S. Separate visual representations in the planning and control of action. Behav Brain Sci. 2004;27: 3–78.

63. Petersen SE, Corbetta M, Miezin FM, Shulman GL. PET studies of parietal involvement in spatial attention: Comparison of different task types. Can J Exp Psychol. 1994;48: 319–338.

64. Renier L a, Anurova I, De Volder AG, Carlson S, VanMeter J, Rauschecker JP. Multisensory integration of sounds and vibrotactile stimuli in processing streams for “what” and “where”. J Neurosci. 2009;29: 10950–10960.

65. Skakoon-Sparling SP, Vasquez BP, Hano K, Danckert J. Impairments in tactile search following superior parietal damage. Brain Cogn. 2011;76: 341–348.

66. Brown S, Martinez MJ, Parsons LM. The neural basis of human dance. Cereb Cortex. 2006;16: 1157–1167.

67. Molenberghs P, Cunnington R, Mattingley JB. Is the mirror neuron system involved in imitation? A short review and meta-analysis. Neurosci Biobehav Rev. 2009;33: 975–980.

68. Vingerhoets G, Clauwaert A. Functional connectivity associated with hand shape generation: Imitating novel hand postures and pantomiming tool grips challenge different nodes of a shared neural network. Hum Brain Mapp. 2015;36: 3426–3440.

69. Davis KD, Kwan CL, Crawley AP, Mikulis DJ. Functional MRI study of thalamic and cortical activations evoked by cutaneous heat, cold, and tactile stimuli. J Neurophysiol. 1998;80: 1533–1546.

70. Hinkley LB, Krubitzer LA, Nagarajan SS, Disbrow EA. Sensorimotor integration in S2, PV, and parietal rostroventral areas of the human sylvian fissure. J Neurophysiol. 2007;97: 1288–1297.

71. Mima T, Nagamine T, Nakamura K, Shibasaki H. Attention modulates both primary and second somatosensory cortical activities in humans: A magnetoencephalographic study. J Neurophysiol. 1998;80: 2215–2221.

72. Mima T, Sadato N, Yazawa S, Hanakawa T, Fukuyama H, Yonekura Y, et al. Brain structures related to active and passive finger movements in man. Brain. 1999;122: 1989–1997.

73. Matteau I, Kupers R, Ricciardi E, Pietrini P, Ptito M. Beyond visual, aural and haptic movement perception: hMT+ is activated by electrotactile motion stimulation of the tongue in sighted and in congenitally blind individuals. Brain Res Bull. 2010;82: 264–270.

74. van Kemenade BM, Seymour K, Wacker E, Spitzer B, Blankenburg F, Sterzer P. Tactile and visual motion direction processing in hMT+/V5. Neuroimage. 2014;84: 420–427.

75. Yang DY-J, Rosenblau G, Keifer C, Pelphrey KA. An integrative neural model of social perception, action observation, and theory of mind. Neurosci Biobehav Rev. 2015;51: 263–275.

76. Chaminade T, Decety J. Leader or follower? Involvement of the inferior parietal lobule in agency. Neuroreport. 2002;13: 1975–1978.

77. Walton ME, Devlin JT, Rushworth MFS. Interactions between decision making and performance monitoring within prefrontal cortex. Nat Neurosci. 2004;7: 1259–1265.

78. Newman-Norlund RD, Noordzij ML, Meulenbroek RGJ, Bekkering H. Exploring the brain basis of joint action: Co-ordination of actions, goals and intentions. Soc. Neurosci. 2007;2:48–65.

79. Radke S, De Lange FP, Ullsperger M, De Bruijn ERA. Mistakes that affect others: An fMRI study on processing of own errors in a social context. Exp. Brain Res. 2011;211:405–13.

80. Leech R, Sharp DJ. The role of the posterior cingulate cortex in cognition and disease. Brain. 2014;137:12–32.

81. Newman-Norlund RD, van Schie HT, van Zuijlen AMJ, Bekkering H. The mirror neuron system is more active during complementary compared with imitative action. Nat Neurosci. 2007;10: 817–818.

82. Ebisch SJH, Ferri F, Romani GL, Gallese V. Reach out and touch someone: Anticipatory sensorimotor processes of active interpersonal touch. J Cogn Neurosci. 2014;26: 2171–2185.

83. Adolphs R. Is the human amygdala specialized for processing social information? Ann N Y Acad Sci. 2003;985: 326–340.

84. Bickart KC, Dickerson BC, Feldman Barrett L. The amygdala as a hub in brain networks that support social life. Neuropsychologia. 2014;63: 235–248.

85. McNeill WH. Keeping together in time: Dance and drill in human history. Cambridge, MA: Harvard University Press; 1997.

86. Ehrenreich B. Dancing in the streets: A history of collective joy. New York: Metropolitan Books; 2007.

87. Berridge KC, Kringelbach ML. Neuroscience of affect: Brain mechanisms of pleasure and displeasure. Curr Opin Neurobiol. 2013;23: 294–303.

88. Floresco SB. The nucleus accumbens: An interface between cognition, emotion, and action. Annu Rev Psychol. 2015;66: 25–52.

89. EI Rawas R, Klement S, Kummer KK, Fritz M, Dechant G, Saria A, et al. Brain regions associated with the acquisition of conditioned place preference for cocaine vs. social interaction. Front Behav Neurosci. 2012;6: 1–14.

90. Gunaydin LA, Grosenick L, Finkelstein JC, Kauvar IV., Fenno LE, Adhikari A, et al. Natural neural projection dynamics underlying social behavior. Cell. 2014;157: 1535–1551.

91. Behrens TEJ, Hunt LT, Rushworth MFS. The computation of social behavior. Science 2009;324:1160–4.

92. Eskenazi T, Rueschemeyer SA, de Lange FP, Knoblich G, Sebanz N. Neural correlates of observing joint actions with shared intentions. Cortex. 2015;70:90–100.

93. Walter H, Abler B, Ciaramidaro A, Erk S. Motivating forces of human actions: Neuroimaging reward and social interaction. Brain Res. Bull. 2005;67:368–81.

94. Jäncke L, Loose R, Lutz K, Specht K, Shah NJ. Cortical activations during paced finger-tapping applying visual and auditory pacing stimuli. Cogn brain Res. 2000;10: 51–66.

95. Schubotz RI. Prediction of external events with our motor system: Towards a new framework. Trends Cogn Sci. 2007;11: 211–218.

96. Jahanshahi M, Jenkins I, Brown R. Self-initiated versus externally triggered movements. I. An investigation using measurement of regional cerebral blood flow with PET and movement-related potentials in normal and Parkinson's disease subjects. Brain. 1995;118: 913–933.

97. Frith CD. The role of dorsolateral prefrontal cortex in the selection of action as revealed by functional imaging. Control Cogn Process. 2000; 549–565.

98. Rowe JB, Stephan KE, Friston K, Frackowiak RSJ, Passingham RE. The prefrontal cortex shows context-specific changes in effective connectivity to motor or visual cortex during the selection of action or colour. Cereb Cortex. 2005;15: 85–95.

99. Petrides M. Lateral prefrontal cortex: Architectonic and functional organization. Philos Trans R Soc Lond B Biol Sci. 2005;360: 781–795.

100. Meister IG, Buelte D, Staedtgen M, Boroojerdi B, Sparing R. The dorsal premotor cortex orchestrates concurrent speech and fingertapping movements. Eur J Neurosci. 2009;29: 2074–2082.

101. Debaere F, Wenderoth N, Sunaert S, Van Hecke P, Swinnen SP. Cerebellar and premotor function in bimanual coordination: Parametric neural responses to spatiotemporal complexity and cycling frequency. Neuroimage. 2004;21: 1416–1427.

102. Kermadi I, Liu Y, Rouiller EM. Do bimanual motor actions involve the dorsal premotor (PMd), cingulate (CMA) and posterior parietal (PPC) cortices? Comparison with primary and supplementary motor cortical areas. Somatosens Mot Res. 2000;17: 255–271.

103. Winstein CJ, Grafton ST, Pohl PS. Motor task difficulty and brain activity: Investigation of goal-directed reciprocal aiming using positron emission tomography. J Neurophysiol. 1997;77: 1581–1594.

104. Chen JL, Penhune VB, Zatorre RJ. The role of auditory and premotor cortex in sensorimotor transformations. Ann N Y Acad Sci. 2009;1169: 15–34.

105. Hickok G, Buchsbaum B, Humphries C, Muftuler T. Auditory-motor interaction revealed by fMRI: Speech, music, and working memory in area Spt. J Cogn Neurosci. 2003;15: 673–682.

106. Smiley JF, Hackett TA, Ulbert I, Karmas G, Lakatos P, Javitt DC, et al. Multisensory convergence in auditory cortex. I. Cortical connections of the caudal superior temporal plane in macaque monkeys. J Comp Neurol. 2007;502: 894–923.

107. Shmuelof L, Krakauer JW. Are we ready for a natural history of motor learning? Neuron. 2011;72: 469–476.

108. Jarvis ED. Learned birdsong and the neurobiology of human language. Ann N Y Acad Sci. 2004;1016: 749–777.

109. Larsson J, Gulyás B, Roland P. Cortical representation of self-paced finger movement. Neuroreport. 1996;7: 463–468.

110. Mayville JM, Jantzen KJ, Fuchs A, Steinberg FL, Kelso JAS. Cortical and subcortical networks underlying syncopated and synchronized coordination revealed using fMRI. Hum Brain Mapp. 2002;17: 214–229.

111. Jantzen KJ, Oullier O, Marshall M, Steinberg FL, Kelso JAS. A parametric fMRI investigation of context effects in sensorimotor timing and coordination. Neuropsychologia. 2007;45: 673–684.

112. Boecker H, Dagher A, Ceballos-Baumann AO, Passingham RE, Samuel M, Friston KJ, et al. Role of the human rostral supplementary motor area and the basal ganglia in motor sequence control: Investigations with $H_2{}^{15}O$ PET. J Neurophysiol. 1998;79: 1070–1080.

113. Lehéricy S, Bardinet E, Tremblay L, Van de Moortele P-F, Pochon J-B, Dormont D, et al. Motor control in basal ganglia circuits using fMRI and brain atlas approaches. Cereb Cortex. 2006;16: 149–161.

114. Prescott TJ, Montes González FM, Gurney K, Humphries MD, Redgrave P. A robot model of the basal ganglia: Behavior and intrinsic processing. Neural Networks. 2006;19: 31–61.

115. Redgrave P, Prescott TJ, Gurney K. The basal ganglia: A vertebrate solution to the selection problem? Neuroscience. 1999;89: 1009–1023.

## 3.7 Supplementary materials

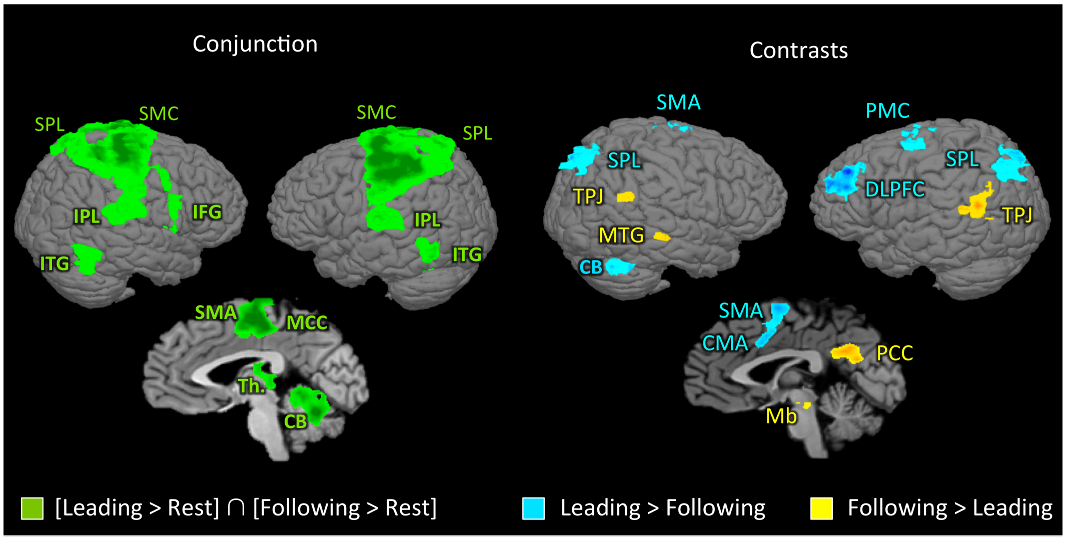

*Figure 3.S1. Direct comparison between leading and following*

The left panel shows the shared network for leading and following with the conjunction [Leading > Rest] ∩ [Following > Rest], at $p < 0.005$ uncorrected (k=20 voxels). The activated areas span over a large sensori-motor network. The right panel shows the bidirectional direct contrasts between leading and following, at $p < 0.005$ uncorrected (k=20 voxels). The leading network (in blue) comprises areas involved in motor and spatial control, including self-initiation and action selection. The following network (in yellow) mostly consists of areas of the mentalizing network involved in social cognition. Abbreviations: CB, cerebellum; CMA, cingulate motor area; DLPFC, dorsolateral prefrontal cortex; IFG, inferior frontal gyrus; IPL, inferior parietal lobule; ITG, inferior temporal gyrus; MCC, middle cingulate cortex; Mb, midbrain; MTG, middle temporal gyrus; PCC, posterior cingulate cortex; PMC, premotor cortex; SMA, supplementary motor area; SMC, sensorimotor cortex; SPL, superior parietal lobule; Th., thalamus. TPJ, temporo-parietal junction.

# Chapter 4

# Multi-person and multisensory synchronization among folk dancers

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## 4.1 Abstract

When people engage in interpersonal interactions, they often do so in a group, employing multiple sensory modalities to coordinate their actions with one another. While a large amount of research has focused on joint action between dyads, the patterns of coordination that emerge from larger groups are not well understood. In the present study, we explored the coordination dynamics of a group of folk dancers, examining the influence of three primary sensory channels on this coordination. Using 3D motion capture, we recorded a group of 13 folk dancers performing to the beat of music (auditory coupling) while holding hands in a circle configuration (haptic coupling) and watching their fellow dancers as well as a leader in the center of the circle (visual coupling). Group synchrony was measured using cluster phase analysis. The results demonstrated that selective elimination of any of the three types of sensory coupling significantly reduces

group synchrony, with haptic coupling having the most widespread effect. The relative phase of the dancers to each source of sensory coupling was also explored. This study sheds new light on how different sensory modalities support multi-person coordination.

## 4.2 Introduction

During any kind of jointly-produced action, individuals need to exchange information using multiple sensory channels in order to coordinate their actions. For example, two people carrying a sofa up a staircase can speak to one another, can visually perceive the sofa and their partner, as well as experience the pushing and pulling forces (i.e., haptic perception) of the sofa that they are jointly moving. A remarkable form of non-verbal coordination is interpersonal synchronization – or mutual entrainment – whereby two or more individuals move rhythmically at the same time. This occurs when two individuals who are walking side by side unconsciously fall into pace, as well as in the form of coordinated group actions such as dance, musical performance, and synchronized swimming. However the coordination that emerges between groups of more than two individuals has not been extensively investigated. Moreover, when engaging in coordinated actions with others, it is likely that individuals rely on multiple sources of sensory information simultaneously. Yet, how individuals integrate visual, auditory and haptic information in order to coordinate their actions with one another is not well understood. The present study attempted to look at both issues together by investigating the relative influence of sensory information on the coordination of a group of 13 folk dancers.

Synchronization studies have focused on when and how different sensory modalities support individual entrainment. For example, an individual tapping his finger to a metronome is more accurate when synchronizing with an auditory metronome compared to a visual metronome (Repp, 2005; Repp & Su, 2013). One explanation for this is that the auditory system has a very high temporal resolution, whereas the visual system has a low temporal resolution. Indeed, more-recent studies have revealed that synchronization performance is more dependent on how each sensory system encodes stimuli than on the modality per se (Hove, Fairhurst, Kotz, & Keller, 2013; Hove, Iversen, Zhang, & Repp, 2013). They showed that while, auditory synchronization is optimized for discrete, rather than continuous, stimuli, the visual system, which has a high spatial resolution, is optimized for moving visual stimuli (Hove, Fairhurst, et al., 2013). Visual entrainment to such moving stimuli, like bouncing balls, is nearly as precise as entrainment to an auditory metronome (Hove, Iversen, et al., 2013; Iversen, Patel, Nicodemus, & Emmorey, 2015). Compared to the auditory and visual channels, synchronization with tactile stimuli has only been assessed by a handful of studies; these studies demonstrated that synchronizing with discrete tactile stimuli (e.g., taps on the body surface) is almost as precise as synchronizing with discrete auditory stimuli (Ammirante, Patel, & Russo, 2016; Elliott, Wing, & Welchman, 2010; Giordano & Wanderley, 2015; Wing, Doumas, & Welchman, 2010). This is likely because the somatosensory system has a relatively high temporal resolution (Gescheider, 1966).

Importantly, active contact often involves more than just tactile information. It includes both touch from the skin and the perception of forces sensed from the position (proprioception) and the movement (kinaesthesia) of the joint and muscles. The combination of touch, proprioception and kinaesthesia is called haptic information (Gibson, 1966). In addition to this perceptual information, haptic coupling is usually constrained by a mechanical link. When an haptic communication channel is formed between individuals, through conveyance of pushing and pulling forces, the partners can coordinate their actions efficiently (van der Wel, Knoblich, & Sebanz, 2011). Haptic entrainment is therefore a major component of interpersonal action coordination. In addition, when comparing across different types of sensory information with respect to mutual entrainment, several studies have shown that haptic coupling between individuals induces a stronger mutual entrainment than either visual or auditory coupling (Nessler & Gilliland, 2009; Sofianidis & Hatzitaki, 2015; Sofianidis, Hatzitaki, Grouios, Johannsen, & Wing, 2012; Zivotofsky & Hausdorff, 2007). For example, when walking side-by-side, people spontaneously fall into pace more often when they are holding hands than when they are only peripherally seeing each other or hearing each other's steps (Nessler & Gilliland, 2009; Zivotofsky & Hausdorff, 2007). Even when the mechanical link is minimal, such as when individuals share light mutual contact through their fingertips, individuals who are swaying side-by side synchronize better to one another, compared to when they both hear the same metronome without interpersonal contact (Sofianidis & Hatzitaki, 2015; Sofianidis et al., 2012).

Pairs of individuals can also coordinate with one another even when communication between them is limited to visual or auditory coupling, but the relative influence of each modality seems to depend on the type of task and on whether the source of the sensory signal is external (e.g., all individuals hearing the same metronome) or if it emerges from the individuals themselves (e.g., reciprocally hearing each other's) (Desmet, Leman, Lesaffre, & Bruyn, 2010; Nessler & Gilliland, 2009; Nowicki, Prinz, Grosjean, Repp, & Keller, 2013; Richardson, Lopresti-Goodman, Mancini, Kay, & Schmidt, 2008; Richardson, Marsh, Isenhower, Goodman, & Schmidt, 2007; Richardson, Marsh, & Schmidt, 2005). In contrast to the external entrainment assessed in the laboratory, during mutual entrainment, the type of signal is optimized within each modality as the visual coupling almost always contains a spatial component (e.g., seeing one's partner moving), whereas auditory coupling is principally temporal (e.g., hearing the pace of a partner's steps).

One important consideration when examining the role of sensory information in interpersonal synchronization is the manner in which an individual is coupled to visual, auditory and haptic information. Bi-directional coupling is when there is mutual adaptation, like in the example of two people moving a sofa together. In this case, the two individual necessarily coordinate and adapt their actions in response to each other movements. Unidirectional coupling is exemplified in the studies where individuals synchronize with a metronome; the metronome's dynamics are fixed and cannot adjust to the person's tapping. The coordination that emerges in a dance group such as folk dancers, for example, involves both bi-directional and unidirectional coupling. The dancers are uni-directionally coupled with the recorded music, but the haptic coupling that occurs among the dancers is bidirectional, where each dancer can be responsive to forces from the others. Another important distinction during mutual interactions involves the differentiation of role-functions into leading and following, where leaders *influence* followers, and followers *adapt* to leaders. For example, in a dance group a leader might demonstrate the dance's steps whereas the other dancers would collectively be the followers. An external signal, such as the recorded music with which the dancers were attempting to synchronize, could be thought of as a "leader" as well since it influences the dancers' movements (Chauvigné, Gitau, & Brown, 2014). Considering that the leader and follower roles make up a fluid continuum and that each individual is leading and following to various degrees, the source of all sensory signals flowing during mutual entrainment can be considered as a collective "leader" to which followers entrain. Followers usually anticipate these leading signals (Gebauer et al., 2016), as they perform their movements slightly ahead of the sensory signal that they are synchronizing with, producing the standard "negative asynchrony" (Repp, 2005). Compared to followers, leaders tend to be more stable spatially and/or temporally (Fairhurst, Janata, & Keller, 2014; Sacheli, Tidoni, Pavone, Aglioti, & Candidi, 2013), and thus serve as reliable sources for others to synchronize with.

Given this complexity, few studies have gone beyond examining mutual entrainment in dyads to investigating how groups of individuals are coupled and coordinate their movements with each other by making use of continuous auditory, visual and haptic information. Only a handful of studies have attempted to assess synchronization in a group settings; these studies have examined teams of three in an origami production task (Wallot, Roepstorff, & Mønster, 2016), groups of six in rocking chairs (Richardson, Garcia, Frank, Gergor, & Marsh, 2012), group of ten in spontaneous arm-swinging (Codrons, Bernardi, Vandoni, & Bernardi, 2014), ten singers in African and Finnish choirs (Himberg & Thompson, 2011) and 46 dancers in a disco club (Ellamil, Berson, Wong, Buckley, & Margulies, 2016). This is likely because many analytical methods are designed to quantify coordination between two actors and are not able to capture the complexity of a group's behaviour (Wallot et al., 2016, Lewis, 1984). Indeed, a group can be conceptualized as single entity, where the emergent behaviour of the group transcends the averaged dyadic interactions between each pair within the group (Richardson et al., 2012; Wallot et al., 2016). Groups, as entities, engage in group-level processes, including decision making, performance, and collective emotional expression (Couzin, 2009; Kerr & Tindale, 2004; King & Cowlishaw, 2009; Meslec, Curseu, Meeus, & Iederan Fodor, 2014). With respect to what kinds of sensory information support group synchrony, studies have shown that shared visual information enhances spontaneous coordination in groups, compared to no sensory information (Codrons et al., 2014; Richardson et al., 2012), and that individuals synchronize best as a group with music that they know the best (Ellamil et al., 2016; Himberg & Thompson, 2011). These studies have only focused on unintentional (unconscious) synchronization, whereas there are multiple situations of shared intentionality where the joint goal is to produce *group synchrony*, and such is the case in group musical or dance performance (Keller, Novembre, & Hove, 2014; Knoblich & Sebanz, 2008; Phillips-Silver, Aktipis, & Bryant, 2010; Reddish, Fischer, & Bulbulia, 2013; Sacheli, Aglioti, & Candidi, 2015). With respect to group synchrony, recent methods allow for the quantification of coordination between multiple time series (Richardson, Garcia, Frank, Gergor, & Marsh, 2012; Wallot, Roepstorff, & Mønster, 2016). Specifically cluster phase analysis assesses the divergence in phasing between each individual of the group and the average of the group (Richardson et al., 2012).

Accordingly, the objective of the present study was to examine the synchrony that emerges between individuals engaged in group-dance, and investigate how coupling with different sensory information supports group coordination. To do so, we examined a group of 13 folk dancers performing in a circle and manipulated the availability of sensory information. We chose folk dancing as, in such group behaviour, dancers reach a sense of group synchronization by relying on three major sources of sensory information: 1) all dancers hear the same music and attempt to entrain their movements to the strong beats of the meter (external auditory coupling), 2) they see one another other and the leader in the circle's center performing identical movement patterns (mutual visual coupling), and 3) they hold hands with their adjacent partners, allowing them to both send and receive forces (mutual haptic coupling). The dancer's full body movements were recorded using 3D motion capture while we manipulated the availability of either auditory, visual or haptic coupling. Synchronization in the dancer's body movements was compared across the different conditions using the cluster phase method (Richardson et al., 2012). Additionally the synchronization and the relative phase between the dancers' movements and each source of sensory information (music, group's leader, adjacent neighbours) were examined to identify which source was leading the dancers the most.

Based on the literature reviewed above on dyadic entrainment, we expected that haptic coupling would have the strongest impact on group synchrony. We also hypothesized that the axes involves in *where* the dancers would step (necessitating spatio-temporal components, i.e., the horizontal antero-posterior and medio-lateral axes) would be more strongly impacted by the lack of vision than axes only involved with *when* the dancers stepped (temporal components, i.e., the vertical axis), as consistent with previous studies examining synchronization with auditory and visual signals. Finally, we hypothesized that synchronization of each dancer with the source of the sensory information would be more reduced than the group synchrony per se when the coupling between the dancers and the source was unavailable.

# 4.3 Methods

## 4.3.1 Participants

14 folk dancers (11 females, 69.3±5.9 years old) participated in the study after giving their informed consent (McMaster University Research Ethics Board). All dancers were recruited from a local recreational folk dancing club, where they had been dancing 14.6±7.4 hours a month for the past 32.3±14.4 years. Six dancers had other dance experience (ballet, contemporary, Scottish, English country). All dancers had normal or corrected-to-normal vision, hearing, and musculoskeletal abilities. They received monetary compensation for their participation.

## 4.3.2 Stimuli

Two Greek folk dances were performed in a closed circle to recorded musical excerpts: Syrtos Pyleas (Dance 1) and Kritikos Syrtos (Dance 2). Both dances were well known to the dancers. Table 4.1 contains information about the basic characteristics of the dance and the music. Figure 4.S1 presents a simplified score of the musical excerpts, a verbal description of the dance steps, and a graphic mapping of those steps onto the musical beats in the score. Each dance contained a basic sequence of 12 steps that was repeated throughout the dance. The musical stimuli used in the experiment permitted six repetitions of the dance sequence (i.e., 72 steps in total).

***Table 4.1.*** *Dance and music characteristics*

| | | **Dance 1: Syrtos Pyleas** | **Dance 2: Kritikos Syrto** |
|---|---|---|---|
| | Excerpt duration | 44s | 56s |
| | Dance sequence fits musical phrase | Yes | No |
| Dance characteristics | Sequence duration | 5.73s | 7.29s |
| | Number of steps per sequence | 12 | 12 |
| | Complexity | Medium | Difficult |
| Music characteristics | Meter | 7/8 | 4/4 |
| | Tempo | 126 bpm | 132 bpm |

## 4.3.3 Procedure

Thirteen dancers formed a closed circle by holding hands, while the leader (the dance group's teacher) was in the center of the circle. Together, they performed the dances under four conditions. In the control condition, they danced as usual with all sensory information present: to music (auditory), while holding hands (haptic), and with the eyes open (visual). This setting is schematized in Figure 4.1. In each of the three other conditions, one sensory modality was selectively inhibited: in the noMusic condition, the dancers danced without music; in the noTouch condition, they danced without handhold as an open circle; and in the noVision condition, they danced with their eyes closed. Because the leader was inside the circle, she was not in physical contact with the other dancers. In addition, her eyes were open during the noVision condition, and she wore wireless headphones (Silent Disco King) during the noMusic condition to permit her to hear the music, which the other dancers could not hear.

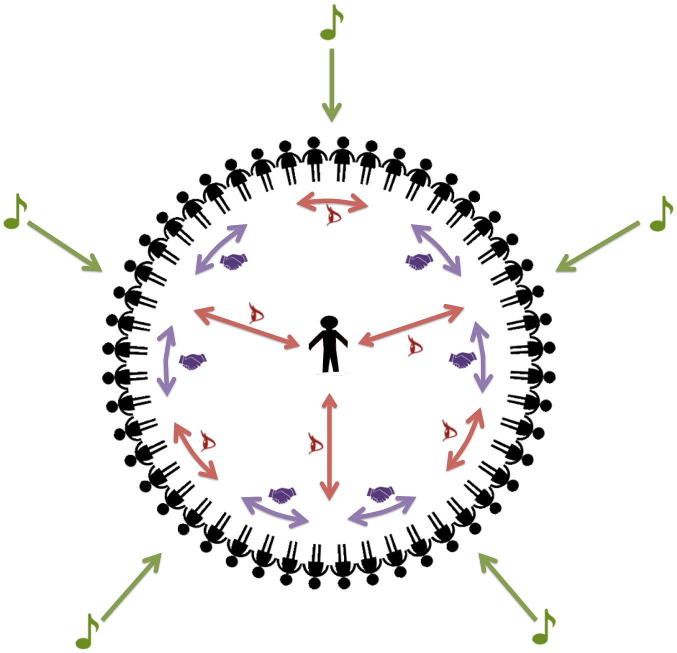


*Figure 4.1: Scheme of the sensory couplings in folk dancing.*

The handholding between each dancer and his/her two neighbours formed a bidirectional haptic coupling (purple arrows). The dancers were seeing each other and the group's leader via semi-bidirectional visual coupling (red arrows). Finally, the dancers were hearing the music via a unidirectional auditory coupling (green arrows).

The dancers performed four dances in total, but only two are included in the present report. For each dance, the dancers performed each of the four conditions five times, resulting in 20 trials per dance. There were 80 trials across the four dances, which were performed in a counterbalanced order. A break was taken after 40 trials. The entire experiment lasted 3 hours, including set-up time. After the experiment, the participants filled out a questionnaire about their dance experience, and reported (on a 5-point scale) their familiarity with and competency at the dances performed and the perceived difficulty and enjoyablility of each condition.

### 4.3.4 Apparatus

The experiment took place on the stage of a large black-box performance theatre. Each dancer was fitted with 10 passive motion-capture markers placed on the right and left foot tips, heels, knees, and waist (iliac crest), with single markers placed on the neck (vertebral level C7) and left hand. The 3-dimentional coordinates of the markers were recorded at 120 Hz using a 23-camera optical motion capture system (Qualisys). The musical stimuli were presented using a speaker (Dynaudio Accoustics BM6A) located approximately 5m from the dancers. To synchronize the music with the motion-capture system, triggers in the audio signal were converted into TTL pulses with an Arduino Uno and then plugged into the Qualisys Track Manager.

### 4.3.5 Data filling and conversion to local coordinates

Missing data were interpolated by means of polynomial interpolation in the Qualisys Track Manager. Correctness of the interpolated data was always visually verified, and data were left missing if they could not be interpolated correctly. Three-dimensional coordinates were then converted to local coordinates centered on each dancer. The two waist markers were used to define the orientation of the local X-axis. The Z-axis (vertical) was not changed. The local Y-axis was defined orthogonally to the X- and Z-axes. Finally, the local origin was defined as the mid-point between the right and left waist markers, projected on the plane z=0 (the floor). The three axes were defined for each dancer in the following manner: the X-axis corresponds to the medio-lateral body axis, with positive values indicating motion in the rightward direction; the Y-axis corresponds to the antero-posterior body axis, with positive values indicating motion in the forward direction; and the Z-axis corresponds to the infero-superior axis, with positive values indicating motion in the upward direction. One dancer was excluded from the analysis of both dances due to the significant amount of data missing from his waist markers (preventing conversion to the local system), and another dancer was excluded from the analysis of Dance 2 for the same reason. For the remaining dancers, 0.60% of the total local data (all dancers, markers and trials) were still missing for Dance 1, and 1.58% for Dance 2. Because the dancers repeated the same sequence six times for each trial, there was enough repetition in the time series to allow for filling in the remaining missing data by averaging the values from the complete sequences. The missing intervals were visually detected in each complete sequence using precise landmarks in the time series. The corresponding intervals were then re-sampled to match the number of frames of the missing interval, averaged, and carefully placed in the missing interval, controlling for drift. Edges were interpolated. When more than one third of a trial (i.e., two dance sequences) was missing due to a marker falling off, the data were left as missing (see Table 4.S1).

### 4.3.6 Pre-processing

Analyses were performed in the X, Y, and Z local trajectories of the foot markers: right and left foot tips and heels. Each time series was detrended to remove drift, normalized across periods to center each period on zero, and low-pass filtered using a 5 Hz Butterworth filter. For normalization, a Z score was obtained at each time point using the local mean and local standard deviation, which were computed using a sliding window approximately the size of the largest period (i.e. between two steps of the same foot). For each dance and axis, the largest period of each trial was computed and averaged across markers, conditions, dancers, and trials, with values ranging from 1.13s to 2.65s.

### 4.3.7 Cluster Phase analysis

A cluster phase analysis (Frank & Richardson, 2010; Richardson et al., 2012) was performed for each dance, axis, condition, marker, and trial for the 12 dancers in Dance 1 and the 11 dancers in Dance 2. As in Richardson et al. (2012), we employed the Hilbert transform to calculate the phase time-series for each movement. Some errors in the phase computation, occurring when a period was not well centered on zero, were detected for each dancer and were removed locally (± 50 frames) from the phase time-series of a dancer. The phase of the group (cluster phase) was computed by averaging the phase time-series of each dancer in the complex domain. The relative phase of each dancer to the group was computed by subtracting the cluster phase from each dancer's phase time-series. The complex magnitude (amplitude) of each dancer's relative phase gives the degree of synchronization of each dancer to the group as a whole. Finally, the degree of synchronization of the group as a whole was computed for each time-point by averaging the mean-centered relative phase of each dancer, and taking the complex magnitude of the resultant. Group and individual synchrony values range from 0 to 1, where 0 indicates a total absence of synchrony and 1 indicates perfect synchrony.

### 4.3.8 Correlational analysis

Using Pearson correlations, we examined the relation between "synchronization with the group" for each individual and his/her self-reported values of dance experience, familiarity with the dances, and ease at dancing in each condition. The significance level was set to $p \leq 0.016$ (i.e., $p=0.05/3$) to correct for the three axes examined.

### 4.3.9 Detection of outliers

The synchronization of individuals with the group was further explored in order to detect outliers. A dancer was considered an outlier if s/he was poorly synchronized with the group over all conditions (i.e., synchrony values close to 0) or if s/he was significantly worse in one subset of the conditions, such that this one condition outweighed the others in the group mean. Outliers were also detected using Procrustes analysis, which compares the 2D shape between objects by determining a linear transformation (translation, reflection, rotation, and scaling) that best allows a given shape to conform to the shape of a model, where the output is a dissimilarity measure between the two shapes. We used the

Procrustes analysis to compare the shape of the trajectories in the XY plane for a given dancer against the group average of the X and Y trajectories for each dance, axis, marker, and condition, without a consideration for the time component (see Figure 4.S2 for examples). Each sequence for each dancer was compared to the corresponding group average. Outliers were identified identically using the cluster phase method and Procrustes analysis, all of them resulting from difficulty in performing the dances in the noVision condition (Figure 4.2 and 4.S2). As a result of this, one participant was excluded from the analysis of both dances, while two additional participants were excluded only from the analysis from Dance 2. In general, dancers had difficulty performing Dance 2 with the eyes closed because

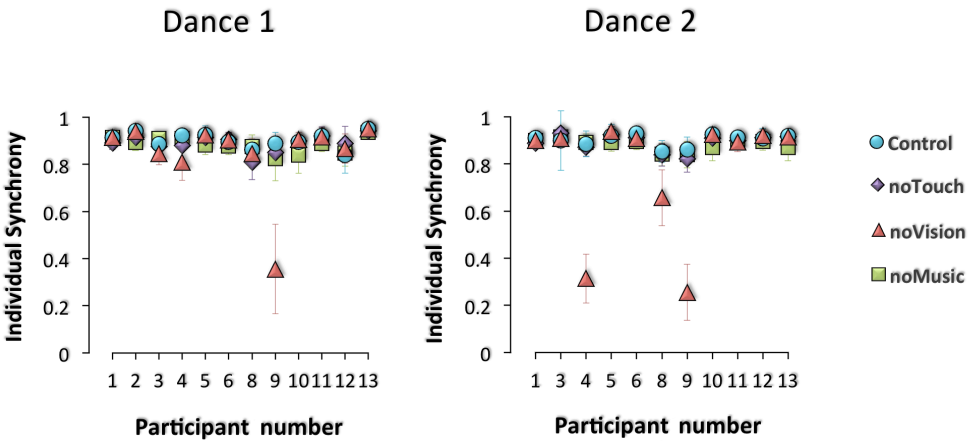


*Figure 4.2: Synchronization of each dancer with the group*

This figure shows individual synchrony from the cluster phase analysis. Most dancers were highly synchronized with the group in all conditions in both dances. However, in Dance 1, participant 9 was not synchronized with the group when dancing with the eyes closed. In Dance 2, participants 5, 8 and 9 were not synchronized with the group when dancing with the eyes closed. These participants were considered as outliers and were removed from the analyses. Note that participant 7 in both dances and participant 2 in Dance 2 are missing due to excessive missing data. Error bars indicate the standard deviation.

the phrase structure of the dance does not map well onto the phrase structure of the music as well as because the dance does not have a clear change of direction. Therefore, if one misses even a single step, it is difficult to use music or haptic information to be able to catch up.

### 4.3.10 Statistical Analysis and Model Reduction

To assess whether the effects were similar in the two dances, and to avoid overly complex models, we first tested, for each analyses, if the dances and interacted with the main factor(s) of interest (thereafter named pre-analysis, see supplementary materials for details). If it was, we performed the analysis on each dance separately. Otherwise, we perform the analysis including both dances, without testing the interaction between dances and other factors. Analyses of variance (ANOVAs) were performed on linear models to test effects on group synchrony in R (R Core Team, 2014), and repeated measure ANOVAs were performed on linear mixed models to test effects on individual synchrony and relative phase, using the LME4 package (Bates, Maechler, Bolker, & Walker, 2015) in R. Effects size were computed using the SJSTATS package (Lüdecke, 2017) in R.

#### 4.3.10.1 Group synchrony

The cluster phase analysis was re-run without outliers, resulting in the analysis of 11 dancers for Dance 1 and 8 dancers for Dance 2. The group synchrony values were averaged within each sequence. We first tested for the effect of axes on the four conditions (see supplementary material for details) and found a significant interaction between conditions and axes. The latter was due to the Z axis, since the interaction between conditions and axes was not significant in a model without the Z axis (i.e. XY), but stayed significant when including it (XZ and YZ, see Table 4.S2). Therefore, in all following analyses we tested the effects using two models: one for the X and Y axes on one side, and the other for the Z axis on the other side. Additionally, the pre-analysis showed no interaction with dances (Table 4.S2) so both dances were included into each model. We ran two ANOVAs looking at the 4 conditions (control, noMusic, noVision, noTouch) x 2 markers (foot tip, heel) x 2 sides (left, right). The two dances and the 30 sequences per dance (6 repetitions x 5 trials) were entered into the models as factors of no interest (interactions were not tested) as were the two axes of the XY model. The significance level of the ANOVAs was set to $p < 0.025$ to correct for the two models ($p=0.05/2$), where significant effects were explored using Bonferroni-corrected post-hoc analyses.

We also ran ANOVAs to test the effect of sequence repetition over the course of the musical excerpt for each dance separately, using two 6 repetitions x 4 conditions (control, noMusic, noVision, noTouch) x 3 axes (X, Y, Z) analyses. The 5 trials and 4 markers were entered into the model as factors of no interest (interactions were not tested). The significance level of the ANOVAs was set to $p < 0.025$ to correct for the two models ($p=0.05/2$), and the significant effects were explored using Bonferroni-corrected post-hoc analyses.

### 4.3.10.2 Synchronization with the leader and with the music

The synchronization of the group and of the individual dancers with the leader and with the musical beat was assessed. For the music, the onset of the principal beats of the musical meter was manually extracted by an expert musicologist. A sinusoidal curve was then extrapolated from the beat's timing such that there was one period between each beat and such that the value of $\sin(\pi)$ (i.e., phase = 0) was always directly on the beat. The synchronization of a dancer with the leader or with the musical beat was then computed in a manner quite similar to the cluster phase. The relative phase of each dancer to the leader (or to the music) was computed by subtracting the leader's phase (or the music's phase) from each dancer's phase time-series. The overall synchronization of the group was computed at each time-point by averaging the mean-centered relative phase of each dancer and taking the complex magnitude of the resultant. We tested the synchronization with the music on the Z axis only, as the dancers were most likely to synchronize their vertical foot steps (floor contact) with the beat of the music (exploratory analyses showed very low synchronization with the music on the X and Y axes). Since the dancers interacted with the leader only visually, and with the music only acoustically, we expected to see an interaction with conditions on the group synchrony values and the mean individual synchrony values.

As with the prior analyses, the group synchrony values were averaged within each sequence and the pre-analysis showed that the effect of references on conditions was identical for both dances (see supplementary materials) so both dances were included into both the XY and the Z models. We tested the influence of the leader and the music on group synchrony with a 3 references (cluster phase, leader, music) [only 2 references of the XY model] x 4 conditions (control, noMusic, noVision, noTouch) x 2 markers (foot tip, heel) x 2 sides (left, right) ANOVA. The two dances and the 30 sequences were entered into the model as factors of no interest (interactions were not tested) as were the two axes of the XY model. The significance level of the ANOVA was set to $p < 0.025$ to correct for the two models ($p=0.05/2$), and significant effects were explored using Bonferroni-corrected post-hoc analyses.

In addition, we tested the mean synchronization of individual dancers with the music and the leader. The individual synchrony values were averaged within each trial and the pre-analysis showed a significant interaction between dances, reference and condition (see supplementary materials) so both the XY and the Z models were tested on each dance separately. We performed 3 references (cluster phase, leader, music) [only 2 references of the XY model] x 4 conditions (control, noMusic, noVision, noTouch) x 2 markers (foot tip, heel) x 2 sides (left, right) repeated measures ANOVAs to account for the dancers.. The five trials were entered into the model as factors of no interest (interactions were not tested) as were the two axes of the XY model. The significance level of the ANOVAs was set to $p < 0.0125$ to correct for the four models ($p=0.05/4$), and significant effects were explored using Bonferroni-corrected post-hoc analyses.

### 4.3.10.3 Relative phase with the leader and with the music

On the Z axis only, we also compared the mean relative phase of individual dancers to the leader and to the music in all conditions. The relative phase values of each dancer were averaged within each trial and the pre-analysis showed a significant interaction between dances, reference and condition (see supplementary materials) so the Z model was tested on each dance separately. We tested the relative phase of the leader and the music using two 3 references (cluster phase, leader, music) x 4 conditions (control, noMusic, noVision, noTouch) x 2 markers (foot tip, heel) x 2 sides (left, right) repeated-measures ANOVAs to account for the dancers. The five trials were entered into the models as a factor of no interest (interactions not tested). The significance level of the ANOVAs was set to $p < 0.025$ to correct for the two models ($p=0.05/2$), and significant effects were explored using Bonferroni-corrected post-hoc analyses.

### 4.3.10.4 Synchronization with the neighbours

Beyond looking at global effects at the group level, we wanted to examine if dancers were more synchronized with their immediate neighbours than with the group. To do this, we developed the concept of a "trio", referring to a given dancer and the two dancers to his/her right and left, respectively. Because we had to exclude trios which contained at least one outlier, the participants were not strictly matched in the trio synchrony and group synchrony analyses. In addition, we expected that it would be easier to synchronize in a group of three individuals than in a larger group. Thus, we normalized the data to the mean of the control condition so as to perform direct comparisons between synchrony within trios and synchrony within the group for each condition. Since the neighbours were the sole source of haptic coupling, we expected to see an interaction with conditions on synchrony values.

The group synchrony values for each trio were averaged within each trial and the pre-analysis showed that the effect of group types on conditions was identical for both dances (see supplementary materials) so both dances were included into both the XY and the Z models. We compared group synchrony and trio synchrony with a 2 group types (whole group, trios) x 4 conditions (control, noMusic, noVision, noTouch) x 2 markers (foot tip, heel) x 2 side (left, right) ANOVAs. The two dances and the five trials were entered into the models as a factor of no interest (interactions were not tested) as were the two axes of the XY model. The significance level of the ANOVAs was set to $p < 0.025$ to correct for the two models ($p=0.05/2$), where significant effects were explored using Bonferroni-corrected post-hoc analyses.

Then, we examined if the dancers were more synchronized with their immediate neighbours than with dancers further along the circle. We measured the synchrony of each dancer with their two neighbours as a function of the neighbour's distance from the reference dancer (graphically displayed in Figure 4.7A in the Results section), where a distance of "1p" refers to those two people directly neighbouring the dancer to the right and left, a distance of "2p" refers to those dancers *two positions out along the circle* from the reference dance, up to a distance of "4p" on either side of the reference dancer, which created the maximum trio distancing in our circle of 13 dancers. Because this analysis investigated the position of dancers along the circle, we included outliers here, although we excluded the worst condition of noVision.

The group synchrony values for each trio were averaged within each trial and the pre-analysis showed that the effect of neighbour's distance on conditions was identical for both dances (see supplementary materials) so both dances were included into both the XY and the Z models. We tested the influence of neighbour distance on group synchrony with a 4 neighbour distances (1p, 2p, 3p, 4p) x 4 conditions (control, noMusic, noVision, noTouch) x 2 markers (foot tip, heel) x 2 sides (left, right) repeated-measures ANOVAs to account for trio members. The two dances and the five trials were entered into the models as factors of no interest (interactions were not tested) as were the two axes of the XY model. The significance level of the ANOVAs was set to $p < 0.025$ to correct for the two models ($p=0.05/2$), where significant effects were explored using Bonferroni-corrected post-hoc analyses.

#### 4.3.10.5 Relative phase within neighbours' trios

Finally, since the dances progressed in a counter-clockwise (rightward) direction, we compared the relative phase of the neighbour directly to the right with that directly to the left, looking only at 1p as the neighbour distance and on the Z axis only. The relative phase values were averaged within each trial and the pre-analysis showed that the effect of neighbour's position on conditions was identical for both dances (see supplementary materials) so both dances were included into the Z model. We tested the influence of the neighbour's position on relative phase with a 2 neighbour's positions (left, right) x 4 conditions (control, noMusic, noVision, noTouch) x 2 markers (foot tip, heel) x 2 sides (left, right) repeated-measures ANOVA to account for trio members. The two dances and the five trials were entered into the model as factors of no interest (interactions were not tested). The significance level of the ANOVA was set to $p < 0.05$, where significant effects were explored using Bonferroni-corrected post-hoc analyses.

## 4.4 Results

### 4.4.1 Correlation analysis

For both dances and all three axes of motion, the synchronization level of each dancer to the group as a whole correlated significantly with the dancer's prior familiarity with the dance, with Pearson r values ranging from 0.35 to 0.54 (Table 4.2). The individual-level synchrony value was also significantly correlated with perceived ease at performing the dance in each condition for Dance 2, but not for Dance 1. Finally, no correlation was found between synchrony and overall experience at dancing.

### 4.4.2 Main effects of conditions

Looking now to the group-level synchrony, the mean group synchrony value was overall high for both dances (Dance 1: 0.89 ±0.05, Dance 2: 0.93 ±0.04, where a

***Table 4.2.** Correlations*

Correlations between the synchronization of each dancer to the group and self-reported values of: familiarity of a dancer with each dance used in the experiment, difficulty of the four conditions (for each dance), and overall folk dancing experience. Significant effects (p < 0.16) are in bold.

| | | **Dance 1** | | | **Dance 2** | | |
|---|---|---|---|---|---|---|---|
| | | X | Y | Z | X | Y | Z |
| **Dance familiarity** | Pearson's r | **0.381** | **0.4** | **0.353** | **0.54** | **0.442** | **0.44** |
| | p-value | **0.008** | **0.005** | **0.014** | **< 0.001** | **0.003** | **0.003** |
| **Condition difficulty** | Pearson's r | 0.289 | 0.015 | 0.299 | **0.56** | **0.62** | **0.59** |
| | p-value | 0.046 | 0.92 | 0.039 | **< 0.001** | **< 0.001** | **< 0.001** |
| **Folk dance experience** | Pearson's r | 0.217 | -0.259 | 0.167 | 0.129 | 0.153 | 0.174 |
| | p-value | 0.138 | 0.076 | 0.256 | 0.404 | 0.322 | 0.259 |

value of 1 is the maximum synchrony), highlighting the clear expertise of this cohort of folk dancers at performing these dances. For both the combined XY (horizontal) axis and the Z (vertical) axis, the effect of inhibiting a single sensory coupling was highly significant (Figure 4.3 and Table 4.3). In the XY axis, all three conditions where one sensory coupling was inhibited elicited a decrease in group synchrony, compared to the control condition, in which the dancers were the most synchronized. The lowest synchrony was seen during the noTouch condition, indicating that the haptic contact was the most important cue for engendering group synchrony in the antero-posterior and medio-lateral dimensions. There was no difference between noMusic and noVision for XY, which elicited an intermediate level of synchrony. For the vertical axis, noMusic elicited the lowest level of group synchrony, noTouch elicited an intermediate level, and noVision was not significantly different from the control condition. We thus observed a dissociation between the horizontal axes (medio-lateral + antero-posterior) – where haptic interaction had the strongest effect on synchrony – and the vertical axis, where music had the strongest effect, and visual coupling has no

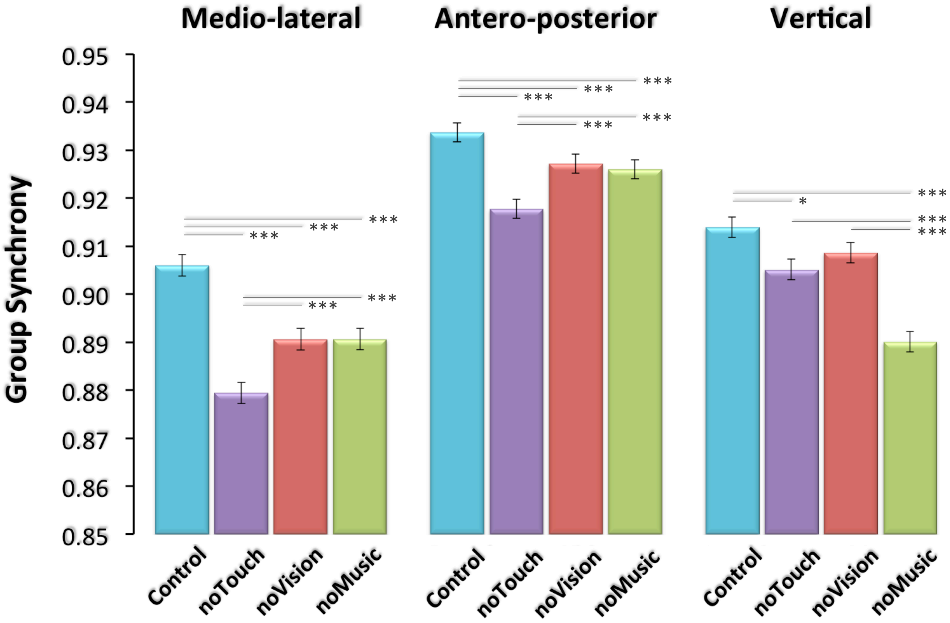


*Figure 4.3:* Group synchrony in the three bodily axes for each condition

In the control condition, the dancers shared haptic (holding the neighbours' hands), visual (the other dancers and the leader), and auditory (music) couplings. In the three other conditions, one of these cues was selectively inhibited. The medio-lateral and antero-posterior axes (spatio-temporal dimension: "where to step") show an effect of all sensory couplings on group synchrony, most significantly for touch. The vertical axis (temporal dimension only: "when to step") shows an effect of all couplings except for vision, and most significantly for music. Note that the medio-lateral and antero-posterior axes were tested in the same model, such that the post-hoc analysis reflects the difference between conditions on the mean of both axes. This was possible because there was no interaction between condition and axis in this model. *** $p<0.001$, **$p<0.01$. *$p<0.05$. The results represent the means for both dances. Errors bars indicate standard errors of the mean.

***Table 4.3.*** *Main effects of conditions*

ANOVAs for the general effect of condition on group synchrony for the XY and Z axes. The factor *condition* has 4 levels (Control, noTouch, noVision, noTouch). Effects of interest are in bold. The significant level is set to p < 0.025 to control for the two models.

| | **XY (horizontal) axes** | | | | | **Z (vertical) axis** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Df | F value | p-value | η2 | part. η2 | Df | F value | p-value | η2 | part. η2 |
| Sequence | 29 | 20.05 | < 0.001 | 0.152 | 0.244 | 29 | 17.78 | < 0.001 | 0.328 | 0.370 |
| **Condition** | **3** | **24.53** | **< 0.001** | **0.019** | **0.039** | **3** | **21.79** | **< 0.001** | **0.042** | **0.069** |
| Marker | 1 | 0.08 | 0.776 | 0.000 | 0.000 | 1 | 0.40 | 0.530 | 0.000 | 0.000 |
| Side | 1 | 65.55 | < 0.001 | 0.017 | 0.035 | 1 | 9.36 | 0.002 | 0.006 | 0.011 |
| Dance | 1 | 847.91 | < 0.001 | 0.222 | 0.320 | 1 | 85.88 | < 0.001 | 0.055 | 0.089 |
| Axis | 1 | 406.42 | < 0.001 | 0.106 | 0.184 | na | na | na | na | na |
| **Condition: marker** | **3** | **0.20** | **0.893** | **0.000** | **0.000** | **3** | **2.67** | **0.047** | **0.005** | **0.009** |
| **Condition: side** | **3** | **5.70** | **0.001** | **0.004** | **0.009** | **3** | **0.55** | **0.645** | **0.001** | **0.002** |
| Marker: side | 1 | 21.86 | < 0.001 | 0.006 | 0.012 | 1 | 6.53 | 0.011 | 0.004 | 0.007 |
| **Condition: marker: side** | **3** | **0.21** | **0.890** | **0.000** | **0.000** | **3** | **0.56** | **0.643** | **0.001** | **0.002** |
| Residuals | 1803 | | | | | 879 | | | | |

effect. There was no interaction between condition and marker and/or side, except between conditions and side for the XY axes. This effect was due to an increased influence of the noTouch condition on the right side, although the same trend was observed on both sides. For both dances, the dancers progressed in the rightward direction, and so it seems that the absence of physical contact with neighbours has its strongest effect on the leading (right) foot.

### 4.4.3 Effect of sequence repetition

During each trial, the dancers repeated the sequence of steps six times over the course of the musical excerpt. There was a significant effect of sequence repetition for both dances (Figure 4.4 and Table 4.S3), such that the group synchrony increased over the course of the musical excerpt. The dancers were the least synchronized in the first sequence, and reached their maximum synchrony at around the third sequence. In Dance 1, the group synchrony dropped slightly in the fourth sequence due to the fact that the transition between sequences 3 and 4 is somewhat complex in this dance. Indeed, sequence 2 is repeated a second time during sequences 3 and 6 only. This occasional repetition, which was removed from the analysis, seemed to reduce the group synchrony at the start of the fourth sequence.

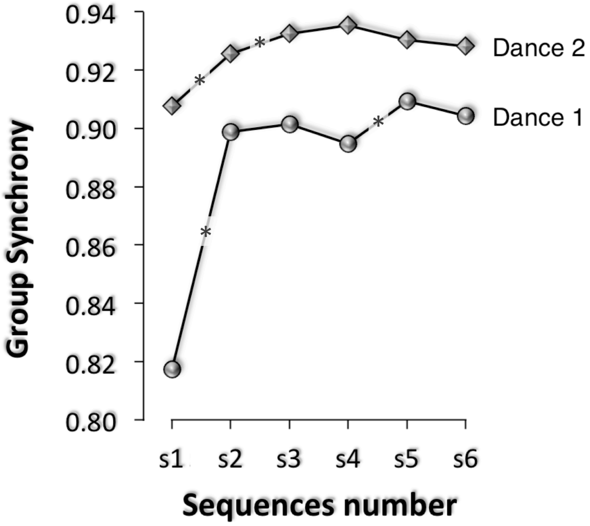


*Figure 4.4: Emergence of group synchrony over sequence repetitions.*
In both dances, the group synchrony increased with sequence repetition. * $p<0.05$ between consecutive sequences. Errors bars indicate standard errors of the mean.

## 4.4.4 Synchronizing with the leader and with the music

We compared the group synchrony relative to the group's average (as above), with two references that could be used for synchronization: the leader and the musical beat. There was no main effect of either reference, nor was there an interaction between reference and condition in any axis (Figure 4.5, Table 4.4).

This means that the dancers synchronized comparably with the leader, with the music, and with the group's average, doing so similarly across all four coupling conditions.

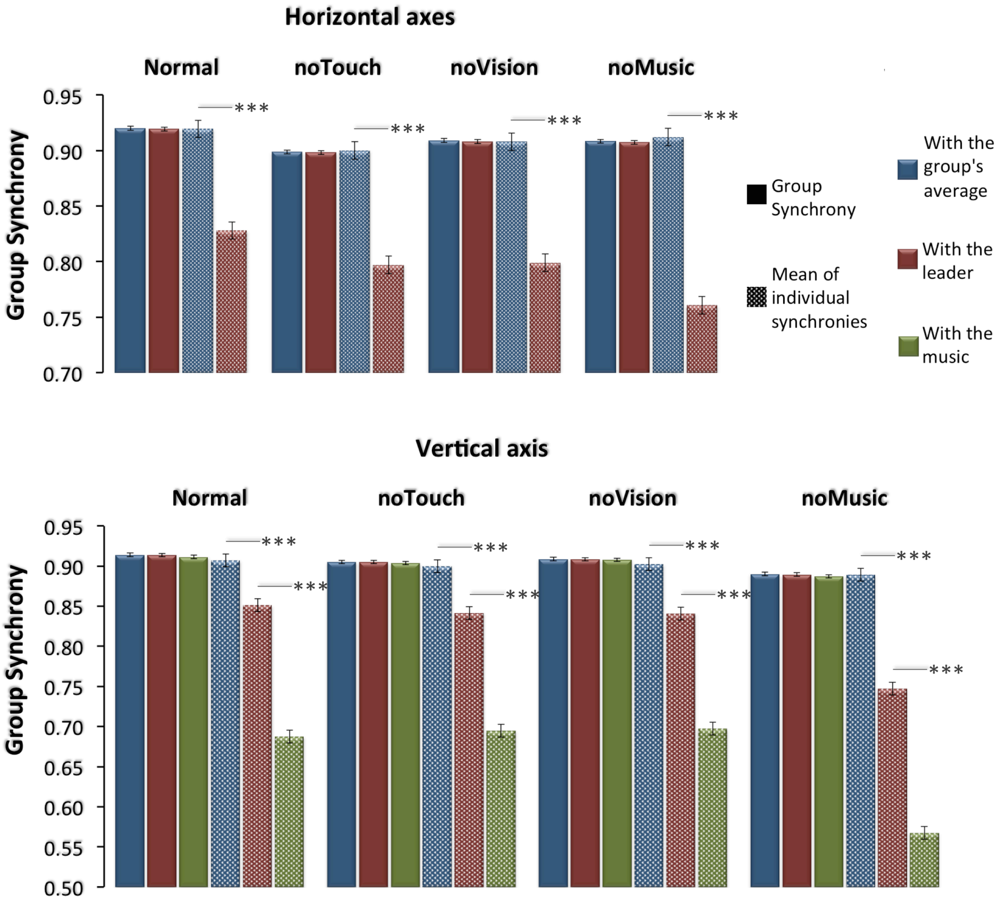


*Figure 4.5: Synchronization with the leader and with the music.*

The results show no main effect or interaction when synchronizing as a group (solid colors), regardless of the reference to which the synchronization is measured from (i.e., the group's average, the leader or the music). There was no effect neither when synchronizing with the group's average as a group or as an individual (solid versus dotted blue). However, the mean of individual synchronies (dotted colors) was higher related to the group's average, intermediate related to the leader and lower related to the music. The decrease in synchrony observed when synchronizing as an individual with the leader or with the music were most important in absence of music. The synchrony with the music was computed only in the vertical axis as we assumed that the dancers synchronized their steps (floor contact) with the musical beat. *** $p<0.001$, **$p<0.01$. *$p<0.05$. The results represent the means for both dances. Errors bars indicate standard errors of the mean.

***Table 4.4.*** *Synchrony with the leader and with the music*

ANOVAs for the effect of synchrony with the leader and with the music. The factor *reference* has two levels (cluster phase, leader) in the XY axes and three levels (cluster phase, leader, music) on the Z axis. Effects of interest are in bold. For the group synchrony, the significant level is set to $p < 0.025$ to control for the two models. For the mean of individual synchronies, the significant level is set to $p < 0.013$ to control for the four models.

| | | **Group Synchrony - both dances** | | | | | **Mean individual Synchronies - Dance 1** | | | | | **Mean individual Synchronies - Dance 2** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Df | F value | p-value | η2 | part. η2 | Df | F value | p-value | η2 | part. η2 | Df | F value | p-value | η2 | part. η2 |
| XY (horizontal) axes | Sequence | 29 | 40.60 | < 0.001 | 0.153 | 0.245 | 4 | 17.40 | < 0.001 | 0.013 | 0.982 | 4 | 10.12 | < 0.001 | 0.009 | 0.986 |
| | **Reference** | **1** | **0.47** | **0.495** | **0.000** | **0.000** | **1** | **4504.40** | **< 0.001** | **0.870** | **1.000** | **1** | **1412.33** | **< 0.001** | **0.290** | **1.000** |
| | Condition | 3 | 49.04 | < 0.001 | 0.019 | 0.039 | 3 | 55.00 | < 0.001 | 0.033 | 0.992 | 3 | 58.44 | < 0.001 | 0.035 | 0.996 |
| | Marker | 1 | 0.31 | 0.576 | 0.000 | 0.000 | 1 | 49.50 | < 0.001 | 0.010 | 0.975 | 1 | 14.72 | < 0.001 | 0.003 | 0.961 |
| | Side | 1 | 126.94 | < 0.001 | 0.017 | 0.034 | 1 | 4.40 | 0.035 | 0.001 | 0.779 | 1 | 0.01 | 0.925 | 0.000 | 0.149 |
| | Dance | 1 | 1728.89 | < 0.001 | 0.104 | 0.181 | na | na | na | na | na | na | na | na | na | na |
| | Axis | 1 | 801.48 | < 0.001 | 0.225 | 0.323 | 1 | 93.40 | < 0.001 | 0.018 | 0.987 | 1 | 3033.97 | < 0.001 | 0.607 | 1.000 |
| | **Reference: condition** | **3** | **0.02** | **0.995** | **0.000** | **0.000** | **3** | **66.30** | **< 0.001** | **0.040** | **0.994** | **3** | **20.91** | **< 0.001** | **0.013** | **0.990** |
| | Reference: marker | 1 | 0.07 | 0.793 | 0.000 | 0.000 | 1 | 27.10 | < 0.001 | 0.005 | 0.954 | 1 | 9.02 | 0.003 | 0.002 | 0.947 |
| | Condition: marker | 3 | 0.62 | 0.602 | 0.000 | 0.001 | 3 | 3.40 | 0.017 | 0.002 | 0.898 | 3 | 0.81 | 0.488 | 0.000 | 0.787 |
| | Reference: side | 1 | 0.10 | 0.749 | 0.000 | 0.000 | 1 | 12.20 | < 0.001 | 0.002 | 0.906 | 1 | 140.12 | < 0.001 | 0.028 | 0.995 |
| | Condition: side | 3 | 10.51 | < 0.001 | 0.004 | 0.009 | 3 | 2.40 | 0.062 | 0.001 | 0.847 | 3 | 2.14 | 0.093 | 0.001 | 0.912 |
| | Marker: side | 1 | 42.00 | < 0.001 | 0.005 | 0.011 | 1 | 9.90 | 0.002 | 0.002 | 0.886 | 1 | 39.80 | < 0.001 | 0.008 | 0.984 |
| | **Reference: condition: marker** | **3** | **0.01** | **0.998** | **0.000** | **0.000** | **3** | **1.50** | **0.216** | **0.001** | **0.788** | **3** | **0.11** | **0.953** | **0.000** | **0.341** |
| | **Reference: condition: side** | **3** | **0.02** | **0.997** | **0.000** | **0.000** | **3** | **1.10** | **0.352** | **0.001** | **0.721** | **3** | **2.77** | **0.040** | **0.002** | **0.927** |
| | Reference: marker: side | 1 | 0.02 | 0.897 | 0.000 | 0.000 | 1 | 0.40 | 0.519 | 0.000 | 0.254 | 1 | 1.51 | 0.219 | 0.000 | 0.708 |
| | Condition: marker: side | 3 | 0.48 | 0.695 | 0.000 | 0.000 | 3 | 0.30 | 0.820 | 0.000 | 0.419 | 3 | 0.77 | 0.511 | 0.000 | 0.784 |
| | **Reference: condition: marker: side** | **3** | **0.01** | **0.998** | **0.000** | **0.000** | **3** | **0.40** | **0.735** | **na** | **na** | **3** | **0.21** | **0.888** | **na** | **na** |
| | Residuals | 3625 | | | | | 3465 | | | | | 2472 | | | | |

***Table 4.4*** *(continued)*

| | | Group Synchrony - both dances | | | | | Mean individual Synchronies - Dance 1 | | | | | Mean individual Synchronies - Dance 2 | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Z (vertical) axes | Sequence | 29 | 55.84 | < 0.001 | 0.334 | 0.376 | 4 | 27.19 | < 0.001 | 0.018 | 0.990 | 4 | 9.90 | < 0.001 | 0.002 | 0.567 |
| | **Reference** | **2** | **0.90** | **0.408** | **0.000** | **0.001** | **2** | **2399.07** | **< 0.001** | **0.715** | **1.000** | **2** | **5430.00** | **< 0.001** | **0.777** | **0.998** |
| | Condition | 3 | 69.00 | < 0.001 | 0.043 | 0.071 | 3 | 313.77 | < 0.001 | 0.139 | 0.999 | 3 | 260.00 | < 0.001 | 0.056 | 0.969 |
| | Marker | 1 | 1.69 | 0.194 | 0.000 | 0.001 | 1 | 67.31 | < 0.001 | 0.010 | 0.982 | 1 | 3.10 | 0.080 | 0.000 | 0.147 |
| | Side | 1 | 29.22 | < 0.001 | 0.006 | 0.011 | 1 | 7.15 | 0.008 | 0.001 | 0.880 | 1 | 27.30 | < 0.001 | 0.002 | 0.558 |
| | Dance | 1 | 241.01 | < 0.001 | 0.050 | 0.082 | na | na | na | na | na | na | na | na | na | na |
| | **Reference: condition** | **6** | **0.07** | **0.999** | **0.000** | **0.000** | **6** | **62.01** | **< 0.001** | **0.055** | **0.997** | **6** | **47.20** | **< 0.001** | **0.022** | **0.923** |
| | Reference: marker | 2 | 0.02 | 0.983 | 0.000 | 0.000 | 2 | 152.62 | < 0.001 | 0.045 | 0.996 | 2 | 6.70 | 0.001 | 0.001 | 0.398 |
| | Condition: marker | 3 | 8.12 | < 0.001 | 0.005 | 0.009 | 3 | 8.59 | < 0.001 | 0.004 | 0.953 | 3 | 16.20 | < 0.001 | 0.004 | 0.700 |
| | Reference: side | 2 | 0.03 | 0.970 | 0.000 | 0.000 | 2 | 3.36 | 0.035 | 0.001 | 0.840 | 2 | 2.50 | 0.080 | 0.000 | 0.216 |
| | Condition: side | 3 | 1.83 | 0.140 | 0.001 | 0.002 | 3 | 3.28 | 0.020 | 0.001 | 0.886 | 3 | 4.30 | 0.005 | 0.001 | 0.401 |
| | Marker: side | 1 | 25.18 | < 0.001 | 0.005 | 0.009 | 1 | 41.28 | < 0.001 | 0.006 | 0.973 | 1 | 623.00 | < 0.001 | 0.045 | 0.962 |
| | **Reference: condition: marker** | **6** | **0.00** | **1.000** | **0.000** | **0.000** | **6** | **1.53** | **0.163** | **0.001** | **0.879** | **6** | **1.70** | **0.125** | **0.001** | **0.394** |
| | **Reference: condition: side** | **6** | **0.00** | **1.000** | **0.000** | **0.000** | **6** | **0.44** | **0.850** | **0.000** | **0.666** | **6** | **7.80** | **< 0.001** | **0.003** | **0.639** |
| | Reference: marker: side | 2 | 0.32 | 0.725 | 0.000 | 0.000 | 2 | 8.58 | < 0.001 | 0.003 | 0.936 | 2 | 555.50 | < 0.001 | 0.080 | 0.978 |
| | Condition: marker: side | 3 | 2.18 | 0.089 | 0.001 | 0.002 | 3 | 1.47 | 0.220 | 0.001 | 0.790 | 3 | 9.00 | < 0.001 | 0.002 | 0.518 |
| | **Reference: condition: marker: side** | **6** | **0.04** | **1.000** | **0.000** | **0.000** | **6** | **0.20** | **0.978** | **na** | **na** | **6** | **4.20** | **< 0.001** | **na** | **na** |
| | Residuals | 2691 | | | | | 2596 | | | | | 1856 | | | | |

However, when looking at mean of individual synchronies, instead of group synchrony, we found a main effect of reference and an interaction (Figure 4.5, Table 4.4). The mean of individual synchronies with the group's average was not different than the group synchrony (Table 4.S4) but the mean of individual synchronies relative to the leader and to the musical beat was significantly lower in both horizontal (XY) and vertical (Z) axes. Moreover, the interaction was due to the fact that the synchronization with the leader and music was even more reduced in absence of music than the synchronization with the group's average, and this was true for all axes. In the horizontal axes and for the mean of individual synchronies with the leader, the noTouch and noVision conditions were significantly lower than the control condition. However, the noTouch and noVision were not different from each other. In the vertical axis and for the mean of individual synchronies with both the leader and the music, the noTouch, noVision and control conditions were not significantly different from each other. These effects were present in both dances so the interaction between dances, references and condition was driven only by magnitude effects.

Regarding the mean *relative* phase, there was a main effect of reference and an interaction between condition and reference (Figure 4.6, Table 4.5). The mean relative phase to the group mean (cluster phase) was zero for all conditions, by definition of the cluster phase analysis. The mean relative phase to the leader was significantly higher than the mean relative phase to the music. It was also different from the relative phase to the group mean, where it was positive for all conditions except for noMusic. This indicates that the dancers lagged behind the leader in most conditions, except in the absence of music, where they anticipated the leader. Furthermore, the relative phase during the noVision condition was significantly higher than during the control condition. This indicates that the dancers lagged even more behind the leader when they were not able to see her. The mean relative phase to the music was not different than the relative phase to the group mean, except in the noMusic condition, where it was significantly lower (keep in mind that the leader was able to hear the music through headphones in

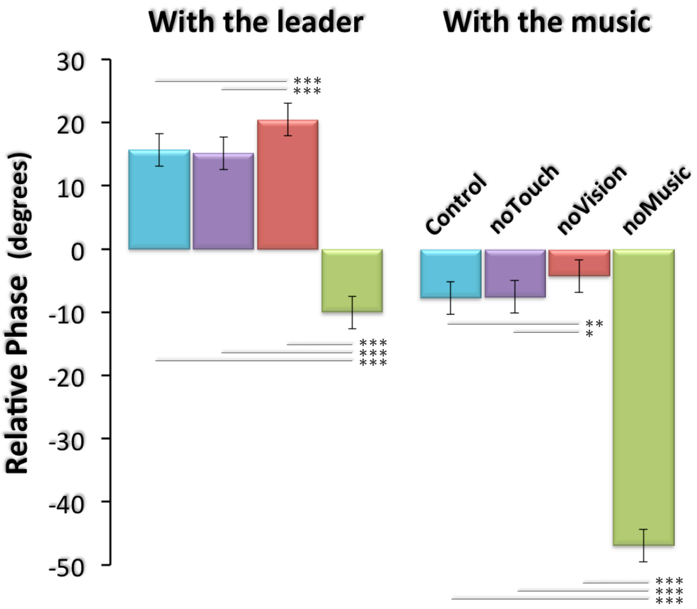


*Figure 4.6: Mean relative phase between the group and the leader or the music*

The results show that dancers lag behind the leader in all conditions, except in the absence of music, where the leader becomes the only reference; note that in the noMusic condition, the leader still hears the music through headphones. The dancers lag behind the leader even more in the absence of visual coupling. The dancers anticipate the music when synchronizing with the music, and they anticipate the leader when they are unable to hear the music. *** $p<0.001$, **$p<0.01$. *$p<0.05$. The results represent the means for both dances. Errors bars indicate standard errors of the mean.

***Table 4.5.*** *Relative phase with the leader and with the music*

ANOVAs for the effect of relative phase with the leader and with the music on the Z axis. The factor *reference* has three levels (cluster phase, leader, music). Effects of interest are in bold. The significant level is set to p < 0.025 to control for the two models.

| | **Relative Phase Dance 1** | | | | | **Relative Phase Dance 2** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Df | F value | p-value | η2 | part. η2 | Df | F value | p-value | η2 | part. η2 |
| Trial | 4 | 3.60 | 0.006 | 0.006 | 0.969 | 4 | 6.00 | < 0.001 | 0.003 | 0.914 |
| **Reference** | **2** | **874.73** | **< 0.001** | **0.307** | **0.999** | **2** | **864.75** | **< 0.001** | **0.236** | **0.999** |
| Condition | 3 | 653.56 | < 0.001 | 0.343 | 0.999 | 3 | 1007.83 | < 0.001 | 0.419 | 0.999 |
| Marker | 1 | 103.21 | < 0.001 | 0.018 | 0.989 | 1 | 198.09 | < 0.001 | 0.025 | 0.990 |
| Side | 1 | 55.96 | < 0.001 | 0.010 | 0.981 | 1 | 108.14 | < 0.001 | 0.014 | 0.983 |
| **Reference: condition** | **6** | **185.59** | **< 0.001** | **0.193** | **0.999** | **6** | **283.01** | **< 0.001** | **0.235** | **0.999** |
| Reference: marker | 2 | 253.13 | < 0.001 | 0.090 | 0.998 | 2 | 97.37 | < 0.001 | 0.026 | 0.991 |
| Condition: marker | 3 | 4.74 | 0.003 | 0.003 | 0.929 | 3 | 1.77 | 0.151 | 0.001 | 0.769 |
| Reference: side | 2 | 54.81 | < 0.001 | 0.020 | 0.990 | 2 | 38.24 | < 0.001 | 0.011 | 0.977 |
| Condition: side | 3 | 0.64 | 0.587 | 0.000 | 0.622 | 3 | 1.65 | 0.175 | 0.001 | 0.710 |
| Marker: side | 1 | 9.52 | 0.002 | 0.002 | 0.898 | 1 | 69.09 | < 0.001 | 0.009 | 0.974 |
| **Reference: condition: marker** | **6** | **1.50** | **0.174** | **0.002** | **0.891** | **6** | **1.05** | **0.393** | **0.001** | **0.764** |
| **Reference: condition: side** | **6** | **0.31** | **0.932** | **0.000** | **0.596** | **6** | **1.02** | **0.413** | **0.001** | **0.735** |
| Reference: marker: side | 2 | 19.11 | < 0.001 | 0.007 | 0.972 | 2 | 65.93 | < 0.001 | 0.018 | 0.986 |
| Condition: marker: side | 3 | 0.38 | 0.766 | 0.000 | 0.514 | 3 | 0.91 | 0.435 | 0.000 | 0.595 |
| **Reference: side condition: marker** | **6** | **0.18** | **0.982** | **na** | **na** | **6** | **0.31** | **0.932** | **na** | **na** |
| Residuals | 2596 | | | | | 1856 | | | | |

this condition). Of note, there was an interaction between marker and reference such that there was an effect of marker only on the relative phase to the music. Indeed, relative to the music, the heel moved before the foot tip in the vertical axis. When looking only at the foot tip, the mean relative phase to the music was significantly higher than the relative phase to the group mean (except for noMusic), whereas when looking only at the heel, the mean relative phase to the music was significantly lower than the relative phase to the group mean in all conditions. In other words, the dancers anticipated the music with their heels. The same effects were found for both dances, indicating that the interaction between dances, references and reference was driven by magnitude effects only.

### 4.4.5 Synchronizing with the neighbours

Having looked at synchronization effects across the group as a whole, we next wanted to look at the more local influence of neighbours. For this, we looked at "trios" of dancers (i.e., a given dancer plus the two dancers on either side of that person, respectively), and compared it with synchrony of the whole group (normalized to the mean of the control condition). We found a significant interaction between condition and group type (Table 4.6). Compared to the group synchrony in the horizontal axes, the synchrony with direct neighbours was significantly higher in the absence of music and touch, and there was no difference between group and neighbour synchrony in the control and noVision conditions. In the vertical axis, the synchrony with direct neighbours was also significantly higher in the absence of music, compared to the group synchrony, whereas there was no difference between group and neighbour synchrony in the other conditions.

Further, we examined synchronization of trios as a function of distance from the neighbours, while including outliers to preserve the continuity of the chain and excluding the noVision condition (Figure 4.7A). There was a main effect of neighbour distance, but no interaction between distance and conditions, nor an interaction between distance, condition, marker, and/or side in all axes

(Figure 4.7B, Table 4.6). The synchronization with neighbours decreased gradually with increasing distance from neighbours (from 1p to 3p, with no difference between 3p and 4p), doing so similarly across all conditions.

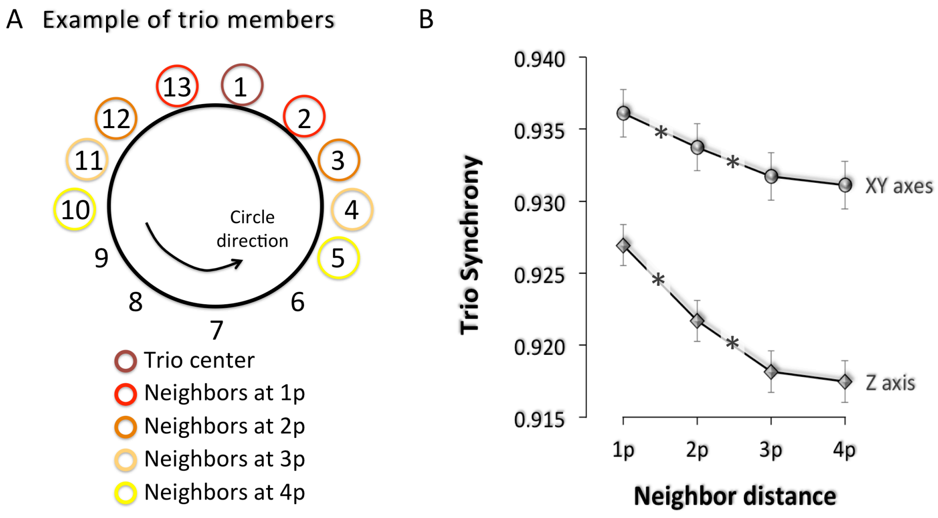


*Figure 4.7: Synchronization in trios of dancers.*

Panel A: Scheme for the circle of 13 dancers. Trios are established based on a reference dancer and the single dancers to his/her right and left, where neighbour distance is measured as the distance in number of participants (1 to 4) between a reference dancer and his/her neighbours. For example, dancers 13 and 2 are at a distance of one participant (1p) from dancer 1, while dancers 12 and 3 are at a distance of 2p from dancer 1, etc. Panel B: Synchrony with neighbours as a function of neighbour distance, showing that synchrony decreases significantly with increasing neighbour distance. * $p<0.05$ between consecutive sequences. The results represent the means for both dances. Errors bars indicate standard error of the mean.

When looking at the relative phase of the right-side versus left-side neighbours (1p only), there was no main effect of neighbour's position, but a significant interaction between neighbour's position and condition (Table 4.6).

***Table 4.6.*** *Synchrony and relative phase for trios of dancers*

ANOVAs for the effect of synchrony and relative phase for trios of dancers. The factor *neighbor* has two levels (neighbor 1p, whole group) in the first ANOVA, four levels (distance: 1p, 2p, 3p, 4p) in the second ANOVA, and two levels (right neighbor, left neighbor) in the third ANOVA. Effects of interest are in bold. For the two synchrony analyses, the significant level is set to $p < 0.025$ to control for the two models (XY and Z). For the relative phase analysis, the significance level is set to $p < 0.05$.

| | | **Trio Synchrony (1p) versus Group synchony** | | | | | **Trio Synchrony (as a function of neighbor distance)** | | | | | **Trio relative phase (neighbor distance = 1p)** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Df | F value | p-value | η2 | part. η2 | Df | F value | p-value | η2 | part. η2 | Df | F value | p-value | η2 | part. η2 |
| XY (horizontal) axes | Trial | 4 | 12.87 | < 0.001 | 0.014 | 0.012 | 4 | 41.54 | < 0.001 | 0.027 | 0.991 | | | | | |
| | Condition | 3 | 41.18 | < 0.001 | 0.033 | 0.030 | 2 | 240.61 | < 0.001 | 0.081 | 0.997 | | | | | |
| | **Neighbor** | **1** | **21.42** | **< 0.001** | **0.006** | **0.005** | **3** | **19.07** | **< 0.001** | **0.008** | **0.968** | | | | | |
| | Marker | 1 | 1.56 | 0.212 | 0.000 | 0.000 | 1 | 56.95 | < 0.001 | 0.009 | 0.973 | | | | | |
| | Side | 1 | 84.43 | < 0.001 | 0.023 | 0.021 | 1 | 288.74 | < 0.001 | 0.048 | 0.995 | | | | | |
| | Dance | 1 | 6.87 | 0.009 | 0.002 | 0.001 | 1 | 1657.00 | < 0.001 | 0.274 | 0.999 | | | | | |
| | Axis | 1 | 27.96 | < 0.001 | 0.008 | 0.007 | 1 | 3027.40 | < 0.001 | 0.501 | 0.999 | | | | | |
| | **Condition: neighbor** | **3** | **3.59** | **0.013** | **0.003** | **0.002** | **6** | **0.57** | **0.753** | **0.001** | **0.688** | | | | | |
| | Condition: marker | 3 | 0.10 | 0.957 | 0.000 | -0.001 | 2 | 2.12 | 0.121 | 0.001 | 0.732 | | | | | |
| | Neighbor: marker | 1 | 0.81 | 0.367 | 0.000 | 0.000 | 3 | 0.66 | 0.578 | 0.000 | 0.544 | | | | | |
| | Condition: side | 3 | 5.18 | 0.001 | 0.004 | 0.003 | 2 | 31.39 | < 0.001 | 0.011 | 0.976 | | | | | |
| | Neighbor: side | 1 | 11.37 | 0.001 | 0.003 | 0.003 | 3 | 3.01 | 0.029 | 0.001 | 0.851 | | | | | |
| | Marker: side | 1 | 39.65 | < 0.001 | 0.011 | 0.010 | 1 | 218.86 | < 0.001 | 0.036 | 0.993 | | | | | |
| | **Condition: neighbor: marker** | **3** | **0.33** | **0.804** | **0.000** | **-0.001** | **6** | **0.44** | **0.854** | **0.000** | **0.624** | | | | | |
| | **Condition: neighbor: side** | **3** | **3.09** | **0.026** | **0.003** | **0.002** | **6** | **0.34** | **0.913** | **0.000** | **0.568** | | | | | |
| | Condition: marker: side | 3 | 0.19 | 0.905 | 0.000 | -0.001 | 2 | 1.51 | 0.220 | 0.001 | 0.660 | | | | | |
| | Neighbor: marker: side | 1 | 1.54 | 0.215 | 0.000 | 0.000 | 3 | 0.58 | 0.630 | 0.000 | 0.524 | | | | | |
| | **Condition: side: neighbor: marker** | **3** | **0.17** | **0.920** | **0.000** | **-0.001** | **6** | **0.26** | **0.955** | **na** | **na** | | | | | |

***Table 4.6** (continued)*

| | | **Trio Synchrony (1p) versus Group synchony** | | | | | **Trio Synchrony (as a function of neighbor distance)** | | | | | **Trio relative phase (neighbor distance = 1p)** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Z (vertical) axes | Trial | 4 | 10.13 | < 0.001 | 0.021 | 0.022 | 4 | 50.19 | < 0.001 | 0.263 | 0.997 | 4 | 0.05 | 0.996 | 0.007 | 0.430 |
| | Condition | 3 | 21.94 | < 0.001 | 0.034 | 0.036 | 2 | 123.14 | < 0.001 | 0.325 | 0.998 | 2 | 0.73 | 0.484 | 0.053 | 0.856 |
| | **Neighbor** | **1** | **6.80** | **0.009** | **0.003** | **0.004** | **3** | **36.57** | **< 0.001** | **0.143** | **0.995** | **1** | **0.01** | **0.912** | **0.000** | **0.036** |
| | Marker | 1 | 1.81 | 0.178 | 0.001 | 0.001 | 1 | 21.05 | < 0.001 | 0.027 | 0.974 | 1 | 0.35 | 0.555 | 0.013 | 0.588 |
| | Side | 1 | 14.71 | < 0.001 | 0.008 | 0.008 | 1 | 54.60 | < 0.001 | 0.071 | 0.990 | 1 | 0.17 | 0.681 | 0.006 | 0.405 |
| | Dance | 1 | 3.35 | 0.067 | 0.002 | 0.002 | 1 | 6.07 | 0.014 | 0.008 | 0.916 | 1 | 1.54 | 0.215 | 0.056 | 0.862 |
| | **Condition: neighbor** | **3** | **4.79** | **0.002** | **0.007** | **0.008** | **6** | **0.66** | **0.680** | **0.005** | **0.876** | **2** | **8.27** | **< 0.001** | **0.603** | **0.985** |
| | Condition: marker | 3 | 4.69 | 0.003 | 0.007 | 0.008 | 2 | 5.57 | 0.004 | 0.015 | 0.952 | 2 | 0.01 | 0.991 | 0.001 | 0.067 |
| | Neighbor: marker | 1 | 0.20 | 0.658 | 0.000 | 0.000 | 3 | 3.01 | 0.029 | 0.012 | 0.942 | 1 | 0.43 | 0.511 | 0.016 | 0.641 |
| | Condition: side | 3 | 0.67 | 0.572 | 0.001 | 0.001 | 2 | 4.54 | 0.011 | 0.012 | 0.943 | 2 | 0.02 | 0.983 | 0.001 | 0.122 |
| | Neighbor: side | 1 | 0.45 | 0.504 | 0.000 | 0.000 | 3 | 1.59 | 0.189 | 0.006 | 0.896 | 1 | 3.41 | 0.065 | 0.124 | 0.933 |
| | Marker: side | 1 | 16.55 | < 0.001 | 0.008 | 0.009 | 1 | 76.06 | < 0.001 | 0.099 | 0.993 | 1 | 0.76 | 0.382 | 0.028 | 0.756 |
| | **Condition: neighbor: marker** | **3** | **0.05** | **0.984** | **0.000** | **0.000** | **6** | **0.26** | **0.957** | **0.002** | **0.732** | **2** | **0.02** | **0.982** | **0.001** | **0.130** |
| | **Condition: neighbor: side** | **3** | **0.06** | **0.980** | **0.000** | **0.000** | **6** | **0.09** | **0.997** | **0.001** | **0.495** | **2** | **0.00** | **0.999** | **0.000** | **0.007** |
| | Condition: marker: side | 3 | 1.05 | 0.369 | 0.002 | 0.002 | 2 | 3.06 | 0.047 | 0.008 | 0.916 | 2 | 0.02 | 0.982 | 0.001 | 0.127 |
| | Neighbor: marker: side | 1 | 0.16 | 0.691 | 0.000 | 0.000 | 3 | 0.49 | 0.688 | 0.002 | 0.725 | 1 | 2.19 | 0.139 | 0.080 | 0.899 |
| | **Condition: side: neighbor: marker** | **3** | **0.22** | **0.882** | **0.000** | **0.000** | **6** | **0.09** | **0.997** | **na** | **na** | **2** | **0.12** | **0.884** | **na** | **na** |
| | Residuals | 1767 | | | | | 4111 | | | | | 2016 | | | | |

The relative phase of the right neighbour (i.e., the front dancer of the trio with respect to the movement of the dance) was negative and tended to be significantly lower than the relative phase of the left neighbour (i.e., the back dancer of the trio), which was positive, but only in the noMusic condition. There was no difference between the relative phase of the right and left neighbours in the other conditions (noVision was not tested due to the large number of outliers). In other words, the right neighbour was ahead of the trio, but only in the absence of music.

## 4.5 Discussion

The present study examined how multisensory interactions affect the coordination dynamics of a group of 13 expert folk dancers performing two familiar Greek dances to music while holding hands in a circle, with the group's leader dancing in the center. The dancers synchronized simultaneously with their immediate neighbours (haptic coupling and visual coupling), the group's leader (visual coupling), and the music (auditory coupling). Using cluster phase analysis to measure group synchrony, we examined how the dancers synchronized overall, and how this synchrony was altered when any one of the sensory couplings was unavailable to the dancers. Similar results were obtained for both dances, indicating that the results were not dependent on any one specific pattern of steps. Globally, we found that all three sensory mechanisms contributed to group synchrony, but that haptic coupling was the most significant. We also found that the auditory modality was most important for synchronizing along the vertical axis, which mainly contains temporal information on when to step, whereas the visual modality was most important for synchronizing along the horizontal axes, which contain spatio-temporal information for where to step. Finally, we established that music was the primary "leader" for the group, such that the dancers' steps tended to anticipate the musical beat. However, in the absence of music, the dancers anticipated the group's leader instead.

The group synchrony was found to be high for all three bodily axes, most likely due to dancers' strong familiarity with the dances and to the fact that the dancers shared an explicit common goal (Ellamil et al., 2016; Keller et al., 2014; Sacheli et al., 2015). Indeed, the synchronization of each dancer to the group significantly correlated with their familiarity with the dances. The absence of haptic coupling between the dancers reduced the group synchrony in all axes, and did so more strongly than vision and audition in all but the vertical axis. Therefore, the results of the current experiment suggest that haptic coupling is the most important means of coordination when dancing in a circle. This is in agreement with several studies of two-person synchronization, where spontaneous mutual entrainment is stronger when two individuals are haptically coupled than when they are only coupled visually or acoustically (Nessler & Gilliland, 2009; Sofianidis & Hatzitaki, 2015; Sofianidis et al., 2012; Zivotofsky & Hausdorff, 2007). When haptically coupled, the movement of one individual is directly perceived by partners as a pushing or pulling force, so the partners can smoothly coordinate their movement with one another (van der Wel et al., 2011). Haptic contact supports both informational (sensory) and mechanical (physical) coupling, resulting in a higher coupling strength than visual or auditory coupling (Harrison & Richardson, 2009; Richardson et al., 2008). It has been suggested that haptic coupling between two individuals allows strong mutual entrainment even when the mechanical contribution is minimized, such as during light interpersonal touch (Sofianidis & Hatzitaki, 2015). However, it was not possible in our study to separate the contribution of purely tactile contact from mechanical sources in haptic coupling. We can assume that the interpersonal mechanical coupling during handholding is important. This may explain why group synchrony was most strongly reduced in the absence of haptic coupling between dancers.

When looking at the influence of visual and auditory coupling on group synchrony, we found an interaction between body axes. The medio-lateral and antero-posterior axes form the horizontal plane in which the dancers performed their steps. The trajectory of the feet in the horizontal plan (see figure 4.S2B) contains spatio-temporal information for the movements: where or how to step. By contrast, the trajectory of the feet in the vertical axis mainly contains temporal information of the movement: when to step and make contact with the floor. We found that the absence of visual coupling between dancers, and between the dancers and the leader, only affected the group synchronization on the horizontal axes, but not the vertical axis. Conversely, the auditory coupling of the dancers to the music influenced group synchrony on all axes, but much more strongly for the vertical axis. This is consistent with the recent synchronization literature showing that an individual synchronizes more accurately to discrete (temporally precise) auditory stimuli, but to continuous (spatially moving) visual stimuli (Hove, Fairhurst, et al., 2013; Hove, Iversen, et al., 2013; Iversen et al., 2015). Sensorimotor synchronization is improved when the stimuli match the perception of the movement in a given modality (Hommel, Müsseler, Aschersleben, & Prinz, 2001; Hove, Fairhurst, et al., 2013). Therefore, the vertical trajectory of the feet (up and down) is more likely to be synchronized with the discrete musical beats (auditory coupling), whereas the spatial trajectory of the feet is more likely to match the shape of the leader's feet (visual coupling). Our study shows that the synchronization mechanisms observed using inanimate stimuli in laboratory-controlled settings apply well in a complex and ecologically realistic environment.

Two caveats need to be mentioned with respect to our experimental setting and the manipulation of auditory and visual couplings. The visual coupling between dancers was prevented by asking the participants to close their eyes while performing the dances, which may have disrupted their balance and in turn their ability to synchronize. However, we did not observe a drastic loss of group synchrony in this condition, and none at all in the vertical axis. Thus, we postulate that a loss of balance did not have a significant impact on our data. Next, we eliminated the auditory coupling by preventing the dancers from hearing the music, but not each other's steps. While we can assume that the dancers could barely hear their steps when the music was playing, it is possible that group synchrony would have been even more decreased in the absence of music if all sources of auditory coupling were successfully masked. Further studies are necessary to disentangle the impact of these two sources of auditory coupling on group synchrony, one being external to the group (the recorded music) and the other emerging from its intrinsic movement patterns.

The measurement of group synchrony in the first set of analyses emerged from the comparison of the phase of each dancer relative to the averaged phase of the group (i.e., group's average, or cluster phase; Frank & Richardson, 2010; Richardson et al., 2012). We next wanted to explore how this overall group synchrony differed from the synchronization of the dancers with each source of sensory coupling (i.e., the synchronization reference): the group's leader seen in the center of the circle, the music that the group jointly heard, and the two neighbours with whom each dancer was in direct physical contact. At the group level, we did not find any interaction between condition (i.e., availability of sensory coupling) and synchronization reference (i.e., source of the sensory coupling). However, we did find an interaction between condition and reference when looking at the mean individual level. This discrepancy highlights the fact that the coordination is a group phenomenon (Richardson et al., 2012; Wallot at al., 2016) as explained by Richardson et al. (2012:8): "The group synchronization measures the extent to which at any moment in time the interactions between all group members establish a *central* group behaviour that acts in turn as an attractor for every individual member […]. This central group behaviour reflects a mutuality and interdependence of influence." At the group level, the dancers were very strongly coordinated as a whole and they fully integrated all coupling sources to achieve their global performance, so the relationship of the group to the leader and the music remained relatively stable too. This is also reflected in the fact that, at the individual level, the dancers were far more synchronized with their group's average than any other sources across all conditions.

At the mean individual level, the conditions interacted with the synchronization reference as both the synchronization with respect to the leader and to the music were drastically more affected by the absence of music than the synchronization with respect to the group's average, regardless of the axis. Even, in the vertical axis, the synchronization of each individual with the leader and the music were affected only by the absence of music. These results potentially suggested that each dancer were synchronized with the leader principally because they both heard the same music. This hypothesis is reinforced by the fact that the synchrony of each dancer to their direct neighbours was less affected by the absence of music than the group synchrony, and that the neighbour synchrony paralleled the group synchrony regarding the visual and haptic couplings. Thus, it seems that the neighbours were the principal source of not only haptic but visual coupling as well. However, we did find that in the horizontal axes the synchronization of each individual with the leader was slightly more affected by the absence of vision than the synchronization with the group's average. So at least regarding the spatial dimension of the steps, the dancers, at the individual level, seemed to refer visually to the leader.

Regarding the synchronizing of each dancers with their neighbours, even if we did not find any specific effect of sensory coupling as a function of distance between them, we did observe that the dancers were more synchronized with their direct neighbours than with the group, and that the farther the dancers were from each other, the less synchronized they were with one another. This effect can only be due to haptic and/or visual coupling, as all dancers heard the same music, but they were in direct contact only with their two immediate neighbours, and could not see all dancers equally well. In a similar vein, Honisch, Elliott, Jacoby, & Wing, (2016) found an accumulative effect of timekeeper variance when participants in a chain had to visually synchronize to their preceding neighbour. Since our chain was a closed circle, we presume that the decreased synchrony observed with increasing neighbour distance was due to an accumulation of synchronization variance that compensated overall. We plan to assess this phenomenon in more detail in the future.

Although global synchronization performance did not depend on the reference to which it was measured, the relative phase of the dancers to the music, the leader, and the neighbours changed as a function of conditions. A general finding in the sensorimotor synchronization literature is that of negative asynchrony (Repp, 2005): individuals (followers) usually anticipate the sensory signal that they synchronize to (the leader). This is also found in cases of interpersonal synchronization, especially (but not only) if there is a unidirectional coupling from a leader to a follower (Gebauer et al., 2016; Goebl & Palmer, 2009;

Loehr & Palmer, 2011). In our paradigm, the auditory coupling from the dancers to the music was unidirectional, whereas the visual coupling to the leader was semi-bidirectional, as all dancers could see the leader, but the leader could not see all dancers in the circle at once. We observed that the dancers showed the expected negative lag (an anticipation) with the music (at least with their heels), but that they showed a positive lag (a delay) with the leader. We can thus infer that the dancers primarily synchronized with the music. It seems that the leader anticipated the music more than the dancers did, which may be a general leading strategy (Candidi, Curioni, Donnarumma, Sacheli, & Pezzulo, 2015; Sacheli et al., 2013; Vesper & Richardson, 2014). Interestingly, when the dancers were prevented from hearing the music, they anticipated the leader (who could hear the music through headphones). Therefore, when the leader became their only temporal reference, the dancers primarily synchronized with the leader. We want to be cautious regarding the findings related to the music's relative phase, as the music's continuous phase was extrapolated from the discrete beat timing. Further analysis directly measuring the asynchrony between the steps and the beats will be necessary to corroborate these results.

Finally, we explored the relative phase between three dancers who were adjacent in the ring and who were bidirectionally coupled through haptic contact. Specifically, since the circle was moving counter-clockwise (i.e., toward the right), we looked at the difference between the right and left neighbours. We did not find a significant difference between the neighbours' relative phase, except in the absence of music, where the right neighbour (the trio's "leader") tended to have a negative lag to the trio. Therefore, when a precise timekeeper was not provided to the dancers, the coupling between dancers might have had more of an influence so that the "leading" neighbour (with respect to the circle direction) was ahead on average. Our study shows that even though the dancers fully integrated all sources of sensory coupling to achieve their global performance, they did so using various strategies.

In conclusion, this study was the first to examine the multisensory couplings involved during group coordination using a cohort of individuals specialized in group synchronization with physical contact. We showed that the dancers primarily relied on the haptic coupling to synchronize within the group, and that the reliance on the visual and auditory coupling depends on the spatiotemporal context. We also showed that they principally followed the music, and that each dancer was synchronized with the group's leader mostly because the leader followed the music too. Identical findings were found when folk dancers performed two different dances, which suggests that these findings are not limited to one specific dance. We were able to assess a group-level behaviour without reducing it to the average of pairwise comparisons, and found that basic synchronization rules still apply during complex interactions. We also explored the influence of each coupling source on the group: what information the dancers coordinated with and to what degree, furthering our understanding of the dynamics of multi-person coordination in ecological settings.

# 4.6 References

Ammirante, P., Patel, A. D., & Russo, F. A. (2016). Synchronizing to auditory and tactile metronomes: a test of the auditory-motor enhancement hypothesis. Psychonomic Bulletin & Review, 23(6), 1882–1890. http://doi.org/10.3758/s13423-016-1067-9

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1–48. http://doi.org/10.18637/jss.v067.i01.

Candidi, M., Curioni, A., Donnarumma, F., Sacheli, L. M., & Pezzulo, G. (2015). Interactional leader–follower sensorimotor communication strategies during repetitive joint actions. Journal of The Royal Society Interface, 12(110), 1–12. http://doi.org/10.1098/rsif.2015.0644

Chauvigné, L. A. S., Gitau, K. M., & Brown, S. (2014). The neural basis of audiomotor entrainment : An ALE meta-analysis. Frontiers in Human Neuroscience, 8(776), 1–18. http://doi.org/10.3389/fnhum.2014.00776

Codrons, E., Bernardi, N. F., Vandoni, M., & Bernardi, L. (2014). Spontaneous group synchronization of movements and respiratory rhythms. PLoS ONE, 9(9), 1–10. http://doi.org/10.1371/journal.pone.0107538

Couzin, I. D. (2009). Collective cognition in animal groups. Trends in Cognitive Sciences, 13(1), 36–43. http://doi.org/10.1016/j.tics.2008.10.002

Desmet, F., Leman, M., Lesaffre, M., & Bruyn, L. De. (2010). Statistical analysis of human body movement and group interation in response to music. In: Fink A., Lausen B., Seidel W., Ultsch A. (eds) Advances in Data Analysis, Data Handling and Business Intelligence. Studies in Classification, Data Analysis, and Knowledge Organization. Springer, Berlin, Heidelberg (pp. 399–408). https://doi.org/10.1007/978-3-642-01044-6_36

Ellamil, M., Berson, J., Wong, J., Buckley, L., & Margulies, D. S. (2016). One in the dance: Musical correlates of group synchrony in a real-world club environment. PLoS ONE, 11(10), 1–15. http://doi.org/10.1371/journal.pone.0164783

Elliott, M. T., Wing, A. M., & Welchman, A. E. (2010). Multisensory cues improve sensorimotor synchronisation. European Journal of Neuroscience, 31(10), 1828–1835. http://doi.org/10.1111/j.1460-9568.2010.07205.x

Fairhurst, M. T., Janata, P., & Keller, P. E. (2014). Leading the follower: An fMRI investigation of dynamic cooperativity and leader-follower strategies in synchronization with an adaptive virtual partner. NeuroImage, 84, 688–697. http://doi.org/10.1016/j.neuroimage.2013.09.027

Frank, T. D., & Richardson, M. J. (2010). On a test statistic for the Kuramoto order parameter of synchronization: An illustration for group synchronization during rocking chairs. Physica D: Nonlinear Phenomena, 239(23–24), 2084–2092. http://doi.org/10.1016/j.physd.2010.07.015

Gebauer, L., Witek, M. A. G., Hansen, N. C., Thomas, J., Konvalinka, I., & Vuust, P. (2016). Oxytocin improves synchronisation in leader-follower interaction. Scientific Reports, 6(1), 38416. http://doi.org/10.1038/srep38416

Gescheider, G. A. (1966). Resolving of Successive Clicks By the Ears and Skin. Journal of Experimental Psychology, 71(3), 378–381. http://doi.org/10.1037/h0022950

Gibson, J. J. (1966). The senses considered as perceptual systems. (H. Mifflin, Ed.). Boston. http://doi.org/10.2307/1571911

Giordano, M., & Wanderley, M. M. (2015). Follow the tactile metronome : Vibrotactile stimulation for tempo synchronization in music performance. In Sound and Music Computing Conference. Maynooth, Ireland.

Goebl, W., & Palmer, C. (2009). Synchronization of timing and motion among performing musicians. Music Perception, 26(5), 427–438. http://doi.org/10.1525/mp.2009.26.5.427

Harrison, S. J., & Richardson, M. J. (2009). Horsing around: Spontaneous four-legged coordination. Journal of Motor Behavior, 41(6), 519–24. http://doi.org/10.3200/35-08-014

Himberg, T., & Thompson, M. R. (2011). Learning and synchronising dance movements in South African songs - Cross-cultural motion-capture study. Dance Research, 29(2), 305–328. http://doi.org/10.3366/drs.2011.0022

Hommel, B., Müsseler, J., Aschersleben, G., & Prinz, W. (2001). The Theory of Event Coding (TEC): A framework for perception and action planning. Behavioral and Brain Sciences, 24(5), 849–878. http://doi.org/10.1017/S0140525X01000103

Honisch, J. J., Elliott, M. T., Jacoby, N., & Wing, A. M. (2016). Cue properties change timing strategies in group movement synchronisation. Scientific Reports, 6(1), 19439. http://doi.org/10.1038/srep19439

Hove, M. J., Fairhurst, M. T., Kotz, S. A., & Keller, P. E. (2013). Synchronizing with auditory and visual rhythms: an fMRI assessment of modality differences and modality appropriateness. NeuroImage, 67, 313–21. http://doi.org/10.1016/j.neuroimage.2012.11.032

Hove, M. J., Iversen, J. R., Zhang, A., & Repp, B. H. (2013). Synchronization with competing visual and auditory rhythms: Bouncing ball meets metronome. Psychological Research, 77(4), 388–398. http://doi.org/10.1007/s00426-012-0441-0

Iversen, J. R., Patel, A. D., Nicodemus, B., & Emmorey, K. (2015). Synchronization to auditory and visual rhythms in hearing and deaf individuals. Cognition, 134, 232–244. http://doi.org/10.1016/j.cognition.2014.10.018

Keller, P. E., Novembre, G., & Hove, M. J. (2014). Rhythm in joint action: Psychological and neurophysiological mechanisms for real-time interpersonal coordination. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 369, 1–12. http://doi.org/10.1098/rstb.2013.0394

Kerr, N. L., & Tindale, R. S. (2004). Group Performance and Decision Making. Annual Review of Psychology, 55(1), 623–655. http://doi.org/10.1146/annurev.psych.55.090902.142009

King, A. J., & Cowlishaw, G. (2009). Leaders, followers and group decision-making. Communicative & Integrative Biology, 2(2), 147–150. http://doi.org/10.4161/cib.7562

Knoblich, G., & Sebanz, N. (2008). Evolving intentions for social interaction: from entrainment to joint action. Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 363(1499), 2021–2031. http://doi.org/10.1098/rstb.2008.0006

Lewis, M. (1984). Beyond the Dyad. New York: Springer. http://doi.org/10.1007/978-1-4757-9415-1

Loehr, J. D., & Palmer, C. (2011). Temporal coordination between performing musicians. The Quarterly Journal of Experimental Psychology, 64(11), 2153–2167. http://doi.org/10.1080/17470218.2011.603427

Lüdecke, D. (2017). sjstats: Statistical Functions for Regression Models. R package version 0.11.2. https://cran.r-project.org/package=sjstats

Meslec, N., Curseu, P. L., Meeus, M. T. H., & Iederan Fodor, O. C. (2014). When none of us perform better than all of us together: The role of analogical decision rules in groups. PLoS ONE, 9(1). http://doi.org/10.1371/journal.pone.0085232

Nessler, J. A., & Gilliland, S. J. (2009). Interpersonal synchronization during side by side treadmill walking is influenced by leg length differential and altered sensory feedback. Human Movement Science, 28(6), 772–85. http://doi.org/10.1016/j.humov.2009.04.007

Nowicki, L., Prinz, W., Grosjean, M., Repp, B. H., & Keller, P. E. (2013). Mutual adaptive timing in interpersonal action coordination. Psychomusicology: Music, Mind, and Brain, 23(1), 6–20. http://doi.org/10.1037/a0032039

Phillips-Silver, J., Aktipis, C. A., & Bryant, G. A. (2010). The ecology of entrainment: Foundations of coordinated rhythmic movement. Music Perception, 28(1), 3–14.

R Core Team. (2014). R : A language and environment for statistical computing. R Foundation for Statistical Computing,Vienna, Austria. http://www.r-project.org/.

Reddish, P., Fischer, R., & Bulbulia, J. (2013). Let's dance together: Synchrony, shared intentionality and cooperation. PLoS ONE, 8(8), 1–13. http://doi.org/10.1371/journal.pone.0071182

Repp, B. (2005). Sensorimotor synchronization: A review of the tapping literature. Psychonomic Bulletin & Review, 12(6), 969–992. https://doi.org/10.3758/BF03206433

Repp, B. H., & Su, Y.-H. (2013). Sensorimotor synchronization: a review of recent research (2006-2012). Psychonomic Bulletin & Review, 20(3), 403–52. http://doi.org/10.3758/s13423-012-0371-2

Richardson, M. J., Garcia, R. L., Frank, T. D., Gergor, M., & Marsh, K. L. (2012). Measuring group synchrony: A cluster-phase method for analyzing multivariate movement time-series. Frontiers in Physiology, 3(405), 1–10. http://doi.org/10.3389/fphys.2012.00405

Richardson, M. J., Lopresti-Goodman, S., Mancini, M., Kay, B., & Schmidt, R. C. (2008). Comparing the attractor strength of intra- and interpersonal interlimb coordination using cross-recurrence analysis. Neuroscience Letters, 438(3), 340–5. http://doi.org/10.1016/j.neulet.2008.04.083

Richardson, M. J., Marsh, K. L., Isenhower, R. W., Goodman, J. R. L., & Schmidt, R. C. (2007). Rocking together: Dynamics of intentional and unintentional interpersonal coordination. Human Movement Science, 26(6), 867–891. http://doi.org/10.1016/j.humov.2007.07.002

Richardson, M. J., Marsh, K. L., & Schmidt, R. C. (2005). Effects of visual and verbal interaction on unintentional interpersonal coordination. Journal of

Experimental Psychology. Human Perception and Performance, 31(1), 62–79. http://doi.org/10.1037/0096-1523.31.1.62

Sacheli, L. M., Aglioti, S. M., & Candidi, M. (2015). Social cues to joint actions: The role of shared goals. Frontiers in Psychology, 6(1034), 1–7. http://doi.org/10.3389/fpsyg.2015.01034

Sacheli, L. M., Tidoni, E., Pavone, E. F., Aglioti, S. M., & Candidi, M. (2013). Kinematics fingerprints of leader and follower role-taking during cooperative joint actions. Experimental Brain Research, 226(4), 473–486. http://doi.org/10.1007/s00221-013-3459-7

Sofianidis, G., & Hatzitaki, V. (2015). Interpersonal entrainment in dancers: Contrasting timing and haptic cues. Posture, Balance and the Brain International Workshop Proceedings, 34–44.

Sofianidis, G., Hatzitaki, V., Grouios, G., Johannsen, L., & Wing, A. (2012). Somatosensory driven interpersonal synchrony during rhythmic sway. Human Movement Science, 31(3), 553–566. http://doi.org/10.1016/j.humov.2011.07.007

van der Wel, R. P. R. D., Knoblich, G., & Sebanz, N. (2011). Let the force be with us: Dyads exploit haptic coupling for coordination. Journal of Experimental Psychology: Human Perception and Performance, 37(5), 1420–1431. http://doi.org/10.1037/a0022337

Vesper, C., & Richardson, M. J. (2014). Strategic communication and behavioral coupling in asymmetric joint action. Experimental Brain Research, 232(9), 2945–2956. http://doi.org/10.1007/s00221-014-3982-1

Wallot, S., Roepstorff, A., & Mønster, D. (2016). Multidimensional recurrence quantification analysis (MdRQA) for the analysis of multidimensional time-series: A software implementation in MATLAB and its application to group-level data in joint action. Frontiers in Psychology, 7(1835), 1–13. http://doi.org/10.3389/fpsyg.2016.01835

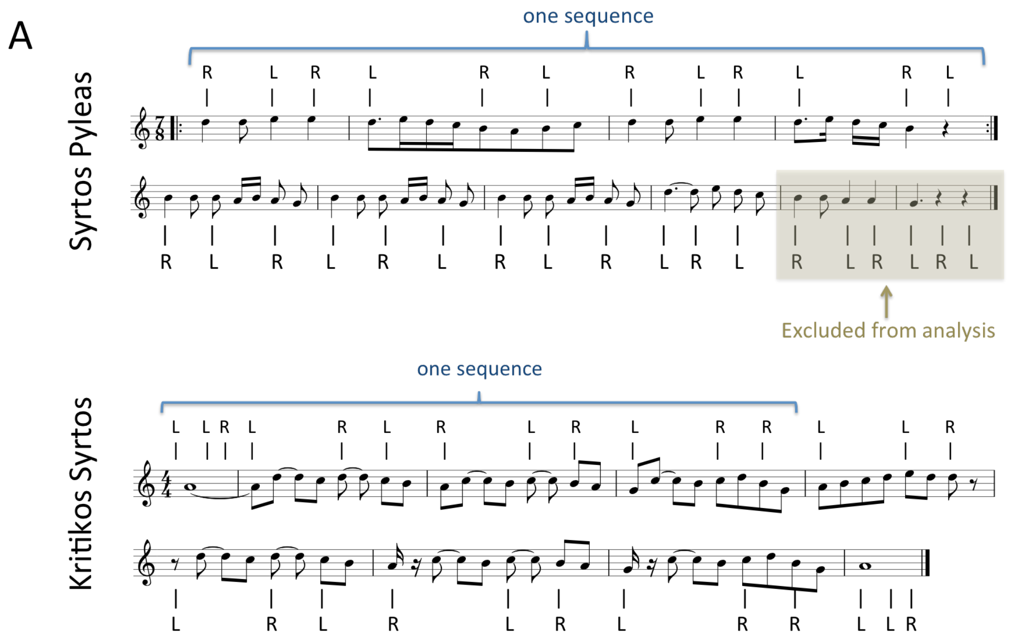
Wing, A. M., Doumas, M., & Welchman, A. E. (2010). Combining multisensory temporal information for movement synchronisation. Experimental Brain Research, 200(3–4), 277–282. http://doi.org/10.1007/s00221-009-2134-5

Zivotofsky, A. Z., & Hausdorff, J. M. (2007). The sensory feedback mechanisms enabling couples to walk synchronously: An initial investigation. Journal of NeuroEngineering and Rehabilitation, 4(1), 28. http://doi.org/10.1186/1743-0003-4-28

# 4.7 Supplementary materials

## 4.7.1 Supplementary methods

### 4.7.1.1 Stimuli



B

**Syrtos Pyleas (dance 1)**

Bar 1
Beat 1: right step forward (along the circle)
Beat 2: left stamp (on the spot)
Beat 3: right stamp (on the spot)

Bar 2
Beat 1: left step forward (along the circle)
Beat 2: right stamp (on the spot)
Beat 3: left stamp (on the spot)

Bar 3
Beat 1: right step (on the side toward the right)
Beat 2: left step (cross back toward the right)
Beat 3: right stamp (on the spot)

Bar 4
Beat 1: left step (on the side toward the left)
Beat 2: right step (cross back toward the left)
Beat 3: left stamp (on the spot)

**Kritikos Syrtos (dance 2)**

Bar 1
Beat 1: Left stamp (toward the center of the circle)
Beat 3: left step (cross back toward the right)
Beat 4: right step (on the side toward the right)

Bar 2
Beat 1: left step (cross in front toward the right)
Beat 3: right step (cross in front toward the left)
Beat 4: left step (on the side toward the left)

Bar 3
Beat 1: right step (cross back toward the left)
Beat 3: left step (cross back toward the right)
Beat 4: right step (on the side toward the right)

Bar 4
Beat 1: left step (cross in front toward the right)
Beat 3: right stamp (toward the center of the circle)
Beat 4: right (together)

*Figure 4.S1: Musical scores and descriptions of the sequences of steps for the two dances used in the experiment.*

In panel A, the locations of steps are indicated on each beat with right foot (R) and left foot (L) ticks. The score of Syrtos Pyleas (Dance 1) was repeated twice over the musical excerpt, while the score of Kritikos Syrtos (Dance 2) was repeated three times over the musical excerpt, so that there were six dance sequences in each. In Dance 1, the third and sixth sequences contain a repetition of the last two measures, which were excluded from the analyses. In Dance 2, the dance sequence does not fit the musical phrase, and so the sequence gets shifted over the course of the music. Panel B describes the sequence of steps for the two dances. For each dance, the dance's sequence spans over four musical bars, where each bar contains three steps.

### 4.7.1.2 Gap filling

***Table 4.S1.*** *Missing data*

Listed here are sequences that are entirely missing data in a participant, thus causing empty cells in the ANOVAs.

| **Dance** | **Missing sequence** |
|---|---|
| Syrtos Pyleas | noMusic, trial 5, right foot tip, all 6 sequences |
| Kritikos Syrto | Normal, trial 2, right heel, sequences 2 to 6 |
| | Normal, trial 5, left heel, sequences 3 to 6 |
| | noVision, trial 3, left heel, sequences 5 and 6 |
| | noVision, trial 3, right heel, sequences 5 and 6 |
| | noVision, trial 5, right heel, all 6 sequences |
| | noTouch, trial 5, right heel, all 6 sequences |

### 4.7.1.3 Detection of outliers

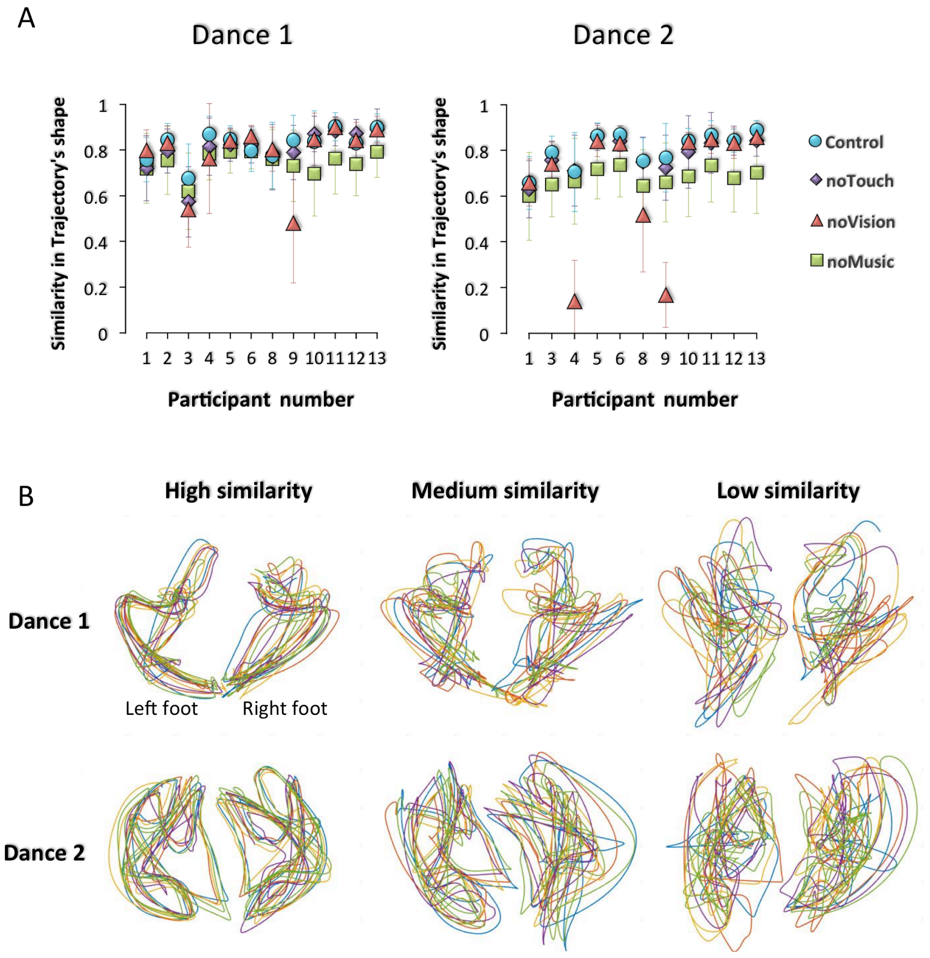


*Figure 4.S2: Procrustes analyses of the shape of the foot trajectories*

A: Mean similarity value (1 – the dissimilarity index) of each dancer compared to the group average's trajectory in a given condition. The same outliers are revealed by this analysis as in the cluster phase analysis. Errors bars indicate standard deviations. B: Examples of trajectories of the foot tip in the XY plane, showing participants with high, medium, and low mean similarity to the group. Each of the six plots displays the left and right foot tip trajectories during an entire trial, where each sequence is represented by a different color. Dance 1: high = p11 control trial 5 (mean similarity [MS] = 0.92), medium = p8 noVision trial 5 (MS = 0.78), low = p3 noTouch trial 3 (MS = 0.43). Dance 2: high = p11 Control trial 5 (MS = 0.91), medium = p8 Control trial 1 (MS = 0.73), low = p9 noVision trial 4 (MS = 0.15).

### 4.7.1.4 Model reduction

The purpose of these pre-analyses is to assess if the effects of interest were similar in the two dances, without having to test the interaction with dances in the full models and therefore avoiding overly complex models.

*Group synchrony*

We first tested for the effect of dances and axes on group synchrony using a 2 dances x 3 axes (X, Y, Z) x 4 conditions (control, noMusic, noVision, noTouch) analysis of variance (ANOVA). As shown in Table S2, the analysis showed no interaction between conditions and dances, no 3-way interaction among conditions, dances and axes, but a significant interaction between conditions and axes. To assess the latter, we repeated this analysis with only two axes. The interaction between conditions and axes was significant in the XZ and YZ models, but not in the XY model, indicating that the effect of conditions on group synchrony was identical in the X and Y axes. No interaction with dances was significant in any model. Therefore, to test the effect of conditions on group synchrony, we ran the full models on both dances combined.

***Table 4.S2.*** *Effect of axes*

ANOVAs testing interaction effects between axes, dances and conditions on group synchrony. Effects of interest are in bold.

| | **XYZ** | | | | | **XY** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Df | F value | p value | η2 | part. η2 | Df | F value | p value | η2 | part. η2 |
| Condition | 3 | 22.77 | < 0.001 | 0.016 | 0.024 | 3 | 19.69 | < 0.001 | 0.019 | 0.031 |
| Axis | 2 | 171.90 | < 0.001 | 0.082 | 0.111 | 1 | 337.76 | < 0.001 | 0.106 | 0.156 |
| Dance | 1 | 662.75 | < 0.001 | 0.158 | 0.194 | 1 | 699.17 | < 0.001 | 0.220 | 0.276 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Condition: axis** | **6** | **6.19** | **< 0.001** | **0.009** | **0.013** | **3** | **1.70** | **0.165** | **0.002** | **0.003** |
| **Condition: dance** | **3** | **1.80** | **0.145** | **0.001** | **0.002** | **3** | **1.20** | **0.308** | **0.001** | **0.002** |
| Axis: dance | 2 | 159.99 | < 0.001 | 0.076 | 0.104 | 1 | 233.00 | < 0.001 | 0.073 | 0.113 |
| **Condition: axis: dance** | **6** | **0.66** | **0.681** | **0.001** | **0.001** | **3** | **0.43** | **0.734** | **0.000** | **0.001** |
| Residuals | 2751 | | | | | 1834 | | | | |

| | **XZ** | | | | | **YZ** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Df | F value | p value | η2 | part. η2 | Df | F value | p value | η2 | part. η2 |
| Condition | 3 | 17.92 | < 0.001 | 0.026 | 0.028 | 3 | 13.44 | < 0.001 | 0.013 | 0.022 |
| Axis | 1 | 41.84 | < 0.001 | 0.020 | 0.022 | 1 | 153.53 | < 0.001 | 0.049 | 0.077 |
| Dance | 1 | 99.22 | < 0.001 | 0.048 | 0.051 | 1 | 793.02 | < 0.001 | 0.252 | 0.302 |
| **Condition: axis** | **3** | **7.85** | **< 0.001** | **0.011** | **0.013** | **3** | **9.21** | **< 0.001** | **0.009** | **0.015** |
| **Condition: dance** | **3** | **0.75** | **0.521** | **0.001** | **0.001** | **3** | **2.59** | **0.052** | **0.002** | **0.004** |
| Axis: dance | 1 | 0.19 | 0.661 | 0.000 | 0.000 | 1 | 291.18 | < 0.001 | 0.092 | 0.137 |
| **Condition: axis: dance** | **3** | **0.67** | **0.573** | **0.001** | **0.001** | **3** | **0.93** | **0.425** | **0.001** | **0.002** |
| Residuals | 1834 | | | | | 1834 | | | | |

### *Synchronization with the leader and with the music*

For the group synchrony and for both the XY and Z axes, we ran a pre-analysis to test if the two dances had a different influence on the interaction between conditions and references. For the XY axes combined, we performed a 2 dances x 2 references (cluster phase, leader) x 4 conditions (control, noMusic, noVision, noTouch) ANOVA, which revealed that the 3-way interaction between dance, reference, and condition was not significant (F (3,3672) = 0.03, p = .992, $\eta^2$ = .000, part. $\eta^2$ = .000). The interaction between dance and reference was not significant either (F (1,3672) = 0.16, p = .689, $\eta^2$ = .000, part. $\eta^2$ = .000). For the Z axis, we performed a 2 dances x 3 references (cluster phase, leader, music) x 4 conditions (control, noMusic, noVision, noTouch) ANOVA, which revealed that the 3-way interaction between dance, reference, and condition was not significant

(F (6,2745) = 0.02, p = 1.000, $\eta^2$ = .000, part. $\eta^2$ = .000). The interaction between dance and reference was not significant either (F (2,2745) = 0.25, p = .775, $\eta^2$ = .000, part. $\eta^2$ = .000). Therefore, to test the effect of synchronizing with the leader and with the music on group synchrony, we ran the full models on both dances combined.

For the mean of individual synchronies and for both the XY and Z axes, we also ran a pre-analysis to test if the two dances had a different influence on the interaction between conditions and references. For the XY axes combined, we performed a 2 dances x 2 references (cluster phase, leader) x 4 conditions (control, noMusic, noVision, noTouch) repeated measures ANOVA, which revealed a significant 3-way interaction between dance, reference, and condition (F (3,5945) = 6.70, p < .001). The interaction between dance and reference was also significant (F (1,5945) = 169.60, p = < .001, $\eta^2$ = .032, part. $\eta^2$ = .894). For the Z axis, we performed a 2 dances x 3 references (cluster phase, leader, music) x 4 conditions (control, noMusic, noVision, noTouch) repeated measures ANOVA, which revealed a significant 3-way interaction between dance, reference, and condition (F (6,4459) = 7.3, p < .001). The interaction between dance and reference was also significant (F (2,4459) = 380.00, p < .001, $\eta^2$ = .069, part. $\eta^2$ = .946). Therefore, to test the effect of synchronizing with the leader and with the music on individual synchrony, we ran the full models on each dance separately.

*Relative phase with the leader and with the music*

For the Z axis, we ran a pre-analysis to see if the two dances had a differential influence on the interaction between conditions and references using a 2 dances x 3 references (cluster phase, leader, music) x 4 conditions (control, noMusic, noVision, noTouch) repeated-measures ANOVA, which revealed a significant interaction between dance and reference (F (6,4460) = 29.47, $p < .001$), and a 3-way interaction between dance, reference and condition (F (2,4460) = 60.94, $p < .001$, $\eta^2 = .015$, part. $\eta^2 = .410$). Therefore, to test the effect of relative phase with the leader and with the music, we ran the full model on each dance separately.

*Synchronization with the neighbors*

For the comparison between trios synchrony and group synchrony, and for both the XY and Z axes, we ran a pre-analysis to test if the two dances had a differential influence on the interaction between conditions and neighbors with a 2 dances x 2 group types (whole group, trios) x 4 conditions (control, noMusic, noVision, noTouch) ANOVAs, which revealed that the 3-way interaction between dances, neighbors and conditions was not significant (XY: F (3,3592) = 1.32, $p = .267$, $\eta^2 = .001$, part. $\eta^2 = .001$; Z: F (3,1788) = 0.33, $p = .807$, $\eta^2 = .001$, part. $\eta^2 = .001$). The interaction between dance and neighbor was not significant either (XY: F (1,3592) = 3.24, $p = .072$, $\eta^2 = .001$, part. $\eta^2 = .001$; Z: F (1,1788) = 0.09, $p = .762$, $\eta^2 = .000$, part. $\eta^2 = .000$). Therefore, to test the effect of synchronizing with the neighbors, we ran the full models on both dances combined.

For the effect of trios synchrony as a function of neighbor's distance, and for both the XY and Z axes, we also ran a pre-analysis to test if the two dances had a differential influence on the interaction between conditions and neighbor's distances using a 2 dances x 4 neighbor's distances (1p, 2p, 3p, 4p) x 4 conditions (control, noMusic, noVision, noTouch) repeated-measures ANOVAs, which revealed that the 3-way interaction between dance, neighbor's distance and condition was not significant (XY: F (6,8234) = 0.19, p = .980; Z: F (6,4111) = 0.79, p = .579). Therefore, to test the effect of trios synchrony, we ran the full models on both dances combined. There was however a significant interaction between dance and neighbor's distance (XY: F (3,8243) = 7.9, p < .001, $\eta^2$ = .015, part. $\eta^2$ = .954; Z: F (3,4116) = 4.47, p < .001, $\eta^2$ = .037, part. $\eta^2$ = .738). As we focused on the main effect of neighbor's distance in the full model, we note that the interaction between dance and neighbor's distance was due to the following: while the synchrony decreased as a function of neighbor's distance in both dance, it decreased from 1p to 3p (with no difference between 3p and 4p) in dance 1 and from 1p to 4p in dance 2, and this in all axes.

*Relative phase within neighbors' trios*

For the Z axis, we ran a pre-analysis to test if the two dances had a differential influence on the interaction between conditions and neighbor's position using a 2 dances x 2 neighbors (left, right) x 4 conditions (control, noMusic, noVision, noTouch) repeated-measures ANOVA, which revealed that the 3-way interaction between dance, neighbor and condition was not significant (F (2,2016) = 2.19, p <

.113). Therefore, to test the effect of relative phase within neighbors' trios, we ran the full model on both dances combined. There was however a significant interaction between dance and neighbor's position (F (1,2033) = 11.52, $p < .001$, $\eta^2 = .317$, part. $\eta^2 = .725$), but we did not focus on the main effect of neighbor's position in the full model.

## 4.7.2 Supplementary results

***Table 4.S3.*** *Effect of sequence repetition*

ANOVAs for the effect of sequence repetition on group synchrony for both dances. The factor *sequence* has six levels and the factor *trial* has five levels. Effects of interest are in bold. The significant level is set to $p < 0.025$ to control for the two models.

| | **Dance 1** | | | | | **Dance 2** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Df | F value | p-value | η2 | part. η2 | Df | F value | p-value | η2 | part. η2 |
| **Sequence** | **5** | **446.87** | **< 0.001** | **0.412** | **0.678** | **5** | **50.59** | **< 0.001** | **0.051** | **0.203** |
| Trial | 4 | 41.57 | < 0.001 | 0.031 | 0.136 | 4 | 10.29 | < 0.001 | 0.008 | 0.040 |
| Condition | 3 | 26.25 | < 0.001 | 0.015 | 0.069 | 3 | 57.32 | < 0.001 | 0.035 | 0.148 |
| Axis | 2 | 36.61 | < 0.001 | 0.013 | 0.065 | 2 | 1111.96 | < 0.001 | 0.451 | 0.692 |
| Marker | 1 | 9.97 | 0.002 | 0.002 | 0.009 | 1 | 4.49 | 0.034 | 0.001 | 0.005 |
| Side | 1 | 0.17 | 0.684 | 0.000 | 0.000 | 1 | 146.64 | < 0.001 | 0.030 | 0.129 |
| Sequence: trial | 20 | 11.13 | < 0.001 | 0.041 | 0.174 | 20 | 9.79 | < 0.001 | 0.040 | 0.165 |
| Sequence: condition | 15 | 12.41 | < 0.001 | 0.034 | 0.149 | 15 | 8.60 | < 0.001 | 0.026 | 0.115 |
| Trial: condition | 12 | 9.80 | < 0.001 | 0.022 | 0.100 | 12 | 7.31 | < 0.001 | 0.018 | 0.081 |
| Sequence: axis | 10 | 10.46 | < 0.001 | 0.019 | 0.090 | 10 | 3.77 | < 0.001 | 0.008 | 0.037 |
| Trial: axis | 8 | 3.21 | 0.001 | 0.005 | 0.024 | 8 | 1.80 | 0.073 | 0.003 | 0.014 |
| Condition: axis | 6 | 6.67 | < 0.001 | 0.007 | 0.036 | 6 | 13.17 | < 0.001 | 0.016 | 0.074 |
| Sequence: trial: condition | 60 | 14.28 | < 0.001 | 0.158 | 0.447 | 60 | 6.95 | < 0.001 | 0.084 | 0.296 |
| Sequence: trial: axis | 40 | 1.35 | 0.073 | 0.010 | 0.049 | 40 | 0.61 | 0.975 | 0.005 | 0.024 |
| Sequence: condition: axis | 30 | 1.46 | 0.052 | 0.008 | 0.040 | 30 | 0.97 | 0.507 | 0.006 | 0.029 |
| Trial: condition: axis | 24 | 1.10 | 0.336 | 0.005 | 0.024 | 24 | 0.46 | 0.987 | 0.002 | 0.011 |
| Segment: trial: condition: axis | 120 | 1.06 | 0.324 | 0.023 | 0.107 | 120 | 0.64 | 0.999 | 0.016 | 0.072 |
| Residuals | 1060 | | | | | 991 | | | | |

***Table 4.S4.*** *Group versus individual synchrony*

ANOVAs comparing the group synchrony with the individual synchronies of each dancer related to the group's average (cluster phase). The factor *level* has two levels (group, individual). Effects of interest are in bold. The significant level is set to $p < 0.025$ to control for the two models. These analyses show no main effect or interaction with the factor *level*.

| | **XY (horizontal) axes** | | | | | **Z (vertical) axis** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Df | F value | p value | η2 | part. η2 | Df | F value | p value | η2 | part. η2 |
| Trial | 4 | 6.35 | < 0.001 | 0.007 | 0.012 | 4 | 5.77 | < 0.001 | 0.019 | 0.022 |
| Condition | 3 | 23.59 | < 0.001 | 0.020 | 0.032 | 3 | 17.74 | < 0.001 | 0.044 | 0.048 |
| **Level** | **1** | **0.24** | **0.621** | **0.000** | **0.000** | **1** | **0.07** | **0.789** | **0.000** | **0.000** |
| Marker | 1 | 0.15 | 0.694 | 0.000 | 0.000 | 1 | 0.06 | 0.802 | 0.000 | 0.000 |
| Side | 1 | 73.79 | < 0.001 | 0.021 | 0.034 | 1 | 7.65 | 0.006 | 0.006 | 0.007 |
| Dance | 1 | 809.67 | < 0.001 | 0.229 | 0.276 | 1 | 67.81 | < 0.001 | 0.056 | 0.061 |
| Axis | 1 | 388.81 | < 0.001 | 0.110 | 0.155 | na | na | na | na | na |
| **Condition: level** | **3** | **0.13** | **0.943** | **0.000** | **0.000** | **3** | **0.07** | **0.978** | **0.000** | **0.000** |
| Condition: marker | 3 | 0.09 | 0.965 | 0.000 | 0.000 | 3 | 2.44 | 0.063 | 0.006 | 0.007 |
| Level: marker | 1 | 0.02 | 0.900 | 0.000 | 0.000 | 1 | 0.10 | 0.755 | 0.000 | 0.000 |
| Condition: side | 3 | 5.22 | 0.001 | 0.004 | 0.007 | 3 | 0.54 | 0.653 | 0.001 | 0.002 |
| Level: side | 1 | 1.60 | 0.206 | 0.000 | 0.001 | 1 | 0.03 | 0.863 | 0.000 | 0.000 |
| Marker: side | 1 | 21.34 | < 0.001 | 0.006 | 0.010 | 1 | 6.09 | 0.014 | 0.005 | 0.006 |
| **Condition: level: marker** | **3** | **0.02** | **0.996** | **0.000** | **0.000** | **3** | **0.02** | **0.995** | **0.000** | **0.000** |
| **Condition: level: side** | **3** | **0.04** | **0.989** | **0.000** | **0.000** | **3** | **0.02** | **0.997** | **0.000** | **0.000** |
| Condition: marker: side | 3 | 0.22 | 0.880 | 0.000 | 0.000 | 3 | 0.48 | 0.697 | 0.001 | 0.001 |
| Level: marker: side | 1 | 0.01 | 0.943 | 0.000 | 0.000 | 1 | 0.01 | 0.910 | 0.000 | 0.000 |
| **Condition: level: marker: side** | **3** | **0.01** | **0.999** | **0.000** | **0.000** | **3** | **0.01** | **0.999** | **0.000** | **0.000** |
| Residuals | 2126 | | | | | 1045 | | | | |

# Chapter 5

# General Discussion

*Léa Chauvigné*

This dissertation described a series of experiments that extend our understanding of haptic mutual entrainment, which refers to the ability of individuals in physical contact with one another to coordinate and/or synchronize their movements in a rhythmic fashion. In Chapter 2, I identified the general brain network for audiomotor entrainment by statistically meta-analyzing the existing neuroimaging literature on finger tapping. I found the cerebellar vermis to be the best candidate for a brain area responsible for aligning rhythmic motor responses to a rhythmic sensory signal, where pulse-based movements were supported by the putamen. In Chapter 3, I used functional magnetic resonance imaging (fMRI) to assess for the first time brain activity during a haptic mutual interaction, using a novel 2-person scanning arrangement. The results revealed that individuals rely on areas that process somatosensation and sensation of the internal body during these types of interactions, as well as regions involved in social-stimulus processing and social cognition. I also showed that leading is internally driven, with a focus on motor control and spatial navigation, whereas following is externally driven, with an enhanced focus on sensory inputs and social processing.

Finally, in Chapter 4, I examined group coordination kinematically by looking at multisensory coupling during folk dancing using 3D motion capture. The results revealed that dancers rely most extensively on haptic coupling for coordination, and that auditory and visual couplings more strongly influence the temporal and spatial parameters of the dance, respectively.

## 5.1 A general brain network for entrainment

In the statistical meta-analysis of the audiomotor entrainment literature (Chapter 2), the cerebellar vermis was revealed as the best candidate for mediating entrainment ability. The cortico-cerebellar loop has very often been associated with externally-triggered actions (Jantzen et al. 2002; Taniwaki et al. 2006; Kornysheva and Schubotz 2011; Hackney et al. 2015). We suggested that this pathway aligns external timing – extracted from the rhythmic sensory signal through a network encompassing auditory areas, premotor cortices, and the basal ganglia (Grahn and Rowe 2009; Kung et al. 2013; Sameiro-Barbosa and Geiser 2016) – to internal motor timing, generated in the cortico-striatal network (Jenkins et al. 2000; Cunnington et al. 2002; Hackney et al. 2015). The basal ganglia, which are key structures for both internal motor timing and external sensory timing, have anatomical projections to the cerebellum from the subthalamic nucleus and the pontine nuclei (Bostan and Strick 2010; Bostan et al. 2010). Thus, timing information processed in the basal ganglia can provide input to the cerebellum. In addition, feedback loops encoding the sensory consequences of motor activity are likely to be integrated by the cerebellum during the entrainment process (Jantzen et al. 2002; Ross and Balasubramaniam 2014). By regulating processes of prediction and error correction (Bastian 2006; Lappe et al. 2017; Sokolov et al. 2017), the cerebellum is able to compare and align motor timing to self- and external-sensory timing signals, and thus serve as a key area for sensorimotor entrainment.

If the cerebellar vermis is a general structure for entraining movement to a rhythmic signal, one would expect that the vermis would be activated whether or not the source of the rhythmic signal is an invariant stimulus (i.e., external entrainment) or an adaptable one (i.e., mutual entrainment). However, in our fMRI study of movement partnering (Chapter 3), we did not observe a greater recruitment of the vermis during mutual entrainment compared to self-paced tasks. Indeed, following, leading and mutual are mutually-paced tasks, whereas solo and alone movement, can be seen as self-paced. We thus expected that the former conditions would rely more on the cerebellar vermis than the latter conditions, but found that the vermis was activated equally in all conditions. A potential explanation is that the vermis activation is enhanced by audiomotor entrainment but not by haptic-motor entrainment, compared to self-paced movement. However, the vermis has also been shown to be sensitive to periodic tactile stimuli (Tesche and Karhu 2000; Restuccia et al. 2007) and so this explanation seems unlikely. An alternative explanation is that the participants in our study, who were trained dancers, imagined music or an underlying beat in all conditions, as post-experimental reports tended to suggest. Participants reported having auditory imagery of music in the MRI scanner, especially during the improvisation tasks. Exploratory analyses (not reported in this dissertation) showed that the cerebellar vermis (at the location found in the meta-analysis) was recruited in all conditions, but tended to be more activated during the improvised conditions. Imagery can engage the entrainment network of the brain (Oullier et al. 2005), and we showed in our meta-analysis that the memory of an auditory rhythmic signal (memory-pacing) activated the vermis during finger tapping. Since entrainment studies have shown that auditory stimuli tend to dominate in cases of multi-sensory integration, (Repp and Penel 2004; Elliott et al. 2010), it is possible that our participants were more entrained (in a pulsed-based manner) to imagined music than to their partner. Further experimental research that directly compares haptic and auditory entrainment is necessary to test this hypothesis and more thoroughly assess the role of the cerebellar vermis in mutual entrainment. For example, music could be added as a stimulus to our two-person fMRI protocol to see if entrainment to the combination of a musical beat and a haptically-interacting partner creates an additive effect in the vermis.

The literature on joint action has highlighted a specific set of areas devoted to social processing. This “mentalizing” network, which principally encompasses the medial prefrontal cortex (mPFC), temporo-parietal junction (TPJ), posterior superior temporal sulcus (pSTS), and posterior cingulate cortex (PCC), was engaged as expected in our fMRI study (Chapter 3). However, we were not able to assess how this network interacts with the entrainment network during mutual entrainment (Figure 5.1). The entrainment network mediates the need to adapt and align body movements to an external stimulus (Thaut et al. 2008; Bijsterbosch et al. 2011; van der Steen and Keller 2013), while the social network is engaged when people adapt to one another and thereby take other people into account (Newman-Norlund et al. 2007, 2008; Keller et al. 2014; Gallotti et al. 2017). It is thus unclear how the social and entrainment networks interactively respond to the reciprocal adaptation that comes into play during mutual entrainment. This is an open area for future research.

## 5.2 Following the leader

During most interactions between people, there is a tendency for role asymmetry to emerge such that one individual becomes the source of signals to which others entrain. In Chapter 3, we showed that while both interacting partners recruited sensorimotor networks, as well as areas of the social (mentalizing) network, leaders and followers engaged these networks differently, in accordance with the function of their respective roles (Figure 5.1). Participants who were engaged in leading showed enhanced activity in the dorsal premotor cortex (dPMC), supplementary motor area (SMA), cingulate motor area (CMA), inferior frontal gyrus (IFG), and dorso-lateral prefrontal cortex (DLPFC), as related to the motor preparation, planning and sequencing, as well as the monitoring of self-

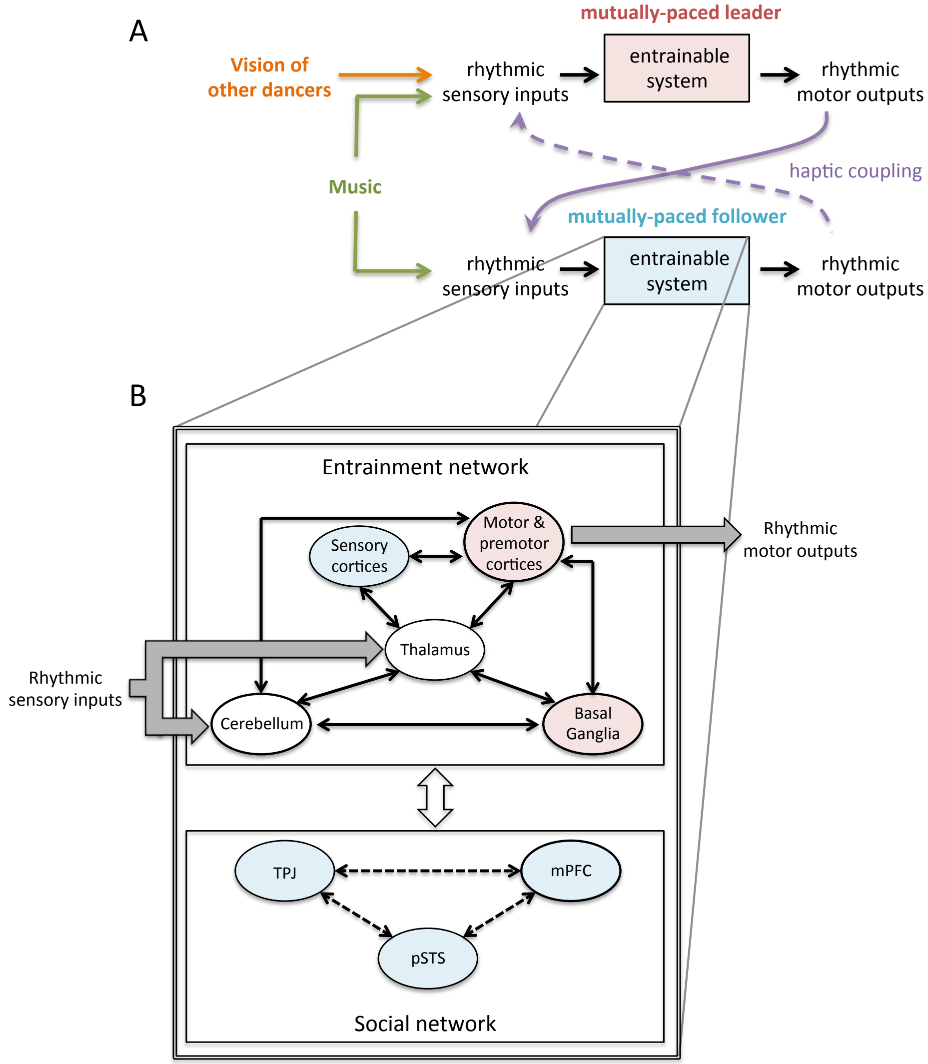


*Figure 5.1: The entrainable system at play during dance partnering*

**A: Entrainment and multi-sensory integration during dance partnering.** The Leader (in red) and Follower (in blue) are bidirectionally coupled through haptic contact (mutual entrainment) that allows them to coordinate their movements along a fine spatio-temporal frame. They also both align temporally to the music (external entrainment) and coordinate their general displacement with other dance couples (mutual entrainment). All cues are integrated by the entrainable system. **B: The entrainable system during joint action.** The figure shows areas and interconnections that are most pertinent during rhythmic entrainment (top) and the main areas involved in joint action (bottom). Dashed arrows show indirect connections. During mutual entrainment, the red areas are enhanced in leaders (motor networks), whereas the blue areas are enhanced in followers (sensory and social networks). Abbreviations: mPFC, medial prefrontal cortex; pSTS, posterior superior temporal sulcus; TPJ, temporo-parietal junction. Adapted from Bostan and Strick (2010), Hackney et al. (2015), and Teki et al. (2011).

initiated action. Leaders also recruited the superior parietal lobule (SPL) to a larger extent than followers, as they were responsible for navigating the couple through space. In contrast, participants who were engaged in following showed enhanced activity in higher-level sensory areas that process tactile inputs (secondary somatosensory cortex, SII), social stimuli (pSTS), and motion perception (middle temporal motion area, MT+), as well as in the anterior cingulate cortex (ACC), which monitors the outcomes of externally-triggered actions. Followers also recruited the TPJ, PCC and mPFC, which belong to the social and mentalizing networks. We therefore validated at a neural level the functions of leading and following described in Chapter 1: leaders are self-driven and devote more resources toward carrying out the spatio-temporal motor task per se, whereas followers are externally-driven (by the leader) and devote more resources toward stabilizing the mutual interaction (Fairhurst et al. 2014; Konvalinka et al. 2014; Gallotti et al. 2017).

In Chapter 4, we adopted a more holistic and behavioural perspective so as to assess multisensory, multi-person, and full-body entrainment. This chapter mainly focused on followers (i.e., the dancers), but ongoing work in the lab is currently exploring results from the perspective of the group's leader. The results demonstrated that, while participants integrated all leading signals during mutual entrainment, they followed them differently. The dancers' movements anticipated the music but not the group's leader. This anticipation seems to be a general behavioural characteristic of following, operating through a predictive mechanism that allows followers to stay aligned with the signal (Repp 2005; Gebauer et al. 2016). Interestingly, when the participants were prevented from hearing the music, they anticipated, and thus entrained to, the group's leader. When dancers have the need to integrate information from both a non-responsive auditory signal (recorded music) and a responsive visual signal (a live person), they primarily follow the music (external entrainment), but are able to follow a human leader if needed (mutual entrainment). This may be the case because recorded music is more reliable (less irregular) than a live person (Konvalinka et al. 2010) or because auditory entrainment is more automatic than visual entrainment (Repp and Penel 2004; Elliott et al. 2010). It should be noted that the fact that one individual anticipates the other is an indication, but not proof, of leading and following dynamics, as the mean asynchrony gives no evidence of adaptive or predictive relationships between the individuals. We would need to test the serial dependence between consecutive dancers' steps and either the musical beat or the leader's steps to confirm this hypothesis and see whether the music, or the group's leader, is leading the dancers. To precisely measure how the dancers predict and adapt to each leading signal, it would be interesting to investigate the dataset with lagged cross correlations or Granger causality analyses, or to measure the phase and period corrections between the dancers, the leader, and the music (van der Steen and Keller 2013).

Further research is needed to fully link the behavioural and neural findings presented here regarding leading and following dynamics during mutual entrainment. First, while there is research about this at the behavioural level (Elliott et al. 2010; Wing et al. 2010; Armstrong and Issartel 2014), it is not known how the leader's and follower‘s brains integrate multisensory sources during entrainment. We could replicate our fMRI study using background music or metronome beats, or potentially a visual display of the partner's hand (see Guionnet et al. 2012). In addition, by recording behavioural data in the scanner, we could assess which cues the participants follow the most and how the brain reacts to each sensory cue depending on whether it is the primary leader. Second, when the partners' roles are not pre-assigned, leaders and followers may switch back and forth as the dynamics of mutual adaptation change over time (Vesper et al. 2013; Fairhurst et al. 2014; Gallotti et al. 2017). Analyzing these dynamics across time has never been attempted, nor has measuring how the brain changes in accordance with them.

## 5.3 Communicating through haptic interaction

The dissertation has focused on mutual entrainment and on leading and following dynamics during haptic interaction. We showed that interpersonal entrainment through haptic contact is possible and that it is even more effective than auditory or visual coupling (Chapter 4). We have shown that mutual haptic interaction engaged, in addition to the social network, areas that process somatosensation (SI and SII) and sensation of the internal body (midcingulate cortex and insula), and that followers can extract dynamic information from haptic coupling via somatosensory areas (SII) as well as motion-processing areas (MT+, pSTS) (Chapter 3). Previous research has shown that humans can transfer information through the haptic channel to coordinate between several individuals (Zivotofsky and Hausdorff 2007; Nessler and Gilliland 2009; Sofianidis et al. 2012; Sofianidis and Hatzitaki 2015), and even to communicate emotion (Hertenstein et al. 2006, 2009; Gallace and Spence 2010; App et al. 2011; Thompson and Hampton 2011). Haptic coupling is therefore an effective means of interpersonal communication (Reed et al. 2006; van der Wel et al. 2011).

While haptic coupling seems very suitable for mutual entrainment, since the movement of one individual is directly perceived by partners as a pushing or pulling force (van der Wel et al. 2011), it seems at first glance that it might not be as efficient for conveying pulse-based entrainment. Auditory system might be better suited for this since music, to which people entrain most often, inherently contains regularly-spaced accents or pulses. However, I would argue that entrainment can be pulse-based only if the rhythmic signal to which one entrains is pulse-based as well, and that it does not depend on the sensory system per se. Indeed, people would probably entrain very poorly to non-pulse-based music, but much better to a human partner that moves in a pulse-based manner. However, in the case of haptic mutual entrainment, the point of contact between the individuals might not be the body part that performs the rhythmic movement. In this regard, it would be very informative to quantitatively analyze behavioural entrainment and activation of the entrainment network to pulse-based signals compared to non-rhythmic signals in all sensory modalities. There is evidence related to external entrainment that humans entrain well to pulsed-based tactile stimuli and that such stimuli can engage the core of the entrainment network (Tesche and Karhu 2000; Giordano and Wanderley 2015; Ammirante et al. 2016). An extension of this research to a joint-action context is currently lacking.

It is important to distinguish between the source of entrainment and the effector within the body of the entrained individual. In the auditory and visual modalities, the signal source is separated from the motor effector that is moving rhythmically (i.e., the body of that individual), whereas in the haptic modality, the body is *both the source and the effector* of entrainment. In Chapter 3, the participant's hands were both the source of the haptic coupling and the motor effector, but we ensured that the participant's hands could not be passively moved by the experimenter. However, in real dance partnering, as in Chapter 4, the upper body is the source of haptic coupling (e.g., the ballroom embrace in couple dances, or the handhold in folk dances), whereas the lower body is the main effector. The transmission of the signal from the contact point to the body part that is entraining is then dependent on within-individual synergies. To my knowledge, this is an unexplored issue in the literature devoted to mutual entrainment. We are planning to replicate our fMRI study with an experimenter leading the participant's hands through forces applied on the feet instead of the hands. However, this paradigm can only assess the role of the follower, as the scanned participant cannot lead the experimenter in this way. However, the follower is probably most impacted by this issue since the leader is responsible for his own movement and so has less of a need to integrate information from the contact point to move another body part.

Finally, as mentioned earlier, haptic coupling has such a powerful influence potentially because it contains both informational (tactile and proprioceptive) and mechanical (physical) couplings (Richardson et al. 2008; Harrison and Richardson 2009). Dissociating those three coupling sources during joint action is a challenge. Tactile information can be eliminated through local anesthesia (Aschersleben et al. 2001), but proprioception and mechanical sources are not easily inhibited. To prevent mechanical coupling, it would be possible in theory to record the forces applied at the point of contact between two individuals and then apply them remotely to a third person. This experiment would be very informative toward understanding the powerful mechanisms at play during haptic interaction.

## 5.4 Concluding remarks

Coordination of movement with the environment, including conspecifics, is a fundamental process in the animal kingdom, especially in social species. Humans display a specific kind of rhythmic coordination, namely entrainment, as seen during the production of music and dance. This dissertation extends our understanding of the neural and kinematic bases of haptic mutual entrainment, which is the rhythmic coordination of movement between several individuals who are in physical contact with one another, as seen during dance partnering. I have identified the vermis of the cerebellum as a key neural marker of entrainment, acting within a large network that includes the basal ganglia and the motor cortex. As stated by M. Molinari in a consensus paper: "Sensorimotor synchronization and cerebellar processing can be considered the basis of human adaptation to environmental changes—not only at the motor level but for virtually all human abilities in general" (Manto et al. 2012: 472). I therefore proposed that the entrainment networks play a general role in any kind of entrainment, including interpersonal entrainment, and encompassing all sensory channels. However, further research is needed to corroborate this hypothesis. I then argued that mutual interaction necessarily implicates leading and following dynamics. I described the brain network involved in haptic mutual entrainment and its dissociation depending on who is leading or following the interaction. The observed brain activations were compatible with the complementary emphases of leading (self- and motor-focused) and following (other- and sensory- focused), respectively. Finally, I showed in the holistic context of group dancing that people rely most extensively on haptic coupling, compared to visual or auditory coupling, to entrain within a group, even though they were mostly led by the music. This dissertation extends our understanding of the features of entrainment to ecological settings involving multi-person haptic interaction.

## 5.5 References

Ammirante P, Patel AD, Russo FA. 2016. Synchronizing to auditory and tactile metronomes: a test of the auditory-motor enhancement hypothesis. Psychon Bull Rev. 23:1882–1890.

App B, McIntosh DN, Reed CL, Hertenstein MJ. 2011. Nonverbal channel use in communication of emotion: how may depend on why. Emotion. 11:603–617.

Armstrong A, Issartel J. 2014. Sensorimotor synchronization with audio-visual stimuli: limited multisensory integration. Exp Brain Res. 232:3453–3463.

Aschersleben G, Gehrke J, Prinz W. 2001. Tapping with peripheral nerve block. Exp Brain Res. 136:331–339.

Bastian AJ. 2006. Learning to predict the future: the cerebellum adapts feedforward movement control. Curr Opin Neurobiol. 16:645–649.

Bijsterbosch JD, Lee K-H, Hunter MD, Tsoi DT, Lankappa S, Wilkinson ID, Barker AT, Woodruff PWR. 2011. The role of the cerebellum in sub- and supraliminal error correction during sensorimotor synchronization: evidence from fMRI and TMS. J Cogn Neurosci. 23:1100–1112.

Bostan A, Strick P. 2010. The cerebellum and basal ganglia are interconnected. Neuropsychol Rev. 20:261–270.

Bostan AC, Dum RP, Strick PL. 2010. The basal ganglia communicate with the cerebellum. Proc Natl Acad Sci. 107:8452–8456.

Chauvigné LAS, Gitau KM, Brown S. 2014. The neural basis of audiomotor entrainment : An ALE meta-analysis. Front Hum Neurosci. 8:1–18.

Cuijpers LS, Zaal FTJM, De Poel HJ. 2015. Rowing crew coordination dynamics at increasing stroke rates. PLoS One. 10:1–18.

Cunnington R, Windischberger C, Deecke L, Moser E. 2002. The preparation and execution of self-initiated and externally-triggered movement: a study of event-related fMRI. Neuroimage. 15:373–385.

de Poel HJ. 2016. Anisotropy and antagonism in the coupling of two oscillators: Concepts and applications for between-person coordination. Front Psychol. 7:1–6.

Demos AP, Chaffin R, Begosh KT, Daniels JR, Marsh KL. 2012. Rocking to the beat: Effects of music and partner’s movements on spontaneous interpersonal coordination. J Exp Psychol Gen. 141:49–53.

Ellamil M, Berson J, Margulies DS. 2016. Influences on and measures of unintentional group synchrony. Front Psychol. 7:1–6.

Elliott MT, Wing AM, Welchman AE. 2010. Multisensory cues improve sensorimotor synchronisation. Eur J Neurosci. 31:1828–1835.

Fairhurst MT, Janata P, Keller PE. 2014. Leading the follower: An fMRI investigation of dynamic cooperativity and leader-follower strategies in synchronization with an adaptive virtual partner. Neuroimage. 84:688–697.

Gallace A, Spence C. 2010. The science of interpersonal touch: An overview. Neurosci Biobehav Rev. 34:246–259.

Gallotti M, Fairhurst MT, Frith CD. 2017. Alignment in social interactions. Conscious Cogn. 48:253–261.

Gebauer L, Witek MAG, Hansen NC, Thomas J, Konvalinka I, Vuust P. 2016. Oxytocin improves synchronisation in leader-follower interaction. Sci Rep. 6:38416.

Giordano M, Wanderley MM. 2015. Follow the tactile metronome : Vibrotactile stimulation for tempo synchronization in music performance. In: Sound and Music Computing Conference. Maynooth, Ireland.

Goebl W, Palmer C. 2009. Synchronization of timing and motion among performing musicians. Music Percept. 26:427–438.

Grahn JA, Rowe JB. 2009. Feeling the beat: Premotor and striatal interactions in musicians and nonmusicians during beat perception. J Neurosci. 29:7540–7548.

Guionnet S, Nadel J, Bertasi E, Sperduti M, Delaveau P, Fossati P. 2012. Reciprocal imitation: Toward a neural basis of social interaction. Cereb Cortex. 22:971–978.

Hackney ME, Lee HL, Battisto J, Crosson B, McGregor KM. 2015. Context-dependent neural activation: Internally and externally guided rhythmic lower limb movement in individuals with and without neurodegenerative disease. Front Neurol. 6:1–16.

Harrison SJ, Richardson MJ. 2009. Horsing around: Spontaneous four-legged coordination. J Mot Behav. 41:519–524.

Hertenstein MJ, Holmes R, McCullough M, Keltner D. 2009. The communication of emotion via touch. Emotion. 9:566–573.

Hertenstein MJ, Keltner D, App B, Bulleit BA, Jaskolka AR. 2006. Touch communicates distinct emotions. Emotion. 6:528–533.

Hove MJ, Iversen JR, Zhang A, Repp BH. 2013. Synchronization with competing visual and auditory rhythms: Bouncing ball meets metronome. Psychol Res. 77:388–398.

Hove MJ, Keller PE. 2010. Spatiotemporal relations and movement trajectories in visuomotor synchronization. Music Percept. 28:15–26.

Issartel J, Marin L, Cadopi M. 2007. Unintended interpersonal co-ordination: "can we march to the beat of our own drum?" Neurosci Lett. 411:174–179.

Iversen JR, Patel AD, Nicodemus B, Emmorey K. 2015. Synchronization to auditory and visual rhythms in hearing and deaf individuals. Cognition. 134:232–244.

Jantzen KJ, Steinberg FL, Kelso JAS. 2002. Practice-dependent modulation of neural activity during human sensorimotor coordination: A functional Magnetic Resonance Imaging study. Neurosci Lett. 332:205–209.

Jenkins IH, Jahanshahi M, Jueptner M, Passingham RE, Brooks DJ. 2000. Self-initiated versus externally triggered movements. II. The effect of movement predictability on regional cerebral blood flow. Brain. 123:1216–1228.

Keller PE, Novembre G, Hove MJ. 2014. Rhythm in joint action: Psychological and neurophysiological mechanisms for real-time interpersonal coordination. Philos Trans R Soc Lond B Biol Sci. 369:1–12.

Kimmel M, Preuschl E. 2016. Dynamic coordination patterns in Tango Argentino: A cross-fertilization of subjective explication methods and motion capture. In: Laumond J-P,, Abe N, editors. Dance Notations and Robot Motion. Springer T. ed. p. 361–376.

Konvalinka I, Bauer M, Stahlhut C, Hansen LK, Roepstorff A, Frith CD. 2014. Frontal alpha oscillations distinguish leaders from followers: Multivariate decoding of mutually interacting brains. Neuroimage. 94:79–88.

Konvalinka I, Vuust P, Roepstorff A, Frith CD. 2010. Follow you, follow me: continuous mutual prediction and adaptation in joint tapping. Q J Exp Psychol. 63:2220–2230.

Kornysheva K, Schubotz RI. 2011. Impairment of auditory-motor timing and compensatory reorganization after ventral premotor cortex stimulation. PLoS One. 6:e21421.

Kung S-J, Chen JL, Zatorre RJ, Penhune VB. 2013. Interacting cortical and basal ganglia networks underlying finding and tapping to the musical beat. J Cogn Neurosci. 25:401–420.

Kurgansky A V. 2008. Visual-motor synchronization: analysis of the initiation and stable synchronization phases. Hum Physiol. 34:289–298.

Lappe C, Bodeck S, Lappe M, Pantev C. 2017. Shared neural mechanisms for the prediction of own and partner musical sequences after short-term piano duet training. Front Neurosci. 11:1–11.

Loehr JD, Palmer C. 2011. Temporal coordination between performing musicians. Q J Exp Psychol. 64:2153–2167.

Manto M, Bower JM, Conforto AB, Delgado-García JM, Da Guarda SNF, Gerwig M, Habas C, Hagura N, Ivry RB, Marien P, Molinari M, Naito E, Nowak DA, Ben Taib NO, Pelisson D, Tesche CD, Tilikete C, Timmann D. 2012. Consensus paper: Roles of the cerebellum in motor control-the diversity of ideas on cerebellar involvement in movement. Cerebellum. 11:457–487.

Merchant H, Honing H. 2014. Are non-human primates capable of rhythmic entrainment? Evidence for the gradual audiomotor evolution hypothesis. Front Neurosci. 7:274.

Merker BH, Madison GS, Eckerdal P. 2009. On the role and origin of isochrony in human rhythmic entrainment. Cortex. 45:4–17.

Nessler JA, Gilliland SJ. 2009. Interpersonal synchronization during side by side treadmill walking is influenced by leg length differential and altered sensory feedback. Hum Mov Sci. 28:772–785.

Nessler JA, Gilliland SJ. 2010. Kinematic analysis of side-by-side stepping with intentional and unintentional synchronization. Gait Posture. 31:527–529.

Newman-Norlund RD, Bosga J, Meulenbroek RGJ, Bekkering H. 2008. Anatomical substrates of cooperative joint-action in a continuous motor task: Virtual lifting and balancing. Neuroimage. 41:169–177.

Newman-Norlund RD, Noordzij ML, Meulenbroek RGJ, Bekkering H. 2007. Exploring the brain basis of joint action: Co-ordination of actions, goals and intentions. Soc Neurosci. 2:48–65.

Oullier O, de Guzman GC, Jantzen KJ, Lagarde J, Kelso J a S. 2008. Social coordination dynamics: Measuring human bonding. Soc Neurosci. 3:178–192.

Oullier O, Jantzen KJ, Steinberg FL, Kelso J a S. 2005. Neural substrates of real and imagined sensorimotor coordination. Cereb cortex. 15:975–985.

Phillips-Silver J, Aktipis CA, G.A. B. 2010. The ecology of entrainment: Foundations of coordinated rhythmic movement. Music Percept. 28:3–14.

Ragert M, Schroeder T, Keller PE. 2013. Knowing too little or too much: The effects of familiarity with a co-performer's part on interpersonal coordination in musical ensembles. Front Psychol. 4:368.

Reddish P, Fischer R, Bulbulia J. 2013. Let's dance together: Synchrony, shared intentionality and cooperation. PLoS One. 8:1–13.

Reed K, Peshkin M, Hartmann MJ, Grabowecky M, Patton J, Vishton PM. 2006. Hapitically linked dyads: Are two motor-contol systems better than one? Psychol Sci. 17:365–366.

Repp B. 2005. Sensorimotor synchronization: A review of the tapping literature. Psychon Bull Rev. 12:969–992.

Repp BH. 2010. Sensorimotor synchronization and perception of timing: Effects of music training and task experience. Hum Mov Sci. 29:200–213.

Repp BH, Penel A. 2004. Rhythmic movement is attracted more strongly to auditory than to visual rhythms. Psychol Res. 68:252–270.

Repp BH, Su Y-H. 2013. Sensorimotor synchronization: a review of recent research (2006-2012). Psychon Bull Rev. 20:403–452.

Restuccia D, Marca G Della, Valeriani M, Leggio MG, Molinari M. 2007. Cerebellar damage impairs detection of somatosensory input changes. A somatosensory mismatch-negativity study. Brain. 130:276–287.

Richardson MJ, Lopresti-Goodman S, Mancini M, Kay B, Schmidt RC. 2008. Comparing the attractor strength of intra- and interpersonal interlimb coordination using cross-recurrence analysis. Neurosci Lett. 438:340–345.

Richardson MJ, Marsh KL, Isenhower RW, Goodman JRL, Schmidt RC. 2007. Rocking together: Dynamics of intentional and unintentional interpersonal coordination. Hum Mov Sci. 26:867–891.

Richardson MJ, Marsh KL, Schmidt RC. 2005. Effects of visual and verbal interaction on unintentional interpersonal coordination. J Exp Psychol Hum Percept Perform. 31:62–79.

Ross JM, Balasubramaniam R. 2014. Physical and neural entrainment to rhythm: human sensorimotor coordination across tasks and effector systems. Front Hum Neurosci. 8:1–6.

Sacheli LM, Aglioti SM, Candidi M. 2015. Social cues to joint actions: The role of shared goals. Front Psychol. 6:1–7.

Sameiro-Barbosa CM, Geiser E. 2016. Sensory entrainment mechanisms in auditory perception: Neural synchronization cortico-striatal activation. Front Neurosci. 10:1–8.

Sänger J, Müller V, Lindenberger U. 2012. Intra- and interbrain synchronization and network properties when playing guitar in duets. Front Hum Neurosci. 6:312.

Schmidt RC, Fitzpatrick P, Caron R, Mergeche J. 2011. Understanding social motor coordination. Hum Mov Sci. 30:834–845.

Schmidt RC, O'Brien B. 1997. Evaluating the dynamics of unintended interpersonal coordination. Ecol Psychol. 9:189–206.

Sofianidis G, Hatzitaki V. 2015. Interpersonal entrainment in dancers: Contrasting timing and haptic cues. Posture, Balanc Brain Int Work Proc. 34–44.

Sofianidis G, Hatzitaki V, Grouios G, Johannsen L, Wing A. 2012. Somatosensory driven interpersonal synchrony during rhythmic sway. Hum Mov Sci. 31:553–566.

Sokolov AA, Miall RC, Ivry RB. 2017. The cerebellum: Adaptive prediction for movement and cognition. Trends Cogn Sci. 21:313–332.

Taniwaki T, Okayama A, Yoshiura T, Togao O, Nakamura Y, Yamasaki T, Ogata K, Shigeto H, Ohyagi Y, Kira J ichi, Tobimatsu S. 2006. Functional network of the basal ganglia and cerebellar motor loops in vivo: Different activation patterns between self-initiated and externally triggered movements. Neuroimage. 31:745–753.

Teki S, Grube M, Griffiths TD. 2011. A unified model of time perception accounts for duration-based and beat-based timing mechanisms. Front Integr Neurosci. 5:90.

Tesche CD, Karhu JJT. 2000. Anticipatory cerebellar responses during somatosensory omission in man. Hum Brain Mapp. 9:119–142.

Thaut MH, Demartin M, Sanes JN. 2008. Brain networks for integrative rhythm formation. PLoS One. 3:e2312.

Thompson EH, Hampton JA. 2011. The effect of relationship status on communicating emotions through touch. Cogn Emot. 25:295–306.

Trainor LJ, Gao X, Lei J jiang, Lehtovaara K, Harris LR. 2009. The primal role of the vestibular system in determining musical rhythm. Cortex. 45:35–43.

van der Steen MCM, Keller PE. 2013. The ADaptation and Anticipation Model (ADAM) of sensorimotor synchronization. Front Hum Neurosci. 7:253.

van der Wel RPRD, Knoblich G, Sebanz N. 2011. Let the force be with us: Dyads exploit haptic coupling for coordination. J Exp Psychol Hum Percept Perform. 37:1420–1431.

Vesper C, Richardson MJ. 2014. Strategic communication and behavioral coupling in asymmetric joint action. Exp Brain Res. 232:2945–2956.

Vesper C, van der Wel RPRD, Knoblich G, Sebanz N. 2013. Are you ready to jump? Predictive mechanisms in interpersonal coordination. J Exp Psychol Hum Percept Perform. 39:48–61.

Wing AM, Doumas M, Welchman AE. 2010. Combining multisensory temporal information for movement synchronisation. Exp Brain Res. 200:277–282.

Yang DY-J, Rosenblau G, Keifer C, Pelphrey KA. 2015. An integrative neural model of social perception, action observation, and theory of mind. Neurosci Biobehav Rev. 51:263–275.

Zhou G, Bourguignon M, Parkkonen L, Hari R. 2016. Neural signatures of hand kinematics in leaders vs. followers: A dual-MEG study. Neuroimage. 125:731–738.

Zivotofsky AZ, Hausdorff JM. 2007. The sensory feedback mechanisms enabling couples to walk synchronously: An initial investigation. J Neuroeng Rehabil. 4:28.