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When we move together

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1. Introduction

The well-known movie *Modern Times* (1936) caricaturizes how being forced to act/work in isolation can influence the human condition. In the movie, Charlie Chaplin casts a “modern” factory worker who is employed on an assembly line. In one shot, we see him tightening bolts in the company of several co-workers. In a next shot, the assembly line speeds up tremendously and he works with great effort, struggling miserably, but nobody comes to help him. In another shot, he is being fed by an automatic feeding machine introduced by the employers. At the end, Charlie experiences a mental breakdown due to social alienation. Indeed, during the 1930’s, when “modern” working conditions reduced the likelihood of social interactions between workers, many of them began to suffer from isolation (Frisby, 1987; Marx, 1973).

In contemporary Western societies, regardless of claims about their individualistic orientation, many aspects of everyday life are fundamentally based on socially coordinated actions of human beings. With a quick gaze around us, we may see many socially coordinated actions performed almost effortlessly, ranging from two friends jointly carrying a heavy table to sports teams that skillfully coordinate their movements to defeat their adversaries, to musicians playing together in an orchestra. These types of actions, performed by two or more individuals who coordinate their actions in space and time to bring about a change in the environment, are often referred to as joint actions (Sebanz et al., 2006a). Although joint actions play an important role in many everyday activities and are at the core of our ability to cooperate, the question of how we accomplish these seemingly simple actions remains an issue of debate in social neuroscience.

The neural systems recruited while participants observe the actions of others and execute actions by themselves have been explored extensively (Buccino et al., 2004; Chong et al., 2008; Gazzola et al., 2007; Iacoboni, 2005; Iacoboni et al., 1999; Kilner et al., 2009; Rizzolatti and Craighero, 2004; Rizzolatti et al., 1996a; Rizzolatti et al., 1996b; Rizzolatti et al., 2001). However, during most social interactions, there is not a single actor and a single observer; instead individuals are simultaneously observers as well as actors who need to adjust their own actions to those of others (Keysers and Fadiga, 2008). Recently, the interest in this reciprocal nature of social interactions and its underlying neural processes has surged. Researchers increasingly try to tackle the difficult question of how interactions between self-propelled agents unfold in space and time by probing the brain activity of humans (Kokal et al., 2009; Newman-Norlund et al., 2008; Newman-Norlund et al., 2007b; Schippers et al., 2009; Sebanz et al., 2006b; Sebanz et al., 2007) and monkeys (Fijii et al., 2008).

Likewise, this thesis aimed at advancing the present knowledge on the neural signature of social interactions, in particular during joint actions, in humans. We first present two functional magnetic resonance imaging (fMRI) experiments (Experiment 1 and 2) exploring the neural mechanisms involved in joint actions when two agents mutually coordinate their actions while playing a cooperation game (Chapter 2). Second, we demonstrate information flow between the brain areas identified in

Experiment 1 by employing an effective connectivity method (Chapter 3). Third, we present an fMRI experiment (Experiment 3) in which we examine the responses of the reward system in the brain during a social drumming task to reveal the rewarding effects of engaging in musical joint actions. In addition, we demonstrate the results of a prosocial commitment test performed immediately after the Experiment 3, which investigates the influence of drumming together on helping behavior between the drum partners (Chapter 4).

1.1. Background Information

Before describing the experiments in detail I will provide a brief overview of the current knowledge about action planning and coordination in social context, the mirror neuron system and joint music making that paved the way for this thesis.

Action Planning and Coordination in Social Context

The mechanisms that enable a single agent to coordinate his or her own actions have been investigated through a variety of experimental paradigms such as task switching and multi-tasking paradigms (Allport, 1993; Mayr and Keele, 2000; Meyer and Kieras, 1997). Results of such studies have shown that individuals do not merely act upon external stimuli but adapt their own actions according to their plans on how to achieve a goal (Bekkering et al., 2000). Importantly, these plans to achieve an action are usually internal to the actor (Allport, 1993; Hommel et al., 2001; Prinz, 1997).

A joint action involves two or more actors who lack insight into each other's mind. When each individual tries to coordinate his/her actions according to his/her own internally generated plans, acting together to achieve a common goal may prove difficult. Consider, for example, a young couple picnicking in the park. If it suddenly starts raining, they would both get up and grasp the heavy picnic basket in order to carry it together to a sheltered place. Although carrying a basket is a simple action, to achieve this goal with another agent is a difficult task as these two agents execute their actions according to their own internally generated action plans. Thus, on the way to the shelter, they will need to coordinate a chain of actions on how to grab the basket and on where and when to walk. Clark (1996) suggested language¹ as a powerful coordinating device for such situations (Clark, 1996). However, as engaging in joint action entails great timing demands, verbal communication between individuals would often be too slow and inefficient.

How is it then possible that individuals can coordinate their actions in space and time to achieve a common goal? Early research revealed that observing others acting affects one's own action planning and control. It has been demonstrated that an individual's performance is facilitated when he/she observes a similar action performed by another individual in the proximity whereas observing the opposite action interferes with performing the same action (Brass et al., 2001; Sturmer et al., 2000). Such effects of the sight of others' actions on one's own performance are

¹ The question of if language itself is a form of joint action is out of the scope of this thesis.

addressed by theoretical frameworks such as ideomotor theory (Greenwald, 1970; James, 1980) and the common coding theory (Hommel et al., 2001; Prinz, 1997). These theories propose that observing actions performed by others might activate the same representations that govern one's own planning and control of these actions because the same representations are involved in action production and observation.

As a first step towards understanding joint action coordination, researchers investigated how individuals perform a task with a co-acting agent using a modified version of a spatial stimulus-response (S-R) compatibility task (Atmaca et al., 2008; Sebanz et al., 2003; Sebanz et al., 2005; Tsai et al., 2008). In a typical spatial stimulus-response (S-R) compatibility task, participants press a left key when they see a red light and a right one when they see a green light and are found to respond less accurately and/or slower to stimuli presented contralateral to the correct response than to stimuli presented on the ipsilateral side (Wallace, 1971). Sebanz and colleagues (2003), for instance, distributed this task among two agents (a participant and a confederate). They then compared the task performance of the participant when he/she acts alongside another agent (group condition) to when he/she performs the identical task alone (Sebanz et al., 2003). Their results demonstrated a spatial compatibility effect² in the group condition in which a participant and the confederate performed their own half of the task. More importantly, there was no spatial compatibility effect when participants performed their half of the task alone, although the participant's task was identical to the task in the group condition (Sebanz et al., 2003). Similar group effects were also found when participants knew the confederate's task but did not see the actions of him/her (Sebanz et al., 2005; Tsai et al., 2008). The conclusion of these studies is that when individuals carry out different parts of a task, each actor represent the whole task (both his/her own and the other's) instead of representing only his/her own part of the task. This suggests that we automatically represent potential actions of others just like our own actions when we perform tasks together with others. This automatic tendency ability to form shared action representations are typically referred to as co-representations or shared representations in the literature (Sebanz et al., 2003; Sebanz et al., 2005).

Although these (and other) behavioral studies did not provide empirical evidence of the neural mechanisms underlying co-representations occurring in group settings, they claimed that the MNS may play a role in representing one's own and other's action in a functionally equivalent way when performing a task together with another agent (Atmaca et al., 2008; Sebanz et al., 2006a; Sebanz et al., 2003; Sebanz et al., 2005; Tsai et al., 2008).

Later, neural correlates of shared representations were investigated with an ERP³ study (Sebanz et al., 2006b). Sebanz and colleagues (2006) compared the ERPs and electrophysiological responses when participants performed a task alone to those when they performed the task together with another individual. Their results demonstrated similar electrophysiological response at frontal brain sites in response to

² A typical spatial compatibility effect indicates that task-irrelevant properties of the stimulus (i.e. the location of the stimulus relative to the participant) interfere with performance.

³ Event-related brain potentials (ERPs) are a non-invasive method of measuring brain activity during cognitive processing.

a stimulus referring to the other's action and to the one referring to one's own action. They suggested that as one's own actions and others' actions were represented in a common domain the mirror neurons system (MNS) might play a role when individuals perform actions in turns with others (Sebanz et al., 2006b).

The Mirror Neuron System and Joint Actions

An accumulating body of studies suggests that perceivers are able to understand the actions of others and the intentions behind these actions while passively observing them (Puce and Perrett, 2003). It has been proposed that seeing actions performed by others may directly trigger motor and somatosensory representations as they would be elicited by one's own actions in similar circumstances (Bastiaansen et al., 2009; Fogassi et al., 2005; Gallese et al., 1996; Gazzola and Keysers, 2009; Keysers et al., 2004; Kilner et al., 2004; Rizzolatti et al., 2001; Umiltà et al., 2001). This intriguing mechanism could allow observers to understand the actions of others based on their own experiences and provides 'a first-person grasp of the motor goals' of others (Rizzolatti and Sinigaglia, 2010).

Originally, the idea of such a mechanism emerged from the discovery of mirror neurons in the ventral premotor cortex (area F5) (Pellegrino et al., 1992) and in the parietal cortex (area PFG located between parietal areas PF and PG) (Fogassi et al., 2005) in the monkey brain with a series of single neuron recording experiments. These neurons were called mirror neurons as they displayed a unique response pattern of being equally responsive to both the execution of the actions performed by the monkey itself and the observation of similar actions performed by an experimenter. Single neuron recording is an invasive technique not commonly used in humans. Following these original observations, several studies using different techniques such as fMRI (Buccino et al., 2001; Buccino et al., 2004; Carr et al., 2003; Chong et al., 2008; Gazzola and Keysers, 2009; Gazzola et al., 2007; Iacoboni, 2005; Iacoboni et al., 1999; Kilner et al., 2009; Kokal et al., 2009), PET (Grafton et al., 1996; Rizzolatti et al., 1996b), MEG (Hari et al., 1998), TMS (Avenanti et al., 2007; Catmur et al., 2009; Fadiga et al., 1995) and extracellular recordings (Mukamel et al., 2010) have provided strong converging evidence for the existence of the MNS in the human brain. The ventral and dorsal premotor areas (BA 44 and BA 6), the inferior parietal lobe (IPL), the middle temporal gyrus (MTG), the supplementary motor area (SMA) and the somatosensory cortex have all been identified as being active during both action observation and execution in humans. These structures together are often referred to as the putative MNS (pMNS). The term 'putative' underlines the fact that an increase in BOLD response both during action observation and execution in a voxel can only suggest that it could contain mirror neurons. Alternative explanations, such as that the voxel contains distinct but interdigitated populations of neurons involved in action observation only and execution only are also possible (Keysers and Gazzola, 2009; Kokal et al., 2009).

As the monkey mirror neurons and the putative human equivalent respond to both action observation and execution, it has been claimed that we directly map the observed actions of others on our motor system, typically referred to as the direct-matching hypothesis (Gallese, 1998; Rizzolatti et al., 2001). This hypothesis claims

that the mirror mechanism unifies perception and action by transforming sensory representations of an action into motor representations of the same action in the observer's brain (Rizzolatti and Sinigaglia, 2010). Therefore, it has been suggested that the functional role of the MNS is action understanding as such mapping would allow one to recognize the goals of others using the link between one's own motor acts and their perceptual consequences (Fogassi et al., 2005; Gallese et al., 1996; Iacoboni, 2005; Rizzolatti and Craighero, 2004; Rizzolatti et al., 1996a; Umiltà et al., 2001).

It has been suggested that the functional role of the mirror neurons includes many aspects of social cognition such as imitation (Iacoboni et al., 1999), empathy (Bastiaansen et al., 2009; Fogassi et al., 2005; Gallese et al., 1996; Jabbi and Keysers, 2008; Keysers and Gazzola, 2006), mind-reading (Gallese, 2003; Gallese, 1998), gestural communication (Schippers et al., 2009; Schippers et al., 2010) and language (Rizzolatti and Arbib, 1998). Maybe not too surprisingly, a number of empirical studies (Newman-Norlund et al., 2008; Newman-Norlund et al., 2007b; Sebanz et al., 2007) and theoretical proposals (Knoblich and Jordan, 2002; Newman-Norlund et al., 2007a; Sebanz et al., 2006a) have also suggested a fundamental role for the MNS during the engagement in joint actions.

Neural Correlates of Joint Actions

In a typical joint action situation mutually acting with others requires the ability to adjust our actions to those of others (Knoblich and Jordan, 2002). According to several experimental and theoretical proposals (Atmaca et al., 2008; Clark, 1996; Knoblich and Jordan, 2003; Knoblich and Jordan, 2002; Newman-Norlund et al., 2008; Newman-Norlund et al., 2007a; Newman-Norlund et al., 2007b; Pacherie and Doherty, 2006; Sebanz et al., 2006a; Sebanz et al., 2006b; Sebanz et al., 2007) the ability to coordinate our actions with those of others depends upon the MNS, a system which allows the direct mapping of observed actions onto one's own motor representations. Such mapping has been claimed to be sufficient to allow an actor to adjust his or her own action plans to the predicted actions of the respective action partner, leading to a successful joint action (Clark, 1996; Newman-Norlund et al., 2008; Newman-Norlund et al., 2007a; Newman-Norlund et al., 2007b; Sebanz et al., 2006a; Sebanz et al., 2006b). Although these proposals suggest a key role for the MNS in joint actions, we know little about its contribution, due to a scarcity of empirical evidence. Existing literature of empirical studies on joint actions includes several behavioral experiments, an ERP experiment and a few fMRI studies.

Behavioral experiments (Atmaca et al., 2008; Knoblich and Jordan, 2003; Sebanz et al., 2003; Sebanz et al., 2005; Tsai et al., 2008) investigating the performance of co-acting individuals have revealed that the actors form shared task representations, yet have not addressed the neural bases of this phenomenon.

The first empirical attempt to reveal the neural processes involved in co-acting with another actor was an fMRI study by Sebanz and colleagues in 2007 (Sebanz et al., 2007). They asked their participants to perform a go-nogo task with a confederate who was present in the scanner room, sitting next to the participants. Their paradigm included single actor conditions in which the participant responded to one of the two

colors alone and co-action conditions in which the participant responded to one color and the confederate responded to the other one by taking turns. They found brain activity in the inferior and superior parietal lobe and supplementary motor area associated with nogo trials in co-acting condition. They conclude that these activations may be the neural correlates of shared representations triggered by observing a co-actor's actions. Although this study was a pioneer in investigating co-acting individuals in fMRI, the task was based on turn taking instead of the continuous adjustment of actions that typically defines joint actions. Thus, it remains unclear how task sharing facilitates choosing a suitable action at the appropriate time when individuals engage in true joint actions.

Recent empirical studies (Kokal et al., 2009; Kokal and Keysers, 2010; Newman-Norlund et al., 2008; Newman-Norlund et al., 2007b) were designed to investigate the role played by the MNS in joint actions. Some of these studies argued that the MNS might be the key neural locus of coordination during joint actions. However, they failed to directly test the contribution of the MNS because they concluded that the brain activations they observed were located in the MNS without actually locating the MNS of their participants. Newman-Norlund and colleagues (2008), for instance, found that the BOLD signal in the inferior frontal gyrus (IFG) was larger when participants balanced a ball together with another agent (a joint action) than when they balanced the ball alone (Newman-Norlund et al., 2008). The authors interpreted this as an evidence for the direct role of the MNS in joint actions. However, they did not confirm that the activations occurred in areas also demonstrating MNS-diagnostic activity. A common test to demonstrate pMNS activity is to identify regions active while viewing an action (another actor balancing a ball) and performing the motor actions alone (the most straightforward definition of the MNS based on single cell recordings). Likewise, in another experiment Newman-Norlund and colleagues (2007) demonstrated greater BOLD signal in the MNS (right IFG and bilateral IPL) during planning of complementary actions compared to imitative actions (Newman-Norlund et al., 2007b). Given that the IFG as well as the IPL are well known to contain other types of neurons in addition to mirror neurons, from the results of these experiments, it is difficult to interpret whether the brain areas identified are really part of the MNS, and hence whether the MNS contributes to joint actions (Kokal et al., 2009; Thioux et al., 2008).

One of the key features of joint actions, which distinguish them from individual actions, is the necessity to continuously adjust one's own actions to those of others. In many cases joint actions do not involve performing identical actions but rather complementary actions. Importantly, we are able to switch between performing same and complementary actions in seconds. In order to shed more light on the contribution of the MNS for this key feature of joint actions, we performed an fMRI study (Experiment 1) specifically aimed at examining the degree to which this adjustment process occurs within or beyond the MNS.

Our results revealed that a typical joint action requires at least three intertwined processes: observing actions of others, executing one's own actions and a task-dependent integration of observed and executed actions (Kokal et al., 2009). As the MNS is known to transform the sight of actions into motor representations of similar actions (Etzel et al., 2008; Gallese et al., 2004; Iacoboni and Dapretto, 2006; Keysers

and Gazzola, 2006; Liepelt et al., 2008; Rizzolatti and Craighero, 2004), it may play a role in representing both partners' actions in a common code. However, the task usually determines the nature of the integration of the observed and executed action. For example, when carrying a picnic basket with another person this integration can vary from doing the same action (e.g. both people lift the basket together) to doing the opposite of the partner (e.g. one moves forward and the other backward to pass a narrow alley). Given that the mirror neurons in the monkey are known to show a fixed relationship between observed and executed actions (Gallese et al., 1996), this task-dependent redefinition of the visuo-motor integration during joint actions is likely to be performed outside the MNS (Kokal et al., 2009; Kokal and Keysers, 2010). In Chapter 2, we propose a potential alternative network of brain areas underlying this key feature of joint actions.

The MNS and Internal Predictive Models in the Service of Joint Actions

Another challenge for motor control during joint actions is the fact that our visual and motor systems have relatively long latencies (several hundreds of milliseconds) (Adam and Van Veggel, 1991; Michie et al., 1976). It has been suggested that the MNS could contribute to solving the time lag issue by allowing one to anticipate future actions of others that are not yet fully visible (Miall, 2003; Ramnani and Miall, 2004; Umiltà et al., 2001; Wolpert et al., 2003).

According to influential action models (Kilner et al., 2007b; Miall, 2003; Wolpert et al., 2003; Wolpert, 2000), the motor system uses two forms of internal models, namely inverse and forward models, while executing actions. It has been proposed that the inverse model maps the relationship between the goals and the motor commands necessary to reach a goal while the forward model maps the relationship between motor commands and the sensory outcomes of a motor action (Miall, 2003). It has been claimed that the MNS may act as both models: the circuit linking the superior temporal sulcus (STS)⁴, PF and F5 acting as an inverse model, whereas the circuit linking the F5, PF and STS as a forward model (Gazzola and Keysers, 2009; Miall, 2003).

Wolpert & Ghahramani (2000) demonstrated that individuals continuously compare the actual and predicted consequences of their actions by utilizing these internal models (Wolpert, 2000). These models have also been hypothesized to support making predictions about others' actions in the immediate future (Gazzola and Keysers, 2009; Kilner et al., 2007a; Kilner et al., 2004; Miall, 2003; Wolpert et al., 2003; Wolpert, 2000). In such situations, predictions about the actions of others could be formed by comparing the potential motor commands transformed from observation by utilizing the inverse model through which the visual information is converted to a predicted motor plan. Simultaneously, the sensory outcomes of the observed motor action could be predicted by utilizing the forward model (Ramnani and Miall, 2004; Wolpert et al., 2003).

⁴ The STS also contains neurons that respond to action observation, yet they do not discharge during action execution. Therefore, STS cannot be considered part of the MNS.

In Chapter 3 we propose that the MNS, as a predictive device, may be involved in joint actions as part of a forward model to predict the future somatosensory and visual consequences of the observed and executed actions, overcoming the otherwise inevitable neural delays. We provide empirical evidence from effective connectivity analysis demonstrating a predominantly backwards information flow from BA44 to the posterior sites of the MNS (BA 2) and the visual areas (i.e. MOG) during joint actions (Kokal and Keysers, 2010). A similar backwards information flow within the MNS during a gestural communication task, a task employing skills similar to those needed for joint action, has also been recently demonstrated (Schippers and Keysers, 2010).

From Joint Actions to Prosocial Behavior

We humans are the only primates that engage in the special form of joint actions that is synchronizing movements or voices during music making and dancing (Wallin et al., 2000). This proclivity for synchronizing one's own actions with those of others is found across all cultures (Wallin et al., 2000) and emerges very early in childhood (Kirschner and Tomasello, 2009).

Why people enjoy joint music making and dancing across all times and cultures remains an open question. Unlike food or sex, jointly acting in a musical context does not provide any obvious fitness advantage, though may increase fitness through social bonding, akin to grooming in non-human primates. One hypothesis on the original adaptive function of such behavior is that our human ancestors invented joint music making and dance as a tool for supporting group cohesion, ultimately increasing prosocial in-group behavior (Huron, 2001; McNeil, 1995; Roederer, 1984). This hypothesis predicts that synchronizing movements or vocalizations with other people should not only be experienced as a pleasurable activity, but also increase prosocial commitment and foster subsequent cooperation among the performers. Indeed, in traditional cultures music making and dancing are often collective actions, integrated in important group ceremonies such as initiation rites, weddings, or preparations for battle. This seems to hold for many modern cultures as well: Kirschner and Tomasello (2010) showed that joint music making facilitates prosocial and cooperative behaviors in four-year-old children (Kirschner and Tomasello, 2010). Similar effects have been observed among adults: Anshel and Kipper (1988) found that adult Israeli males score higher on a questionnaire on trust after a group singing lesson in comparison to passive music listening, active poetry reading, or watching a film together (Anshel and Kipper, 1988). Likewise, Wiltermuth and Heath (2009) demonstrated that American students cooperate more after joint singing sessions compared to sessions without singing (Wiltermuth and Heath, 2009).

These wide-ranging prosocial effects of engaging in joint musical activities suggest that our brain may link synchronized actions to a change in social attitude towards the interaction partners. So far, however, the brain areas mediating this linking process remain entirely unknown. In Chapter 4 we provide evidence suggesting that this link may be provided by the brain's reward system, which is known to play a role in our ability to synchronize our actions with an external stimuli (Lewis et al., 2004; Rao et al., 1997; Repp, 2005; Wing, 2002), reinforcement learning (White, 2009) and the modulation of prosocial behavior (Baumgartner et al., 2008;

Delgado, 2008; King-Casas et al., 2005). We suggest that understanding the neural basis of the link between joint musical activity and prosocial behavior may shed light not only on important aspects of human culture but also on the mediators of joint actions.

1.2. Methods and Techniques

Functional MRI (fMRI) is a brain mapping technique developed two decades ago by modifying the structural or classical magnetic resonance imaging (MRI) technique. fMRI detects differences in the magnetic properties of haemoglobin when its configuration changes from the oxygenated to the deoxygenated state (Belliveau et al., 1992; Kwong et al., 1992; Ogawa et al., 1993). Under normal, resting conditions it is assumed that the cerebral blood flow (CBF) and cerebral blood volume (CBV) are regulated by neuronal activity. However, a striking feature of the metabolic responses to functional activation is that rising CBF/CBV uncouples from oxygen consumption (Belliveau et al., 1992). This uncoupling of CBF/CBV and oxygen consumption results in a decrease in deoxyhaemoglobin concentration in the venous pool, providing the blood-oxygen-level dependent (BOLD) contrast used in fMRI studies. By making use of BOLD contrast, fMRI provides an indirect means of assessing neuronal activity.

fMRI has several advantages over other brain imaging techniques. First, it noninvasively records brain signals without the risks associated with radiation exposure inherent in other scanning methods, such as X-ray Computed Tomography (CT) and Positron Emission Tomography (PET) scans. Second, it has high spatial resolution, typically 2–3 mm but resolution can be as good as 1mm. Third, it can record signals from all regions of the brain, unlike Electroencephalography (EEG) and Magnetoencephalography (MEG) which are biased towards recording from the cortical surface.

Although fMRI has been widely used for various fields of neuroscience, studying social interaction as an action related process is relatively challenging, due to the large number of stimulus repetitions required and artifacts resulting from head movements in the scanner. Here, I briefly summarize these two problems, which we encountered, and our efforts to solve them.

First, BOLD changes are typically only one percent above baseline (Ogawa et al., 1990). In order to detect these rather small signal changes it is important to repeat the measurements a large number of times. This necessity for many repetitions of the same stimulus can lead to artificial situations when studying social interactions. In order to overcome this problem, instead of repetitively presenting pictures or videos of social stimuli we asked our participants to interact continuously in real time with social agents (i.e. a game partner, a drummer). Moreover, to motivate our participants we asked our participants to be part of a game during which they could increase their earnings by cooperating with the experimenter.

Another problem that we faced was that, due to the inherent properties of the fMRI equipment, participants had to lie supine on the scanner bed as still as possible while carrying out actions. Even slight head movement may lead to severe reductions in image quality. In addition, upper-arm movements that evoke contractions in the

neck muscles may cause small head movements. Accordingly, we designed tasks involving small movements of the forearm and fingers only. Moreover, we stabilized the upper arms of our participants to avoid head movements yet allow our participants to move comfortably.

1.3. This Thesis

The recently developed line of research devoted to joint action has successfully challenged the traditional ways of studying perception and action in individual minds in isolation. With respect to investigating brains in interaction, a new challenge for social neuroscientists lies in finding ways to explore the neuronal processes underlying true social interactions despite the paradigm limitations imposed by the present brain imaging techniques. Therefore, with the current thesis we not only delineated the brain correlates of joint actions with fMRI, but also explored methods of enabling individuals to interact with other social agents as naturally as possible in the constrained fMRI environment. Hence, we investigated a range of joint actions from playing a simple cooperation game (Experiments 1 and 2) to drumming together (Experiment 3). Although the participants' tasks were experimentally constrained due to the nature of the technique, our experiments always involved real-time interaction with another person in order to keep the interaction as social as possible. These joint action partners varied from an experimenter standing next to the participant (Experiment 1), to a computer (Experiment 2) to drum partners (Experiment 3).

Moreover, we also made advancements in data analysis. In addition to traditional ways of data analysis, we employed an effective connectivity method to test the contribution of the MNS in joint actions in terms of effective connectivity between brain areas (Chapter 3). We did this by employing Granger causality mapping (GCM), which has recently been used to explore the directional information flow between brain areas. This exploratory work of mapping influences between brain areas may suggest a complementary method for neuroimaging studies investigating the neural correlates of joint actions. Therefore, this study not only provides further insight on the neural basis of the joint actions but also a significant methodological advance, that of employing effective connectivity to study social interactions.

In addition, we took the line of research investigating joint action one crucial step further by exploring the continuum from action to social behavior. Recently, interest in the behavioral effects of music making as a collective activity has surged. Many studies have demonstrated a link between joint action in musical context and a change in future social behavior. However, the neural signature of this link is still under-investigated. In the last chapter of this thesis we investigated this link with fMRI by measuring the neural processes associated with synchronized drumming in the reward areas (Experiment 3) and testing the effects of drumming together on social bonding with a prosocial commitment test performed immediately after the Experiment 3 (Chapter 4).

The results presented in this thesis may advance the present knowledge on the neural signature of social interactions, in particular joint actions, in three ways: First, by employing truly interactive paradigms in our first two experiments, we provide one

of the very first direct investigations of the neural basis of joint action, a topic that has previously been restricted to speculative theoretical papers and a few empirical studies (Chapter 2). Second, we shed new light on the contribution of the MNS to joint action by presenting empirical evidence on the information flow within the brain during joint actions (Chapter 3). Finally, we provide the first empirical evidence of both the neural foundation of acting together in a musical context and the subsequent change in prosocial behavior after joint musical activity (Chapter 4). To our knowledge this is not the first study investigating how social synchrony changes future prosocial behavior, but it represents one of the very first studies in which a link between actual prosocial behavior (helping a person pick up dropped pencils) and neural activity in the reward areas is measured. Therefore, it bridges a gap in the fractured literature of the life sciences: behavioural studies of musical behaviour across cultures and the emerging understanding of the neural basis of social reward and affiliation.

Outline of the Thesis

Chapter 1 introduces the concepts, terms and methods used in this thesis.

Chapter 2 presents the first two experiments of this thesis:

Experiment 1 explored the neural mechanisms involved in joint actions when two agents mutually coordinate their actions in real time while playing a cooperation game. For this game we used a custom-made MRI-compatible response box. This box had two arms made of fiberglass sticks resembling the hands of an analog clock, but with the hour hand and minute hands of equal length, was placed on the lower abdomen of the participant lying on the scanner bed. The cooperation game involved two actors: a participant in the scanner and an experimenter standing next to the scanner bed. Participants were able to see the entire response box (via the mirror of the head coil), their own fingers, and the experimenter's fingers. The participant's task was to manipulate his/her stick on the box simultaneously with the experimenter to create a geometrical shape (an angle or a straight line).

In detail, at rest, on the box the experimenter's stick pointed up (12:00 of an analog clock) and the participant's down (06:00). For each game/trial, before the start of actual movements, the experimenter received auditory instructions indicating where (left or right) and when to move her stick. The participant was unaware of these instructions, and received auditory instructions only indicating the final geometrical shape whether to create an angle or a straight line. Accordingly, the experimenter initiated the cooperation game by start pushing the top arm of the clock to the left or right with her index finger according to her instructions. Thereafter the participant pushed his/her stick with the index finger to a direction suitable to achieve the instructed geometrical shape. Actors had 2 seconds to complete the shape and they had to be virtually simultaneous (within 200 ms of each other to convey a mutual feeling of cooperation) while pushing their sticks in order a game/trial to be successful. We introduced this tight time constraint in order to ensure that the participant and experimenter monitors and coordinate the velocity of their movements carefully and continuously throughout the trial as both the spatial and temporal coordination define joint actions. This way, our laboratory paradigm resembled to

real-world joint actions such as lifting a basket together, where the velocity of actions have to be coordinated to avoid tipping over the basket.

In addition to the cooperation games, in the control conditions the participant was asked to (a) passively watch the experimenter moving her stick alone or (b) move his stick alone. With these control conditions we could identify the common voxels for both observation and execution, and thus map the putative MNS in our participants. This revealed that the pMNS involved in both (a) observation and (b) execution included the BA 44, BA 6, IPL and the middle temporal gyrus (MTG). Given that engaging in joint actions requires an integrative processing of two streams of information (visual input and motor output) corresponding to the two agents' actions depending on the task requirements, we mapped the brain areas specifically involved in this integration by comparing the activity during joint actions to the activity during the sum of solo action execution and observation. A network of brain areas showed evidence for this integration during joint actions; we refer to these regions as the integration network. The integration network included the prefrontal, posterior parietal and temporal lobe adjacent to the pMNS: in the frontal lobe the joint action clusters were anterior to those of the pMNS, while in the parietal lobe they were posterior to those of the pMNS. Voxels common to both networks were rare and restricted to the superior parietal lobe and the middle occipital gyrus (MOG). This suggests that, as opposed to previous claims, the integration of observed actions of others with one's own actions is likely to be computed outside of the pMNS in the frontal lobe (Kokal et al., 2009).

Experiment 2 tests whether the activity in the integration network would be as strong as the activity during a task that requires only one-way coordination (one agent adapts his/her behaviors to another). Our experimental task in Experiment 1 was a joint action task, in which two actors had to explicitly take each other's actions into account (mutual coordination). However, we suspected that the motor task this demanded of the participants might have been more complex and difficult in the joint actions conditions (cooperation game) than in the solo conditions (control conditions). For example, in clay pigeon shooting the shooter does not know in advance precisely where and when the clay will go and so has to track the movement of the clay. However, this is clearly not a joint action since the movement of the clay is entirely unaffected by the movement of the shooter. In Experiment 2, we implemented such a task in our paradigm and acquired brain activity while the participants cooperate with a human agent (two-way coordination) or react to the computer to shape the two sticks of the 'clock-like' device in an angle or a straight line (one-way coordination).

This time, movies of a virtual game box replaced the game box of Experiment 1 and were presented to the participants via a data projector on a screen that the participant could view through a mirror. The experimenter stayed in the control room not next to the participant. At the beginning of each game/trial, an index finger holding the edge of the lower stick appeared. After that, the participants controlled that virtual finger using an MR compatible joystick with their right index finger. For the games with the human agent, an index finger holding the edge of the upper stick appeared and the experimenter used her joystick in the control room to control the finger. For the games with the computer, no such finger appeared on the upper stick. For the computer condition, although the participant was led to believe that the

computer controlled the upper stick the experimenter actually controlled the stick, again using her joystick from the control room. The experimenter in the control room was able to view a clone of the movies viewed by the participant. The critical manipulation was that in the human condition, the experimenter viewed both the upper and lower halves of the screen, and could therefore adjust her actions to those of the participant, as in Experiment 1, while in the computer condition; the lower half was occluded, preventing her from reaching to the participants' actions. In the computer condition, the participant therefore had to coordinate his/her actions to those of the 'computer' to reach the target within 200 ms, but the computer (actually the experimenter) did not adjust its movements (one-way coordination).

We extracted brain activity in the peak voxels of the region of interests (ROIs) that we identified in Experiment 1 while participants played with the human agent and reacted to the computer, and then performed comparisons between conditions. Our results revealed that while playing with the human agent brain activity in both the integration network and the pMNS was higher than while playing with the computer. This suggests that, despite the presence of similar biological movement in both conditions (a human experimenter blind to the participant's actions actually played the role of the computer), these brain areas were sensitive to the presence of the mutual coordination that characterizes joint actions (Kokal et al., 2009).

In the previous chapter we concluded that the MNS does not, by itself, directly underlie our ability to integrate our own actions with those of others. In **Chapter 3**, we explored the functional role that premotor sites of the MNS may play in joint actions. By employing Granger causality mapping we demonstrated that the two functionally separate networks (the MNS and the integration network) identified in Chapter 2 were effectively connected. Thus, the MNS may not integrate the actions of the participant with those of the experimenter directly, but rather sends information to a network of regions that do. The MNS could thus play an indirect role by transforming the observed and executed actions into a single code and then sending this information to the brain areas responsible for integration. In addition, we identified predominantly backwards information flow from premotor to posterior regions such as the MOG, primary somatosensory cortex (SI) and the cerebellum. This backward information flow is compatible with forward models proposing that the premotor areas actually send predictions to the sensory areas, and shows that this backward flow can predominate under joint action conditions. This suggests that our brain seems to overcome sensory delays by relying on the predicted actions of others when engaging in joint actions (Kokal and Keysers, 2010).

Chapter 4 presents both an fMRI experiment (Experiment 3) investigating a special form of joint action, namely music making, and a behavioral test (prosocial commitment test) following the scanning sessions.

Every culture has some form of group musical activity. People chant together in churches, dance together in clubs and march together in armies. But why? Unlike sex or food, joint action in a musical context does not provide any obvious fitness advantage, so why is it so universal? To move towards an answer to this question we had people drum together with a drum partner while measuring the participant's brain activity using fMRI. The participants drummed a simple rhythm, in alternating blocks, with two experimenters: one drummed in-synchrony and the other drummed out-of-

synchrony relative to the participants (Experiment 3). After the experiment, we measured the effect of synchronized drumming on ‘real-life’ prosocial behavior, by ‘accidentally’ dropping eight pencils in front of the participant and counting the number of pencils the participant picked up to help the experimenter (prosocial commitment test).

We hypothesized that reward areas would be active when individuals are in synchrony with a drum partner (joint drumming), and that these reward signals would facilitate prosocial commitment among drum partners. First, our results revealed that the caudate within the reward system was more active during joint musical activity (synchronous drumming) than asynchronous drumming. Second, in line with previous behavioral studies, participants helped the experimenter who drummed in synchrony with the participants more than the asynchronous one. Importantly, how much they helped was predicted by the amount of activity in the caudate during joint drumming. This demonstrates how the reward system can create a bridge between musical joint activities such as synchronized drumming and prosocial behaviour (Kokal, et al., under review).

Chapter 5 discusses and integrates the main outcomes of this thesis and their implications on further research.