5. Conclusion

This thesis explored how our brain processes joint actions with truly social paradigms, in which a participant directly interacted with another agent or believed to interact with one. We delineated brain areas that play a role in a series of social tasks performed during functional Magnetic Resonance Imaging (fMRI) experiments in which participants (1) engaged in joint actions with an experimenter standing next to them during a cooperation game, (2) played the same game with a computer, and (3) drummed a simple rhythm with a drum partner (Chapters 2 and 4). By employing Granger causality mapping (Chapter 3) and exploring the information flow from and to the anterior sites of the Mirror Neuron System (MNS) during our cooperation game, we gained further insight into the contribution of the MNS to joint actions. In addition to investigating the neural substrates involved when a participant acts together with an agent, we also tested how this activity relates to the actual social behavior of the drum partners (Chapter 4). This chapter briefly summarizes the results of the experiments and discusses their implications.

Moving a set dinner table often takes two people, and in doing so requires the close coordination of actions between two agents. A number of studies have proposed that the MNS is involved in responding to the actions of others by doing the same as they do (imitation) (Iacoboni et al., 1999), as well as complementing others’ actions (Newman-Norlund et al., 2007b). Hence, some have argued that the MNS could promote joint actions by integrating one’s own actions with those observed while individuals act together (Knoblich and Jordan, 2002; Newman-Norlund et al., 2007a; Newman-Norlund et al., 2007b; Sebanz et al., 2006; Sebanz et al., 2007). However, we argue here that during a typical joint action, unlike imitation, the task determines the nature of this integration which can vary depending on whether one is carrying out an action that is the same or opposite to that of a partner (Kokal et al., 2009). Therefore, the integration of observed actions of others with one’s own actions necessary in joint actions has to be more flexible than previously thought. As opposed to previous claims, we presented evidence demonstrating that the integration is computed outside of the MNS during our cooperation game.

The first fMRI experiment of this thesis investigated the circuitry involved in task-dependent integration of observed and executed actions that distinguishes joint action from action observation and execution performed in isolation. In particular, we tested the degree to which this process occurs within or beyond the MNS (Chapter 2). To do so, we created a real-time joint action paradigm in which participants acted together with an experimenter in shaping sticks of a game box to create a geometrical shape (joint action conditions). Depending on the goal of the trial (i.e forming an angle or a straight line respectively), in some trials the participant performed a similar action to that of the experimenter and in some trials he/she performed the opposite actions. In addition, the participant (a) passively watched the experimenter moving her stick alone or (b) moved his/her stick alone. Identifying the common voxels for both (a) observation and (b) execution, revealed activity in the putative MNS (pMNS) of
our participants corresponds to those areas previously reported in the literature such as; the premotor (BA6, BA44), parietal (SI, SII, IPL) and high-level visual areas.

Given that engaging in joint actions requires the 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 action observation and solo execution. We formulated this as follows: if integration > 0 then (joint action = observation + execution + integration) > observation + execution. A network of brain areas (integration network) showed evidence for this integration process in the prefrontal, posterior parietal and temporal lobe adjacent to the pMNS. Although both the integration network and the pMNS were in anatomically similar locations, voxels common to both networks were rare and restricted to the superior parietal lobe (SPL) and the middle occipital gyrus (MOG). Importantly, there was no overlap in the premotor cortex between regions showing evidence of integration and the pMNS. This suggests that, as opposed to previous claims, the integration of observed actions of others with one’s own actions during joint actions is likely to be computed outside of the pMNS in the premotor cortex (Kokal et al., 2009).

Further investigation of the functional properties of the pMNS in joint action conditions using region of interest (ROI) analysis revealed significant activity above baseline in all ROIs of the pMNS. This suggests that although the pMNS is not involved in the integration process directly, it nevertheless plays a role in joint action. Therefore, we proposed that joint action might be a dual process: the MNS transforming the observed actions into representations of similar actions (common code) allowing one to tune his/her actions to the expected actions of the other without lagging behind due to the latencies of the visual and motor systems. The integration network, on the other hand, seems to play a role in utilizing these common codes to select the most adequate action in order to flexibly tune one’s own actions to those of others.

These results are in line with the theoretical papers re-evaluating strong claims previously made about the key role of the MNS in grounding joint actions. In an influential paper, Pacherie and Dokic (2006) argue that the MNS cannot, by itself, provide a sufficient basis for our ability to engage in joint action. They claim that the function of the MNS might be to provide better control of one’s own actions and the understanding of other’s actions (Gallese, 2003) thus facilitating joint action control when individuals adjust their actions to those of others (Pacherie and Dokic, 2006). Likewise, Knoblich and Jordan (2002) propose that the simple perception-action matching provided by the MNS itself cannot be enough for successfully coordinating our actions with others (Knoblich and Jordan, 2002). They point out a necessity of additional machinery to modulate one’s own actions in response to perceived effects of other’s actions. We suggest that the integration network that we identified in Chapter 2 might be the neuronal signature of this additional machinery.

While the results of Experiment 1 revealed a network of brain areas (integration network) that are involved in the integration of a visual input and a motor output, we cannot distinguish whether this integration activity is specific for the mutual coordination that defines joint actions or whether it could be just as strong
during a task requiring only one-way coordination. Therefore, to examine whether the brain areas identified in Experiment 1 are sensitive to the mutual coordination, in Experiment 2 we scanned half of our participants a second time. Participants played the same cooperation game with an experimenter who a) adapted her actions to those of the participant (mutual coordination, true joint actions) or b) with a computer that did not (one-way coordination). By examining the activity in all ROIs of Experiment 1, we showed that brain activity in all brain areas within the integration network and the MNS were stronger while cooperating with a human agent in comparison to playing with a computer. This shows that despite the presence of similar biological movement in both conditions (given that the experimenter who was 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 (Kokal et al., 2009). The presence of a human finger in the display, the belief to be playing with a human agent and/or the contingency that participants detected between the human agent and their own actions (mutual coordination) must have made both networks sensitive to the presence of the social loop that characterizes joint actions (Liepelt et al., 2008). Furthermore, our results cannot be explained by the participants paying less attention to the actions of the computer, as the number of correct trials did not differ in the two conditions, nor can it be explained by differences in the time spent moving with the human agent or the computer, as the playing time did not differ significantly.

In Chapter 2, we presented evidence suggesting that the anterior sites of the MNS do not play a direct role in the integration of observed and executed actions. In Chapter 3, we focused on testing the contribution of the MNS in joint action with a different method: Granger causality mapping (GCM). We employed GCM on our fMRI data and explored the directed information flow between the anterior sites of the MNS (BA 44 and BA 6) and the brain areas previously identified in Experiment 1.

GCM of fMRI data employs a differential Granger approach (Roebroeck et al., 2005). Simulations have shown that GCM applied to fMRI signals cannot accurately infer whether information is sent from one region to another per se, however it can establish whether more information is sent from one region to another than vice versa (Roebroeck et al., 2005). By following this approach, our results revealed three main findings (1) effective connectivity between the BA 44 and BA 6 and the integrative areas, (2) the predominant direction of these effective connections, and (3) the contribution of the cerebellum in joint actions.

First, when analyses were confined to the joint action blocks, we found significantly more Granger causality (GC) from voxels within the left BA 44 (part of the MNS) to voxels within the right MOG, left thalamus, left cerebellar vermis and right cerebellum (within the integration network) than vice versa. Similarly, the GC was significantly larger from voxels within the left BA 6 (part of the MNS) to the voxels of the left cerebellar vermis (within the integration network) than vice versa (Kokal and Keysers, 2010). This implies that these two functionally separate networks are effectively connected in the service of joint actions. In addition, a direct comparison calculated between the Granger Causality maps (GCMs) relating to the joint action versus the execution blocks revealed significant differences in the GCMs originating from the left BA44 voxels to voxels within the bilateral cerebellum (these values were significantly larger during joint action blocks compared to execution.
blocks). This demonstrates that the directed influence of the left BA44 on bilateral cerebellum was significantly stronger during joint actions than during execution. This implies that the information transfer between the left BA 44 and bilateral cerebellum is specific for cases in which participants need to coordinate their own actions to those of the experimenter rather than acting alone. Similar direct comparison of GCMs between joint action and observation blocks did not reveal any significant difference.

In the context of our results from Chapter 3, when an individual needs to coordinate his/her actions with the sight of another individual’s actions (e.g. while creating a straight line on our game box), this task would be computationally more demanding if the participants’ own actions were represented in a different code to those of the observed agent, and less demanding if they were represented in the same code. The MNS seems to facilitate the role of the integrative brain areas by representing the participant’s and the experimenter’s actions in the same code (Etzel et al., 2008). According to our results, the anterior sites the MNS (left BA 44 and BA 6) play an indirect role in the integration process by feeding information into the areas that are part of the integration network. This suggests that the MNS and the integration network work in concert during joint actions.

Furthermore, recent reviews (Caspers et al., 2010; Keysers et al., 2010) provide strong evidence for the fact that BA2 is systematically activated while we perform and observe the actions of others. We found that the left BA 44 evidenced significant positive dGC values with bilateral BA 2 (localized within SI of the MNS) during joint action conditions but not solo conditions (observation and execution). Thus, this suggests that the left BA 44 not only sends information to the integration network but also to the posterior sites of the MNS during joint actions. This information flow between the BA44 and the BA2 suggests that the motor and somatosensory representations interact during joint actions.

Another main finding of Chapter 3 was the predominant direction of the effective connections during joint actions. Our results revealed predominantly backwards information flow (i.e. from frontal left BA44 to more posterior areas: bilateral BA2, right MOG etc). This suggests that the premotor areas send more predictions to the sensory areas than the other way around when one engages in joint actions with another agent. This is compatible with the increasingly prominent concept of forward models (Gazzola and Keysers, 2009; Keysers and Perrett, 2004; Kilner et al., 2007; Kilner et al., 2004; Miall, 2003; Wolpert et al., 2003; Wolpert and Miall, 1996). Given that it takes approximately 200–300 ms to respond to a stimulus (Adam and Van Veggel, 1991; Michie et al., 1976) and that, when acting together with another agent, our actions would lag several hundreds of milliseconds behind the perceived actions of our partner, it seems likely that, the MNS acting as a forward model plays more of a role in overcoming the sensory delays by relying on the predicted somatosensory and visual consequences of observed and executed actions of others. This finding has been recently supported by another study where premotor regions also sent more information to visual areas than the other way around during gestural communication task, a task employing skills similar to those needed for joint action (Schippers and Keysers, 2010).

Finally, in this chapter we found that both left BA44 and BA6 sent more information to the cerebellum, than they received from it (Kokal and Keysers, 2010).
The cerebellum is known to play crucial role in motor control and is thought to be part of the forward model (Blakemore et al., 2001; Blakemore and Sirigu, 2003; Dum and Strick, 2003; Kawato et al., 2003; Stein and Glickstein, 1992). During motor control, the convergence of input from the premotor cortex and sensory structures makes the cerebellum an ideal site for calculating in real time the error between intended and actual movement, and using this error to improve motor performance (Wolpert et al., 1998). The fact that the cerebellum receives more input from the premotor cortex during joint actions compared to solo motor execution suggests that the cerebellum is of greater importance during actions performed with others such as joint actions than those performed singly. These findings emphasize that the cerebellum merits more attention in understanding of the neural correlates of joint actions.

In summarizing the results of Chapter 3 we presented the first empirical evidence, to our knowledge, demonstrating predominantly backwards information flow from the anterior sites of the MNS to the posterior (sensory) areas such as the SI and MOG during joint actions. In addition, we showed that the cerebellum is effectively connected with the premotor areas of the MNS when adjusting our actions to others’.

After gaining insight into the neural signature of a simple type of joint action (i.e. moving an arm of a clock-like device together with another agent), we extended our research to a different type of joint action, namely music making. In Chapter 4, we described an fMRI experiment together with a prosocial commitment test that investigated the neural mechanisms underlying interpersonal synchrony and its subsequent affiliated effects among synchronized individuals, respectively. Our aim was to test the prediction that the caudate plays a major role in linking the experience of being in synchrony to that of the brain’s reward system, modulating the future prosocial behavior. The striatum, in particular the caudate, has long been implicated in processing both social and monetary reward (Delgado et al., 2004; Izuma et al., 2008; Saxe and Haushofer, 2008), modulating prosocial behavior (Delgado, 2008; Kosfeld et al., 2005) and voluntary motor control especially during tapping with an external stimuli (Grahn and Brett, 2007). Thus, separate studies place the caudate at the intersection between two phenomena relevant to the question at hand: 1) the capacity to synchronize with others, and 2) modulations of prosocial behavior via the reward system. However, prior to the study presented in Chapter 4 it had not been addressed whether the reward system, in particular the caudate, modulates prosocial behavior following synchronized activity.

We measured neural activity in the caudate, which we showed to respond to monetary reward in the same participants, while manipulating the degree of synchronicity between drum partners in a social drumming task. During this task, participants believed to drum with one of two co-drumming experimenters in alternating blocks in the MR scanner. One co-drummer was in-synchrony and the other out-of-synchrony relative to the participants during scanning. Our last run of the fMRI experiment was designed as a manipulation run in which only one experimenter drummed continuously with half of the participants in- and with the other half out-of-synchrony. After scanning, the same experimenter ‘accidentally’ dropped eight pencils in the proximity of the participant and the participant had a choice to behave
altruistically or not. We used the number of pencils collected by the participant as a measure of prosocial commitment.

The prosocial commitment test results revealed that the participants collected more pencils to help the drum partner when she drummed synchronously compared to when she drummed asynchronously with the participants before the test, during scanning. Our fMRI results revealed that synchronized drumming does trigger activity in a reward area, the caudate. In addition, the activity in the caudate during synchronized drumming in the scanner predicted the number of pencils the participant later collected to help her drum partner (Kokal, under review). These results imply that our brain transforms synchronized activity into basic reward activity, and this then, through the caudate, influences future decisions to act altruistically towards the person with whom the synchronized activity is performed. This reveals that the caudate might be the mediating structure that links the synchronized actions performed with others and the prosocial effects of engaging in joint musical activities. This provides a hint for why synchronized activity and its affiliated effects are wide-ranging in many cultures by showing that it ties into the basic reward system, just as money does.

In Chapter 4, we used music making in a social context because this activity is more amenable to the scanner environment than other cases of synchronized actions (marching, rowing etc). Our results might not be specific to synchrony in music but may apply to any forms of temporally coordinated (synchronized) actions in general. We expect that similar effects might exist for non-musical activities such as rowing in synchrony (Cohen et al., 2010), or making similar bodily movements (van Baaren et al., 2004). This possibility should be tested in future experiments using non-musical tasks.

Last, in Chapter 4 we investigated not only the behaviour outcome of synchronized actions but also the neural mechanisms that link the joint musical activity with the prosocial behaviour. Hence, our study is a pioneer in bridging different but related research questions and methods in one study. Although we recruited a sufficient number of participants for a conventional fMRI study (18 participants), discovering that the results were dependent on individual differences in rhythm imitation introduced the challenge of applying correlational analyses to only half of our participants leading to a moderate effect size. Albeit this fact, we reported the trends and marginally significant results in addition to the significant ones to inspire future studies with new hypotheses to test.

Outlook

“Individuals possess a remarkable ability to coordinate their actions with others to reach common goals” (Sebanz et al., 2006). With the accumulation of knowledge in the last decade, we are just beginning to understand the underlying mechanisms of this remarkable ability. Nonetheless, we have to underline that further research extending our knowledge about the functional properties of the brain areas reported in this thesis is crucial. We hope that the empirical evidence that we presented in this thesis will contribute to the understanding of the neural basis of medical conditions characterized by deficits in social interactions.
Over the last years, interest in the behavioural study of social music-making and the neural basis of social reward has surged as separate disciplines. In Chapter 4, we combined neuroimaging methods with an actual behavioral test in which we could investigate both neural underpinning of musical joint actions and prosocial behaviour in one study. Hence, we bridged a gap between fractured literatures in the life sciences: the study of musical behaviour and the emerging understanding of the neural basis of social reward and affiliation. We hope other researchers will follow our approach and shed more light on the understanding of the neural basis of prosociality in relation to joint activity. Although we believe in the generality of our results of this study, further research empirically testing joint actions that are not musical is crucial.