Joint Action: Neurocognitive Mechanisms Supporting Human Interaction

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Abstract

Humans are experts in cooperating with each other when trying to accomplish tasks they cannot achieve alone. Recent studies of joint action have shown that when performing tasks together people strongly rely on the neurocognitive mechanisms that they also use when performing actions individually, that is, they predict the consequences of their co-actor’s behavior through internal action simulation. Context-sensitive action monitoring and action selection processes, however, are relatively underrated but crucial ingredients of joint action. In the present paper, we try to correct the somewhat simplified view on joint action by reviewing recent studies of joint action simulation, monitoring, and selection while emphasizing the intricate interrelationships between these processes. We complement our review by defining the contours of a neurologically plausible computational framework of joint action.

Keywords: Joint action; Error monitoring; Goal-directed behavior; Cooperation-competition

1. Introduction

As many casual sports fans have undoubtedly noted when watching their favorite players, human beings are remarkably skilled in adapting their own behavior to that of others. Take the example of playing doubles in tennis. At the start of a rally, the player at the receiving end is usually quite able to anticipate the end location of his or her opponent’s service, thus starting to prepare the return strike long before the ball actually arrives. In the midst of a
rally the situation is no less demanding. The shared decision of who will counter a particular volley is a delicate decision that can easily result in an error when either the partner’s location, posture or movements, or combinations of these, are misjudged. This sports example illustrates an important characteristic of the complexity of joint action. Successful performance in a joint action task requires accurate perception of peripheral actors, as well as accurate predictions regarding the consequences of these actions. Action simulation plays an important role here. Depending on whether the co-actor is friend or a foe, one’s action monitoring system may adopt different criteria to arrive at an appropriate conclusion. Finally, the perception and prediction of other’s behavior have immediate implications for one’s own action selection system because, depending on the output of action simulation and action monitoring processes, a suitable action must be selected from multiple possible alternatives.

In the present paper we will highlight the abovementioned three components: action simulation, action monitoring, and action—selection of joint action. First of all, we claim that task-specific practice must have an impact on motor simulation. Typically, it takes a long learning period to be able to anticipate the final location of a 145-mph serve and respond appropriately. Indeed, it is likely to presume that one’s own motor expertise in a particular task domain provides a basis for one’s perceptual skills in detecting and recognizing nuances in the behavior of one’s opponent and to predict the consequences of these behavioral nuances. Second, we emphasize the crucial role of context-sensitive action monitoring in joint action, which involves keeping track of one’s own task performance and the behavior of a collaborator, competitor, or both. Third, and finally, we will emphasize the critical role of action selection processes in joint action. In particular, joint action is typically not always about imitation. Obviously, when playing tennis you cannot return a service with a similar service motion. Instead, the appropriate response in the case of a 145-mph serve is the kinematically distinct forehand punch return.

After having described recent studies that cover the three elements of joint action briefly alluded to above, we tentatively formulate the contours of a new neurocognitive model of joint action that, framed in Bayesian statistics and thus emphasizing bottom-up belief propagation as well as top-down hypotheses testing and priming effects, complements current theoretical views on joint action.

2. Action simulation

Does the expertise of an observer affect the way in which he or she perceives the actions of others? Acquired motor skills offer a unique way to test this issue, since people differ widely in the actions they have learned to perform. In particular, sport scientists have examined in detail at which level expertise helps us to perceive and understand the behavior of others. For example, a recent review paper showed that experts are better than nonexperts at picking up perceptual cues, as revealed by measures of response accuracy and response time (Mann, Williams, Ward, & Janelle, 2007; see also Shim, Carlton, Chow, & Chae, 2005). Interestingly, experienced tennis players were found to react faster than novices when they
returned balls hit by a live opponent, but not when they returned balls projected from a cloaked ball machine. This example nicely illustrates the idea that observation of another actor, whose actions and goals one can model, is critical to accurate anticipation of actions (cf. Bobick, 1997). Although the effects mentioned above are typically described at a perceptual level, that is, expertise improves the quality of the perceptual system involved, an alternative view is offered in terms of motor resonance.

In a series of functional magnetic resonance imaging (fMRI) studies, Calvo-Merino, Glaser, Grèzes, Passingham, and Haggard (2005) and Calvo-Merino, Grèzes, Glaser, Passingham, and Haggard (2006) compared brain activity in experts in classical ballet, experts in capoeira, and nonexpert control subjects while they viewed videos of ballet or capoeira actions. Comparison of brain activity during observation of their own dance style with observation of the other, unknown style, revealed significant differences in activation at bilateral sites in the premotor cortex and intraparietal sulcus, as well as right superior parietal lobe and left posterior superior temporal sulcus. These differences were presumably due to the fact that expert dancers had been trained in one set of movements but not in the other. In a second study these authors asked whether this effect was related to specialized motor representations or rather general processes of visual inference and knowledge used to understand the observed actions. Male and female dancers viewed videos of gender-specific male and female ballet moves. Given the fact that some ballet moves are performed by only one gender, but that male and female dancers train together, ballet dancers were presumed to have equal visual familiarity with all moves, but greater motor experience with gender-specific moves. Again, observation of moves from one’s own motor repertoire resulted in significantly greater premotor, parietal, and cerebellar activity when compared to opposite-gender moves that participants frequently saw but did not perform. These results fit nicely with ideas propagated lately about a possible human mirror neuron system (see Fig. 1A). Mirror neurons are a particular class of sensorimotor neurons, originally discovered in area 342.
F5 of the monkey premotor cortex, that discharge both when the monkey does a particular action and when it observes another individual (monkey or human) doing a similar action (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). Thus, the neuron “mirrors” the behavior of another animal, as though the observer were itself acting. These neurons have been directly observed in primates and are believed to exist in humans (Iacoboni, Woods, Brass, Bekkering, Mazziotta, & Rizzolatti, 1999) and other species, including birds (Miller, 2008).

In humans, brain activity consistent with mirror neurons has been found in the premotor cortex and the inferior parietal cortex. The studies of Calvo-Merino and colleagues suggest that brain areas in the human mirror system respond purely based on motor experience, over and above any visual representations of an action. In other words, we understand actions not only by visual recognition but also in a strictly motor sense. In a recent study, we extended this finding to the natural development of actions in infants.

To investigate the effect of natural motor experience on motor resonance during action observation, 14–16-month-old infants’ electroencephalograms (EEG) was recorded during observation of action videos (Van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008). Stronger mu- and beta-wave suppression by measuring spectral power decreases in the mu-frequency band (7–9 Hz and beta-wave 17–19 Hz band, respectively) was found for observation of crawling compared to walking videos and the size of the effect was strongly related to the infant’s own crawling experience, suggesting that already early in life one’s own action experiences determine how one perceives the world.

In summary, there is increasing evidence that the mirror system integrates observed actions with actions which already exist in an individual’s own personal motor repertoire. Moreover, the data reviewed here support the claim that we understand the actions of others by means of motor simulation. Importantly, experience not only enables motor simulation but is also a crucial condition for efficient performance in general as it makes the detection of errors in ongoing behavior possible. More research needs to be undertaken to find out how personal experience changes the way we perceive others’ actions. In particular, the kind and amount of expertise and whether motor experience is crucial, or whether also perceptual experiences might enhance activity within the mirror neuron circuitry is a topic hardly understood yet (i.e., Beilock, Lyons, Mattarella-Micke, Nusbaum, & Small, 2008).

3. Action monitoring

Our everyday experience teaches us that human behavior is fallible. We trip over curbs, drop fragile objects, forget to attach promised documents to an e-mail, and fail to return tennis serves. Importantly, however, the detection of our own errors leads us to engage in corrective or adaptive behaviors. We immediately send a second e-mail that does include the attachment and when we fail to return a tennis serve, we tend to pause, re-evaluate the preceding moments, and adjust our behavior in order to minimize the chances of making the same error in the future. In light of the joint action theme of this paper we will discuss investigations into the question of whether the system responsible for these corrective or
adaptive behaviors is also engaged when we observe errors in others. As a viewer of a professional tennis match, do we adjust our own models of the players even though this behavior has no obvious function in our lives (except maybe predicting the outcome of a game or recognizing changes in strategy)? In addition, we address the question of whether the system that initiates remedial actions is flexible. Does the social context in which an action is embedded influence the type of corrective actions we initiate following the observation of errors? In particular, do we react to another person’s error in the same way when this person is not a friend, but rather someone whose errors we enjoy?

Flexible adaptive behavior following one’s own errors in humans has been investigated experimentally using speeded choice-reaction-time tasks. In these tasks, errors are usually the result of responding prematurely. Hence, an appropriate adaptive response to improve performance is to take extra time to process the next stimulus and prevent a similar mistake, an adaptive behavior known as posterror slowing (Rabbitt, 1966). Correct responses following impulsive erroneous responses are usually slower than correct responses that follow correct responses. Posterior slowing will be one of the main measures of interest in the subsequent review on action monitoring in joint action.

Recent EEG and fMRI studies have demonstrated that the posterior medial frontal cortex (pMFC including anterior cingulate and pre-SMA, see Fig. 1B) plays a key role in the detection of errors and in subsequent behavioral adjustments. The error-related negativity (ERN) (Falkenstein, Hohnsbein, Hoormann, & Blanke, 1991; Gehring, Goss, Coles, Meyer, & Donchin, 1993), a component of the event-related brain potential generated in the medial frontal cortex, occurs following errors, and its amplitude is related to the amount of posterror slowing (Debener et al., 2005; Gehring et al., 1993). Interestingly, an ERN is also found when people observe another person making an error, suggesting that the detection of one’s own and other’s errors (observed errors) is mediated by similar neural mechanisms (van Schie, Mars, Coles, & Bekkering, 2004).

In a recent study by Schuch and Tipper (2007), participants either performed a reaction-time task or observed another person performing the same task in an alternating fashion. The results showed that people not only slowed down following their own errors but also when they observed their co-actor perform erroneously, demonstrating posterior slowing in response to observed errors. These results suggest that similar remedial strategies are engaged by own and observed errors. E. R. A. De Bruijn, R. B. Mars, H. Bekkering, and M. G. H. Coles (unpublished data) took this idea one step further and studied the relationship between posterior behavior following own and observed errors in a social speeded choice-reaction task in cooperative and competitive contexts. Whereas own errors are always negative events, observed errors may be negative or positive depending on the context in which the interaction takes place. Observing errors by one’s opponent in a competitive context is actually a good thing. As expected, the results from the study by De Bruijn et al. showed that in both contexts people slow down following their own errors. Also, a strong correlation between posterior slowing following own and observed errors was found in the cooperative context, demonstrating that those subjects who showed large posterior slowing after their own errors also showed posterior slowing after observed errors. This relationship between own and observed posterior slowing in a cooperative context strongly
suggests that similar mechanisms may underlie these remedial actions. However, in a competitive context, the opposite pattern was found. People accelerated after observing their competitor making an incorrect response. This acceleration may be resulting from the competitive speed instructions and thus reflect the preference for speed over accuracy in this context. Indeed, response times in general were faster in the competitive than in the cooperative context supporting such preference but more research is needed to address this question. So, although the exact nature of this acceleration is currently unknown, the study clearly demonstrates that the social context in which a joint action is performed determines the formalization of adaptive behaviors.

Importantly, these recent outcomes demonstrate that the functional systems that feed into remedial-action systems to regulate adaptive behaviors are highly flexible and that they play a central role in optimizing performance not only in individual tasks but also in social tasks. These systems may thus crucially underlie social adaptive behavior, which enables people to respond flexibly to other people’s actions in a wide variety of social interactions and thus facilitate goal-directed behavior in joint actions.

In a series of studies by Sebanz, Knoblich, and Prinz (2003, 2005) and Sebanz, Knoblich, Prinz, and Wascher (2006), participants performed either a task on their own or together with a co-actor. The authors repeatedly demonstrated that knowledge about a co-actor’s task affected reaction times in joint action. Apparently, people not only form representations about their own task but also about the co-actors task and the results indicate that these so-called shared representations may affect one’s own actions. The recent study by De Bruijn, Miedl, and Bekkering (2008) investigated the effects of shared representation in a competitive context, in which it was beneficial to not incorporate the action plan of an opponent, as this would only slow down responses and thus competitive performance. The results showed that in joint action people may differ in the extent to which they incorporate the actions of the other, ultimately determining the success in a competition. Apparently, when the actions of the other interfere with one’s own action plan, some people are efficient in blocking out or ignoring the actions of the person they are interacting with. These participants experienced only little interference of their opponent’s task. Other people, however, seem to take the actions of the other into account even though this may lead to unsuccessful performance. The authors hypothesized that personality characteristics may underlie these individual differences in incorporating other’s actions. It is plausible that people who, for example, score higher on empathy may have increased awareness of the other’s task. Alternatively, modulations in awareness of the other’s task may be the result of performance during the task itself. For example, when one is always responding slower than their opponent, awareness of the other’s task may increase. Additionally, the correlation analyzes from the above study revealed large individual differences in the amount of posterior slowing. Similar individual differences were also recently demonstrated (De Bruijn et al., 2008) while investigating the effects of another’s task knowledge on one’s own actions. Future studies should focus on unraveling the mechanism of individual differences in shared representations.

The previous study showed that context appears to impact the way we adapt to observed errors. But does the neural response to an observed error also vary as a function of context? Two recent fMRI experiments investigated this issue. In the first experiment, the neural
response to observed and executed errors in competitive and cooperative situations was tested (E. R. A. De Bruijn, F. P. de Lange, D. Y. von Cramon, & M. Ullsperger, unpublished data). Depending on their own and their partner’s performance as well as the context of the interaction, participants gained or lost money. As a result, observed errors in the cooperative context yielded a loss of reward, while observed errors in the competitive context resulted in a gain. As could be expected based on results from previous EEG studies, the fMRI data for the cooperative context demonstrated increased activity in pMFC for own and observed error processing. Importantly, activity in this area was error specific and independent from reward. Even when participants observed their competitor make an error and thus gained money, this area was activated. On the other hand, activations in specific areas in the basal ganglia known to be involved in reward processing were error independent. These areas were only activated for the best possible outcome in the two contexts: performing correctly in the cooperative situation and observing an error in the competitive context.

In the second fMRI experiment, participants who were strong fans of their national soccer team (in fact, all students in Nijmegen, an interregional university city including many students who either strongly favor the German national soccer team or the Dutch national soccer team) viewed virtual penalty shootouts which pitted their national team against a rival team (Newman-Norlund, Ganesh, van Schie, De Bruijn, & Bekkering, in press). Brain responses to errors made by both teams were recorded and compared. Analyses of these data revealed that error-specific brain activity at two specific sites in the pMFC did vary based on the degree of support to a specific national team. However, a third site in the pMFC was found to respond more strongly when a friend missed as compared to when a foe missed. These recent findings suggest that humans use similar mechanisms in joint action to detect errors and generate adaptive behavior as in individual action. However, the studies also demonstrate that the social context in which errors are observed does influence the brain’s response to their commission.

In sum, the recent studies on own and observed error detection in joint action demonstrate that humans use similar cognitive and neural mechanisms during both types of tasks. However, the flexibility of the remedial-action system is such that humans do not simply imitate other’s actions in these situations but are able to perform goal-directed behavioral adjustments specifically tailored to the context in which the interaction takes place. These flexible responses to own and observed errors may facilitate the efficiency of joint actions. Flexible adaptive behavior is also reflected in the performance of complementary actions, a specific class of movements prevalent in joint action which we will discuss next.

4. Action selection

The recent explosion in social cognitive neuroscience in general and the study of joint action in particular, has led to a reevaluation of the way we look at the processes governing action selection in complex social environments. Whereas much previous research had focused on imitation as a critical capacity supporting human social interactions, it is actually nonimitative or complementary responses that are especially critical to joint action in
social situations. Engaging in joint action is made possible by capacities for the immediate, noninferential apprehension of others’ activities, emotions and goals (e.g., Sebanz, Bekkering, & Knoblich, 2006). But how do we calculate the appropriate response to a tennis shot which, via the movements of an opponent, is imparted with a particular spin and trajectory if we can not directly copy the observed action?

A pair of recent fMRI experiments designed to test the brain basis of complementary actions have revealed a startling answer to this question. In the first experiment, participants were scanned while preparing to grasp a manipulandum in one of two ways (power or precision grip) after viewing an actor grip the same manipulandum using either a power or a precision grip. Action planning activated the typical action execution network, including bilateral superior temporal gyrus, inferior parietal lobule, and inferior frontal gyrus. Compared to preparation of imitative actions, preparation of complementary actions resulted in increased blood-oxygen-level-dependent (BOLD) signal in the right inferior frontal gyrus, and bilateral inferior parietal lobule (Newman-Norlund, Van Schie, van Zuijlen, & Bekkering, 2007), two core components of the mirror system. In a second experiment, participants lifted and balanced a virtual bar either alone or together with a partner. Joint bar lifting, a process already shown to involve the generation of complementary behaviors in cooperating individuals (Bosga & Meulenbroek, 2007), resulted in greater BOLD signal in the right inferior frontal gyrus (Newman-Norlund, Bosga, Meulenbroek, & Bekkering, 2008).

Taken together, data from these experiments suggest that joint action relies heavily on brain areas that possess response properties quite similar to those of mirror neurons previously reported in primates. One possible explanation for this finding is that joint action conditions depend disproportionately on the activity of broadly and noncongruent mirror neurons, neurons which link nonidentical percepts and actions. In fact, Gallese et al. (1996) discriminated between three categories of mirror neurons: strictly congruent, broadly congruent, and noncongruent. Mirror neurons of the strictly congruent variety responded to observed and executed movements that corresponded both in terms of general action (e.g., grasping) and in terms of the way in which that action was executed (e.g., precision grip). In addition to strictly congruent neurons, Gallese et al. (1996) observed broadly congruent mirror neurons which they divided into three subgroups. Each type of broadly congruent neuron responded to a variety of grips or actions, and consequently no commonality in their response profile could be found at the level of grip. Instead, shared properties could be found one level up, at the level of actions, category of actions (hand-actions vs. nonhand actions for instance), or action goals (these neurons appear to respond to the goal of an action and are indifferent to the means by which this goal is achieved).

Even less strictly defined are the so-called noncongruent mirror neurons that seem to show no clear-cut relationship between the observed action and the movement of the monkey. Hence, at first sight no common property seems available in their response profile. However, when the level of abstraction is raised to the level of object-related versus nonobject-related actions these neuron can be considered congruent and representational again, as mirror neurons only respond to object-related actions, and not to, for instance, mimed actions. The representational content of this type of neurons can thus be characterized as object-related actions. Although it is tempting to suggest that imitation might be
revealed by strictly congruent mirror neurons, whereas joint action depends on broadly and noncongruent mirror neurons, mirroring as a form of representation lacks a principled restriction and a wide variety of content attribution can result from this (S. Uithol, W. F. G. Haselager, I. Van Rooij, & H. Bekkering, unpublished data). Alternatively, it may be that joint action requires more robust and/or more extensive simulation processes as compared to individual action. This could be due to simulation of multiple possible actions (e.g., those of oneself and another) or the simulation of multiple possible responses to a single observed action.

The studies of Newman-Norlund et al. (2007, 2008) also raise the intriguing possibility that joint action preferentially recruits right lateralized components of the mirror system. But why might this be? Are there core differences between the functions carried out by left and right components of the human mirror system? One recently suggested possibility is that right hemisphere components of the mirror system serve to integrate information regarding actions being generated by multiple actors and compute an appropriate response, which is then forwarded to left hemisphere areas better suited to support execution of specific movement trains (Newman-Norlund et al., 2008). Another possibility is that right inferior frontal activations are related to inhibition processes (Brass, Zysset, & von Cramon, 2001; Brass, Derrfuss, & von Cramon, 2005). According to this explanation, planning and execution of complementary actions would first require that we actively inhibit our natural tendency to imitate observed actions.

Future research on joint action may prove critical to clarifying functional differences between various components of the mirror system. One particularly fruitful avenue for future research may be to look at how humans learn to perform complementary responses. In other words, how do we form specific subsets of action perception-linkages (or transformations) that facilitate our performance in specific social situations, like playing tennis, dancing, or building a house? Do we acquire, store, and retrieve these mappings in the same way we manage stimulus response relationships in which the triggering stimulus is nonbiological, or is learning how to interact with other humans somehow treated as a special case? Preliminary analysis of brain data obtained during improvement in a cooperative bar-lifting task suggest that this learning process relies on computations performed by the right superior temporal sulcus (STS), an area typically associated with perception of biological motion and thought to funnel information into mirror areas (Grossman & Blake, 2002; Newman-Norlund et al., 2008, un-reported contrast). The proposed lateralization between left STS—perception of biological motion in general, and right STS—specifically tuned for social interactions is, of course, highly speculative at the time being, but it warrants new investigations.

5. Discussion

In the present paper we have discussed three topics that we consider critical to understanding joint action: action simulation, action monitoring, and action selection. Additionally, we emphasize that complementary actions are crucial to efficient social interactions.
It is gradually becoming clear that the mirror system not only subserves direct perception-action links but also activation of logically related response patterns via inferences from observed activities to actions and goals. Accordingly, the remarkable human capacity to perform joint actions reflects the flexible and adaptive way we can use our own action system to understand and interact with other agents. On the basis of this latter insight we can define the contours of a model of joint action in which the topics that we discussed can be formally situated.

The discovery of mirror neurons has given a boost to simulation theory (Gallese & Goldman, 1998) in the sense that these cells represent a plausible neural mechanism for mapping observed actions onto an observer’s own action repertoire. From a motor control perspective this mapping is called an inverse mapping and its function is to update the estimated state of the (ongoing) action plan (Oztop & Arbib, 2002). More recent models, however, propose that mirror neurons may be more appropriately understood as representing forward models in the sense that they transform action plans into anticipated visual information. As such, mirror neurons provide a feedback control mechanism that eliminates neuronal delays during execution of actions. Current theory holds that, during observation of actions, mirror neurons simulate the perceptual outcomes of the observer’s action repertoire (Oztop, Kawato, & Arbib, 2006); mirror neurons representing the best matching action alternative are most active and inhibit mirror neurons representing competing action alternatives (Wolpert, Doya, & Kawato, 2003).

The models discussed above address crucial themes in motor control theory such as the many-degrees-of-freedom problem and anticipatory control to circumvent neuronal delays. They also explain why it is easier to recognize one’s own actions rather than someone else’s (e.g., Repp & Knoblich, 2004; Knoblich & Flach, 2003). However, they do not focus on the intentional and goal-directed aspects of mirror neurons and the mirror neuron system in general. For example, Fogassi et al. (2005) have shown that, for macaque monkeys, activity of parietal mirror neurons during grasping is modulated by what happens afterwards: grasp-to-put or grasp-to-eat. Also the human mirror neuron system appears to be sensitive to the specific end goal of goal-directed actions (see e.g., Iacoboni et al., 2005).

Presumably, these findings are related to behavioral findings showing that the goal of goal-directed actions is often more important than the way in which the particular goal is achieved (Bekkering, Wohlschläger, & Gattis, 2000). This is especially relevant in the context of joint action because cooperating actors share a common goal but their actions typically need to complement each other rather than being the same. We believe that a higher goal-related level of abstraction is needed to explain joint action and that the mirror neuron system already represents this goal-related level of abstraction.

Cuijpers, van Schie, van Koppen, Erlhagen, & Bekkering (2006; see also Bobick, 1997) created a Bayesian model of action recognition in which the identification and categorization of observed actions occurs at a goal level. The observer still simulates perceptual outcomes of action alternatives from the action repertoire, but decisions are made on the basis of associated goals. Consequently, when an observer imitates an observed actions he may or may not use the same action alternative depending on context and personal preferences. This model fits nicely with the finding that the effector with which an action is performed is not
particularly relevant for activating the mirror neuron system as long as the goal remains the same (Gazzola et al., 2007).

In a joint action context people are typically working toward a common goal, which is usually comprised of a sequence of subgoals. In the framework of Cuijpers et al. model this sort of dynamic interaction can be modeled by modeling the selection of appropriate subsequent subgoals during action observation. This implies that mirror neuron activity should reflect the subgoal of the observed actor before a decision is made and the subsequent subgoal after a decision is made. At present, underlying neurophysiological support for this notion is however lacking. The issue about goals and subgoals, besides other claims and predictions that we can derive from our computational framework of joint action, deserves to be tested in detail in future neurocognitive studies.

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