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Do non-human primates cooperate? Evidences of motor coordination during a joint action task in macaque monkeys

Federica Visco-Comandini, Simone Ferrari-Toniolo, Eleonora Satta, Odysseas Papazachariadis, Rajnish Gupta, Laura Elena Nalbant and Alexandra Battaglia-Mayer[*]

Dipartimento di Fisiologia e Farmacologia, SAPIENZA, Università di Roma, Roma, Italy

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ABSTRACT

Humans are intensively social primates, therefore many of their actions are dedicated to communication and interaction with other individuals. Despite the progress in understanding the cognitive and neural processes that allow humans to perform cooperative actions, in non-human primates only few studies have investigated the ability to interact with a partner in order to reach a common goal. These studies have shown that in naturalistic conditions animals engage in various types of social behavior that involve forms of mutual coordination and cooperation. However, little is known on the capacity of non-human primates to actively cooperate in a controlled experimental setting, which allows full characterization of the motor parameters underlying individual action and their change during motor cooperation. To this aim, we analyzed the behavior of three pairs of macaque monkeys trained to perform solo and joint-actions by exerting a force on an isometric joystick, as to move an individual or a common cursor toward visual targets on a screen. We found that during cooperation monkeys reciprocally adapt their behavior by changing the parameters that define the spatial and temporal aspects of their action, as to fine tune their joint effort, and maximize their common performance. Furthermore the results suggest that when acting together the movement parameters that specify each actor's behavior are not only modulated during execution, but also during planning. These findings provide the first quantitative description of action coordination in non-human primates during the performance of a joint action task.

1. Introduction

The cognitive functions associated to the capacity of subjects to tune their motor behavior with the rules imposed by the environment stay at the core of social cognition. One of these functions refers to the ability to coordinate our actions in a social context.

A joint action can be defined as a form of social interaction whereby two or more individuals coordinate their movement

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[*] *Corresponding author*. Dipartimento di Fisiologia e Farmacologia, SAPIENZA, Università di Roma, P.le A. Moro, 5, 00185, Roma, Italy.
E-mail address: alexandra.battagliamayer@uniroma1.it (A. Battaglia-Mayer).

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in space and time as to reach a common goal (Sebanz, Bekkering, & Knoblich, 2006). How this coordination is achieved is an open issue, since it necessarily requires some kind of interlocking of individuals' perceptions, intentions, action plans and performance (Knoblich, Butterfill, & Sebanz, 2011). Furthermore, individuals can modulate their behavior on the basis of predictions on the consequences not only of their own actions (Blakemore, Frith, & Wolpert, 2001; Blakemore, Wolpert, & Frith, 2000), but also of those of the interacting agent (Frith & Singer, 2008). This, together with expectations from the external world (Reynolds & Bronstein, 2003), can facilitate the construction of 'internal models of interaction' (Wolpert, Doya, & Kawato, 2003). Wolpert et al. (2003) have proposed that the observation of the actions of another agent activates the same feed-forward mechanisms used for controlling our own behavior, thus enabling predictions of what that agent intend to do (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004) or helping to monitor the partner's motor behavior (Aglioti, Cesari, Romani, & Urgesi, 2008). In general, the neural mechanisms that allow the integration in a coherent framework of aspects related to 'own' and 'other' action remain to be understood. Particular attention has been devoted to the role of the 'mirror system', and to its potential contribution to understanding others' action and intentions (Fogassi, Ferrari, Gesierich, Rozzi, Chersi, & Rizzolatti, 2005; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; for a review see Rizzolatti & Sinigaglia, 2010). It is worth stressing that the properties of mirror neurons, originally discovered in macaque monkeys, have not been studied in the context of direct motor interaction between conspecifics, but only in single subjects that perform and observe an action. Nevertheless, it has been hypothesized (Knoblich & Sebanz, 2008; Sebanz, Bekkering and Knoblich, 2006; Sebanz & Knoblich, 2009) that mirror coding is involved in complex forms of joint action, by providing a representational system for simulating and understanding another agent's action, therefore a basis for predicting the what, where, and when of the initiatives of the others in a social arena (Sebanz & Knoblich, 2009). In line with this hypothesis, fMRI studies have shown that in humans the same fronto-parietal areas defining the mirror system are more active during joint actions, as compared to individual ones (Newman-Norlund, Bosga, Meulenbroek, & Bekkering, 2008), with greater activation associated to increasing joint action demands, such as when comparing imitative versus complementary coordinated behavior (Newman-Norlund, van Schie, van Zuijlem, & Bekkering, 2007). Thus, predicting information encoded by the mirror mechanisms could be used not only for imitation, but also for non-imitative, complementary actions that are a frequent form of motor interaction between individuals.

However, another hypothesis postulates that the mirror system subserves only partially the capability to perform complementary actions. In such a case, mirror mechanisms would first translate observed and executed action into a common code, and then this signal would be processed by other components of an integration network specifically tailored to support complementary actions. Coherently with this interpretation, it has been found that the mechanisms of motor resonance, useful for internally simulating the actions performed by others, seem to cease when complementary actions are internally elicited in the observer (Sartori, Betti, & Castiello, 2013; Sartori, Cavallo, Bucchioni, & Castiello, 2012; for a review see Sartori, Bucchioni, & Castiello, 2013). According to this view, different forms of joint action can involve different integrative networks.

Cognitive psychology studies have addressed the issue of how co-actors make use of each other's task representation and how the ability to predict each other's action facilitates on-line coordination (Sebanz, Bekkering and Knoblich, 2006). These studies suggest that ad hoc perceptual, motor, and cognitive processes support joint action, which would depend on the ability to share representations, predict behavior and integrate predicted effects of own and other's actions. Thus, joint attention, action observation and task sharing stay at the core of motor cooperation. Experiments on humans showed that partners engage in joint actions by modifying their kinematics, in particular by making their behavior more predictable and discernible (Pezzulo & Dindo, 2013; Sacheli, Tidoni, Pavone, Aglioti, & Candidi, 2013). This increase in predictability seems to be achieved by minimizing the variability of co-actors' movement (Vesper, van der Wel, Knoblich, & Sebanz, 2011) or by selecting movement trajectories that allow a faster disambiguation of an action from alternative ones (Pezzulo & Dindo, 2013).

On an evolutionary perspective, little is known on the ability of non-human primates to perform goal-directed, cooperative actions. Some studies have indeed examined in monkeys the ability and tendency to spontaneously interact by cooperating with each other (Mendres & de Waal, 2000; Suchak, Eppley, Campbell, & de Waal, 2014; Visalberghi, Quarantotti, & Tranchida, 2000). Chimpanzees show not only cooperative behavior, but also the capability to select the most efficient partner (Hirata & Fuwa, 2007), and seem to be able to engage in various types of joint behavior that involve some form of cooperation among individuals (Melis, Hare, & Tomasello, 2005; Noe, 2006; for a review see Melis & Semmann, 2010). However, all these studies have used an ecological approach and therefore lack quantitative description of the animals' motor behavior during interaction.

This study is aimed at investigating first whether macaque monkeys, when required to coordinate their actions, are able to jointly adapt their motor behavior, in order to achieve a common goal. Second, in the case of a successful performance, we aimed at identifying the motor strategies implemented by the animals, through a quantitative approach.

To this purpose, we trained three couples of macaque monkeys in tasks where they were required to move a visual cursor on a screen by exerting hand forces on an isometric tool during both individual (*SOLO*) and cooperative joint action (*CJA*). To minimize the possibility that joint-action was based on a direct observation/simulation strategy, we used an isometric condition, during which no physical hand movement had to be performed or could be observed by each partner. We have hypothesized that, beyond the model adopted and the underlying neural system, at the basis of *CJA* lays the optimization, through a process of reciprocal adaptation, of the specific motor parameters underlying the selection of spatiotemporal task-dependent variables and strategies. To this goal, we have analyzed in a quantitative fashion several aspects of hand dynamics, that is the hand forces exerted on the