

The boundaries of cooperation: sharing and coupling from ethology to neuroscience

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ABSTRACT

Cooperation is usually described as a human tendency to act jointly that involves helping, sharing, and acting prosocially. Nonetheless clues of cooperative actions can be found also in non-humans animals, as described in the first section of the present work. Even if such behaviors have been conventionally attributed to the research of immediate benefits within the animal world, some recent experimental evidence highlighted that, in highly social species, the effects of cooperative actions on others' wellbeing may constitute a reward per se, thus suggesting that a strictly economic perspective can't exhaust the meaning of cooperative decisions in animals. Here we propose, in the second section, that a deeper explanation concerning cognitive and emotional abilities in both humans and animals should be taken into account. Finally, the last part of the paper will be devoted to the description of synchronization patterns in humans within complex neuroscientific experimental paradigms, such as hyperscanning.

Keywords: Cooperation; Synchronization; Empathy; Humans; Animals

1. INTRODUCTION

The term cooperation conventionally refers to collaborative actions of two or more individuals during the production of common behavioral effects. Such behaviors are planned, implemented and directed towards the achieving of a specific goal or to the completion of actions which imply common interests, and subsequently provide a benefit to all the actors involved. However, a wider definition of the construct can comprise organisms in different domains of activity like helping, sharing, or acting prosocially. Here, this second meaning of the construct will be used: in fact, cooperative actions are also often associated with emotional satisfaction or reward (Crook, 1970), even if these last aspects are more often referred to human beings. In fact it has been suggested that, among all the animal world, human cooperation represents an outlier with respect to other animal societies for at least two reasons: firstly, it leads to the formation of very large groups with detailed and structured division of labor, as can be noted by the large organizations and nation states we build at different levels of complexity (Fehr & Fischbacher, 2003). Secondly, it is not relegated to the family environment like in the case of many animal species, but involves social exchange between genetically unrelated strangers. Indeed, human beings cooperate with people who don't belong to their closer social environment and with whom they won't probably ever communicate again. Thus, in this last case, direct and concrete gains could be small or absent since they may never have the occasion to be reciprocated (Fehr & Gächter, 2002; Milinski, Semmann & Krambeck, 2002; Nowak & Sigmund, 2005; Bshary & Grutter, 2006). In sum, the most striking feature of human cooperation seems to be characterized by the large size of social interaction in combination with extensive cooperative behaviors between unrelated individuals (Melis & Semmann, 2010).

In contrast, it has been generally affirmed that most animal species exhibit little division of labor and that cooperation is usually limited to small groups involving kin. Some exceptions to the group dimension, though, can be found within some social insects such as ants and bees, or the naked mole rat, but, still, their cooperation is based on the genetic relatedness between colony members (Fehr & Fischbacher, 2003). Also, it has been proposed that, in the case on non-kin individuals cooperating each other, one or both partners seem to gain immediate benefits from their actions (Clutton-Brock, 2009).

However, it is still possible to appreciate a set of collective behaviors at different levels of complexity in animals as well, which will be discussed in the present paper. In fact, according to classical points of view on this phenomenon, a qualitative differentiation between human and animal coop-

eration seems to emerge, with humans guided by emotional and prosocial motivations, and animals by instinct and affiliation. Nonetheless a different perspective is proposed here, with cooperation being a social construct that lies on a continuum and that can be structured along different degrees of complexity, in consideration of phylogenetic, ontogenetic, but also subjective variables. Beside the species-specific needs to act collectively and provide resources, that are genetically driven and are typical not only of humans, but of many other social species, a series of other joint actions that involve higher cognitive and emotional processes can be appreciated in humans, but in some case also in non-human animals. As a possible fulcrum of such processes the capacity of perceiving and inferring others' affective states will be proposed, from more basic resonance and mirroring abilities, towards the development of a more complex social sharing based on joint attention and synchronization (Balconi & Bortolotti, 2012). In other words, the higher the capacities of synchronization and inferring the consequences of actions on the other's life are, the more frequent and complex the attempts to act cooperatively will be (Balconi, Falbo & Conte, 2012). The aim is not that of exhausting the topic as a whole, but to furnish some clues and raise questions to trigger a reflection about possible links between biological, social and neural manifestations of cooperative behavior.

In the first part of the paper some interesting examples of cooperation in the animal world will be considered to provide available knowledge on a topic that has scarcely been described objectively and that deserve greater attention. Some of the examples seem to suggest, in fact, the presence of cooperative actions that are based on empathic concern and are independent from material reward. These hints will prompt the idea of a quantitative continuum in cooperation and helping, that a strictly economic perspective is not able itself to explain all the cooperative behaviors and decisions in animals' lives, and that a deeper explanation concerning cognitive and emotional abilities should be taken into account. The second part will gather such suggestions and try to better frame them within a reflection on the role of onto- and phylogenesis in the development of cooperation, while the final part of the paper will be devoted to the description of joint actions in human within complex neuroscientific experimental paradigms. The hyperscanning paradigm, in fact, will be presented as an interesting way to detect high-level synchronization during cooperation in human beings.

2. COOPERATION WITHIN THE ANIMAL KINGDOM

As previously suggested, interesting examples of cooperation and sharing can be observed also in the social life of non-human organizations. It has been shown that, even at very low and simple evolutionary stages, organisms such as viruses, bacteria and social amoebas can cooperate each other. For example, solitary amoebas can form a multicellular differentiated slug when they are starving, with the aim to pass through soil barriers that they couldn't otherwise cross by themselves (Brown, 2001; Kuzdzal-Fick, Foster, Queller & Strassmann, 2007; Brockhurst, Buckling, Racey & Gardner, 2008). A first point of interest to be considered consists in the structural complexity of the species involved: for example, birds or mammals that live solitarily in large territories for the greater part of the year in social units organized around the family have usually a limited repertoire of socially-based interactions. On the contrary, animals living in densely congregated groups with long-term monogamous or polygamous pair-bonding commonly show some emergence of cooperation (Crook, 1970). Usually, it takes the form of group hunting, foraging, food storage and sharing, usage of common pool resources, territorial defense and mutual protection against predators, parental and child care (even in the form of baby-sitting), but also in the control of social interaction in more complex primate organizations (Hauser, Chen, Frances & Chuang, 2003; Fehr & Rockenbach, 2004). To provide some examples, emperor penguins crowd to keep warm and cattle press tightly together to prevent insects' bites. Also, male lions cooperate to defend females from other male competitors (Bateson, 2000). In animals with higher social competencies cooperative actions may also be reciprocated, like in the case of baboons: it has been shown that when a male individual helps another male to fend off competition for a female, the favor will be returned at a later time (Packer, 1977).

Such behaviors are usually explained in consideration of strictly economic perspectives which propose that animals cooperate whenever it entails a benefit (Trivers, 1971). However, other views suggest that in some cases there could be a more complex process underlying such mechanisms consisting in a pro-social propensity of the actors involved. In this case cooperative acts are defined as truly altruistic behaviors that can emerge from a reward value attributed to the perception of benefit to others (Camerer & Fehr, 2006). Nonetheless this last option, as already suggested by Charles Darwin (1859-1958), is a paradox in that it poses a problem to the traditional theory of natural selection, which lies on the assumption that individuals compete to survive and breed (Viana, Gordo, Sucena & Moita, 2010).

Nonetheless, observations made in both natural populations and in laboratory conditions are sometimes controversial. For example, as already

reported in Vanutelli and Balconi (2015), although the growing interests in emotional and social lives of non-human animals, the presence of objective experimental evidence has just begun to emerge. A first interesting example is described in a paper by Church (1959) concerning rats' behaviors towards conspecifics in pain. The experiment was conceived as such: a rat was instructed to press a lever to obtain food, but, if this act was accompanied by an electric shock administered to another rat, the first rat interrupted its activity. Such reaction, however, rises a big question, that is whether the rat was really concerned for its companion or just afraid that something bad might happen to itself. A similar experiment conducted nearly fifty years later by Langford and colleagues (Langford et al., 2006) demonstrated the presence of bidirectional pain modulation in mice during the exposure to their cagemates in pain. More interestingly to the purpose of the present study, Bartal and colleagues (Bartal, Decety & Mason, 2011) conducted an experiment in which a rat was free while its cagemate was trapped in a restrainer. The experiment showed that, after several attempts, the free rat learned to intentionally open the restrainer and free its cagemate, thus providing strong evidence for the presence of cooperation and helping motivated by empathic concern. Also, such mechanisms was not elicited by a painful experience, but just by the psychological distress perceived in the conspecific. Finally, its behavior was not guided by reward. In fact, when the rat had the possibility to choose among liberating the cagemate or obtaining some chocolate contained in another box, not only it continued to free the other rat, but it opened both restrainers and shared the chocolate.

These examples prove that a strictly economic perspective is not able itself to exhaust the theme of animal cooperation just considering decisional processes based on benefits evaluations, and that a wider explanation concerning cognitive and emotional abilities should be taken into account. For example, another paper by Viana and colleagues (Viana et al., 2010) explored cooperation in rats during an iterated Prisoner's Dilemma (iPD) game. In this case the game involved the decision between benefits and costs during a cooperative task, where cooperation was the strategy that entailed the highest benefits for both actors (for an extensive review of this paradigm see Axelrod & Hamilton, 1981; Stephens, McLinn & Stevens, 2002). In this case the authors showed that rats' choices were actually modulated by the relative size of the reward, but also by the motivational state of the animals, thus revealing that environmental factors may influence the perception of the economic outcome during social exchange. Moreover such behaviors could be modulated by social interactions, in that the rats typically used their opponent as a cue. As the authors themselves suggested, a similar outcome has been demonstrated also in humans, who modulate their propensity to

cooperate according to the identity of the adversary (e.g, computer vs other human) (Rilling et al., 2002).

We can finally state that, in the case of highly social animals such as mice and rats, according to the community environment, they could have somehow developed a propensity to perceive cooperative acts as a social reward. In fact, this could have allowed the opportunity to observe and experience cooperative actions and their consequences for the other members, in parallel with the development of increasingly higher and more complex cognitive and emotional abilities. Here it seems that some important phylogenetic aspects intersect with ontogenetic ones. In fact, the acquisition of such capabilities could be traced back to the very early experiences during the development, as proposed in the following section.

3. ONTOGENESIS AND PHYLOGENESIS: HELPING AND SHARING

It has been shown that infants as young as 14-18 months of age spontaneously help adults by picking up the objects that drop on the floor and returning to them (Warneken & Tomasello, 2006; 2007; Over & Carpenter, 2009), or, even in more complex situations, they can open a cabinet for adults who carry something and have the hands full. This is particularly interesting if we consider that they typically renounce to fun activities to do so (Warneken, Hare, Melis, Hanus & Tomasello, 2007; Warneken & Tomasello, 2008). Importantly, it has been shown that chimpanzees can help other individuals in similar ways (Warneken & Tomasello, 2006).

To better explore this issue, Warneken and colleagues (Warneken et al., 2007) directly compared the tendencies of 18-month-old children and mother-raised chimpanzees to help others with out-of-reach objects. Results showed that both species helped in this situation in a quite reliably way, and neither species declined in helping when they were required to provide higher efforts.

The presence at such early age of spontaneous helping in young children and in higher primate suggests that these competencies emerge naturally and do not rely on explicit cultural transmission (Warneken & Tomasello, 2009b). Also, considering studies involving again both young children and chimpanzees, it was demonstrated that the promise of a material reward did not increase the amount of helping (Warneken et al., 2007). In some cases, external rewards could even act as deterrent of cooperative motivations as it has been proven in a study with 20-month-old children. Here, in fact, furnishing material rewards decreased the amount of helping in that it weakened children's intrinsic motivations (Warneken & Tomasello, 2008).

For what concerns sharing, instead, children seem to be more generous with precious resources than chimpanzees: in natural life chimpanzees usually compete over food, but they can offer food to others in some circumstances (Warneken & Tomasello, 2009b). For example, they selectively share food with their desired coalitionary or sexual partners (Muller & Mitani, 2005). Nonetheless, when facing situations that are more similar to those attributed to humans, chimpanzees are often reluctant to share in the absence of an immediate benefit (Brosnan, Grady, Lambeth, Schapiro & Beran, 2008). The communion of food, instead, is quite different in humans since children from a relatively early age show to share food and other resources of interest (Fehr, Bernhard & Rockenbach, 2008; Brownell, Svetlova & Nichols, 2009; Moore, 2009). For example, it has been shown that young children at two different sides of a table tend to share food rewards equally (see Warneken & Tomasello, 2009). On the contrary, chimpanzees are motivated to share only if each chimpanzee's portion of the food is on its own part of the table. Otherwise, the food will be monopolized by the dominant individual (Melis, Hare & Tomasello, 2006a; 2006b; Hare, Melis, Woods, Hastings & Wrangham, 2007).

Thus in this case some possible differences between children and chimpanzees seem to emerge. It has been hypothesized that the presence of different forms of foraging in the two species could explain such results (Warneken & Tomasello, 2009b). In fact, many evolutionary theorists believe in a human transition from more individual to more cooperative hunting and gathering, so that they could have adopted a more cooperative way of living involving more tolerant and altruistic behaviors toward others (Sterelny, 2007).

Nonetheless, if we consider the underlying processes of these two different mechanisms, we could note that the difference consists in the presence or absence of a concrete need and distress expressed by the other individual. In fact, in the first case, both children and chimpanzees recognized the emerging difficulties cued by the situation and decided to cooperate. This important aspect was not present in the second case where the decision of sharing was made in a neutral situation. Specifically, we could hypothesize that in the second case the decisions were made upon economic strategies based on costs/benefits evaluations, while in the first case they could have moved by compassion. This is even more plausible if we consider the results obtained in similar tasks at different stages of the child development. In fact, Brownell and colleagues (Brownell et al., 2009) found that in a task which comprised the subdivision of food between the subject and a receiver, 18-month-old children chose randomly, while 25-month-old children more often chose the option which entailed the same benefit for both themselves and the receiver. More importantly, this behavior occurred only in the case the receiver verbalized his desire for food. This result is very interesting since it indicates that

they required explicit cues to perceive the other person's need in this context, and that this element was essential for the emergence of the cooperative action. In general, we could say that it is important to develop cogent representation of the others for the emergence of complex cooperative actions.

According to what discuss so far, such early behaviors, though, don't seem to be driven by culture. In fact, even before they are physically capable of helping, 6-month-old infants can discriminate between geometrical shapes that are "helping" from those who are "hindering others" (Hamlin, Wynn & Bloom, 2007).

Nonetheless, it has been proven that cultural transmission could become more important over ontogeny. In fact, children gradually learn to discriminate the targets of their altruistic acts, to select specific social partners, and to follow conventional norms and rules. Thus, culture does not seem to create altruism in young children, but later in ontogeny it comes to play a crucial role in mediating their altruistic exchange (Warneken & Tomasello, 2009a).

But how do humans develop such competencies, and why chimpanzees and other animals develop concerns for others and decide to reciprocate and cooperate? It has been suggested that early acquisitions related to maternal care can prompt the emergence of some first cooperative interests. For example, adults communicate with children about the effects of their actions on others since the very first stages of their lives. This set of teaching is called inductive parenting and it has been proven to encourage the internalization of societal norms and values, as well as the emergence of altruistic behavior. Such parenting presumes that children will be naturally cooperative, if only they can see clearly the effects of their actions on others (Tomasello, 2010).

Experimental studies comparing children and chimpanzees seem to support this interpretation, as already demonstrated by Warneken and colleagues (Warneken, Chen & Tomasello, 2006) who presented 18- and 24-month-old children and three human-reared juvenile chimpanzees with a series of collaborative tasks. The experimenter was programmed to quit a previously-begun game in the attempt to trigger subjects' re-engagement. Children at both ages all actively encouraged the adult to restart the game by asking and communicating with him according to their possibilities, suggesting the formation of a shared goal. On the other hand, chimpanzees never tried to re-engage the adult, but tried to solve the task individually. Thus it seems that chimpanzees' participation in group activities is more individualistic, while children's one relies on shared intentionality. In fact, although apes could use others by gathering information, manipulating them as social tools, coordinating actions with them for their own benefit, human children seem to be concerned with sharing psychological states with others by forming joint intentions and attention with them.

To conclude, we hypothesize that the emergence of cooperative behaviors can occur in case of highly social species which show organized and shared living systems. Here cooperation seems like a need to solve complex situations and to guarantee the collective wellbeing. Then, we also think that the emergence of more complex cooperative actions can arise according to the development of empathic and cognitive capabilities that allow producing a representation of others' needs and intentions. This could be probable due to the acquisitions learnt from early parenting and it is visible also in some animal species. In this case it seems that the individual deduce a reward from the cooperative actions per se. In fact, in some cases, animals show a behavioral modulation according to their concern for other group members, even if more objective experimental evidence should be collected. Finally, as we can see in the case of humans, cooperative behavior can take the form of higher-level processes also involving the desire and the active research for psychological and social sharing which is reinforced during the ontogenesis together with the acquisition of cultural-based norms. In the following section, some experimental evidence about the results of such processes on peripheral and brain activities will be furnished in the frame of the latest frontiers in social neuroscience.

4. SHARING A SOCIAL WORLD: BRAIN COUPLING AND HYPERSCANNING

As already pointed out by Hasson and colleagues (Hasson, Ghazanfar, Galantucci, Garrod & Keysers, 2012) many actions that are produced jointly, such as those illustrated in the first section like mating, group cooperation and predator avoidance, depend on an accurate production and evaluation of meaningful social cues. Human and animal research have suggested that the psychophysiological linkages between two conspecifics are an inherent element of social bonding and attachment (Gottman, Swanson & Swanson, 2002; Coan, Schaefer & Davidson, 2006; Feldman, 2007; McAssey, Helm, Hsieh, Sbarra & Ferrer, 2013). As a result, the occurrence and development of these behaviors can be strongly influenced by interactions with other group members. The study of dyadic interactions in humans, in fact, showed that emotional exchanges between the two members of a couple can be highly interdependent (Thompson & Bolger, 1999; Ferrer & Nesselroade, 2003; Song & Ferrer, 2009). Importantly, it has been also suggested that the development of such mechanisms could be adaptive for humans' social lives since it appears to promote successful exchange and determine continuous social

interactions. For example, it has been shown that the adoption of the other's emotional state can promote relationship longevity (Hatfield, Cacioppo & Rapson, 1994). Also, the level of emotional coherence within the pair is related to the length of the relationship between partners (Anderson, Keltner & John, 2003).

Similar synchronizations patterns are visible also through the posture (Shockley, Santana & Fowler, 2003) and some physiological indices such the respiration (McFarland, 2000; Giuliano, Skowron & Berkman, 2015) or the cardiac rhythms (Konvalinka et al., 2011; Ruth Feldman, Magori-Cohen, Galili, Singer & Louzoun, 2011; Smith et al., 2011) of the two individuals. For example, Smith and colleagues (Smith et al., 2011) asked 114 young couples to complete measures of marital quality together with a marital task, preceded and followed by resting baseline recording of High-Frequency Heart Rate Variability (HF-HRV). Then, they were required to discuss about a current marital disagreement. Results showed that resting HF-HRV was correlated with marital quality, suggesting that the capacity for self-regulation is associated with adaptive functioning in close relationships.

Moreover, Feldman and colleagues (Feldman et al., 2011) submitted dyads of mothers and their 3-month old infants to a face-to-face interactions during cardiac recording, together with analyses of behavioral signs like gaze, affect, and vocal synchrony. Results showed that mother and infant coordinated heart rhythms during episodes of affect and vocal synchrony. This is very important in that it demonstrates the modulation of physiological processes through the coordination of visuo-affective social signals. It is important to underline that through this parental exchange the child learns how to interpret others' states according to the stability of such recurrent patterns. Also, it has been shown that the quality of such interactions can strongly predict later developmental functioning (Sroufe, 1979).

Similar peripheral modulations have been also found in some mammals dyads, in which mothers adapt their physiological systems to those of the infant (Giuliano et al., 2015). Moreover, Hofer (1995) demonstrated that the maternal physical presence integrates a set of bio-behavioral provisions among which the heart rhythm. Such mechanisms are able to influence the physiological organization in young individuals (Dettling, Schnell, Maier, Feldon & Pryce, 2007). For example, even if in female rats multiple biochemical and hormonal factors are involved in the establishment of maternal cares, the dyadic bond can be later maintained in the absence of hormonal environment (Rosenblatt, 1992). This means that further mechanisms are involved in the establishment of meaningful synchronization patterns, such as behavioral regulation. Also, during these early interactions, the production of oxytocin produces a facilitating effect on the activation of the reward

system that is thus reinforced during dyadic interactions and may even replace other forms of reward (Ferris et al., 2005).

Recent scientific evidence in humans suggested that the coordination of actions between two interacting persons activate specific mechanisms that transfer not only to behavioral or peripheral synchronization, but also to brain activity in the form of brain-to-brain coupling. To provide an example, perceiving the actions, feelings or emotions of another person typically triggers corresponding cortical representations in the perceiver (Hasson et al., 2012), and such process has been termed as vicarious activation (Keyesers & Gazzola, 2009). Interestingly, if the two (or more) actors possess similar brains and bodies, vicarious activations in the perceiver will get closer and closer to that of the agent, thus leading to coupled neural responses (Keyesers, 2011). In fact, when we interact with another person, the emerging phenomenon can't be solved simply as the sum of the two experiences. Our brains and bodies cannot be considered per se, but they are immersed in a common environment in which we reciprocally adapt our actions (Konvalinka, Vuusta, Roepstorffa & Frith, 2010).

The study of brain coupling and synchronization has been recently taken on by a new neuroscientific paradigm called "hyperscanning" that emerged in contrast to previous research approach based on a more individualistic dimension within social experience. This technique, in fact, allows the simultaneous registration of the cortical activity from two or more participants interacting together (Montague, 2002). The applications could imply different devices, such as dual functional Magnetic Resonance Imaging (fMRI), electroencephalographs (EEG), or Near-Infrared Spectroscopy (NIRS) indices, as well as different tasks, from economic games assessing social decision-making (King-Casas et al., 2005; Astolfi et al., 2011); communication and transfer of information across brains (Stephens, Silbert & Hasson, 2010; Jiang et al., 2012); synchrony during music playing (Lindenberger, Li, Gruber & Müller, 2009; Babiloni et al., 2011; 2012; Sängler, Müller & Lindenberger, 2012); motor synchronization (Tognoli, Lagarde, DeGuzman & Kelso, 2007; Funane et al., 2011; Holper, Scholkmann & Wolf, 2012; Naeem, Prasad, Watson & Kelso, 2012; Yun, Watanabe & Shimojo, 2012; Cui, Bryant & Reiss, 2013; Konvalinka et al., 2014); executive functions and problem-solving (Decety, Jackson, Sommerville, Chaminade & Meltzoff, 2004; Dommer, Jäger, Scholkmann, Wolf & Holper, 2012; Liu, Saito & Oi, 2015), but also shared attention (Saito et al., 2010). The principle lies in the fact that, during joint actions involving motor, perceptual or cognitive abilities, people become implicitly coupled (Knoblich, Butterfill & Sebanz, 2011).

Such studies have revealed typical patterns of inter-brain synchronization with correlated cortical responses, and this is very important in that sim-

ilar results cannot be detected by considering single brain activities (Babiloni & Astolfi, 2012; Chatel-Goldman, Schwartz, Jutten & Congedo, 2013). Starting from few pionieristic experiments, an increased number of researchers have adopted this perspective and founded the bases for new ecologically-valid investigations, thus emphasizing the importance of a “second-person” or a “two-person neuroscience” (Hari & Kujala, 2009).

Studies involving imaging techniques such as fMRI permitted to localize the brain areas that are recruited during cooperative joint actions. Saito and colleagues (Saito et al., 2010), for example, conducted an experiment in which two subjects were engaged in a joint attention task inside MRI scanners combined with an infrared eye-tracking system. Infrared cameras captured video images of each participant’s eyes and eyebrows, which were transferred to the other’s participant in real-time. The task consisted in looking at targets cued either by the eye movement of the partner or by the change in color of the target. Results showed the intervention of the right Inferior Frontal Gyrus (IFG) during the sharing of intentional exchange. The authors interpreted this cortical activation in relation to the detection of the communicative motivation from eye movements (Frith & Frith, 2006), with the intent to make possible collaborative activities with shared goals. In fact, according to previous evidence, the neural synchronization of the right IFG might represent the self-other equivalence in intention in action (Meltzoff, 2007). This is of particular interest if we consider what already discussed in the second section.

Nonetheless, studies involving EEG hyperscanning have the advantage of a higher temporal resolution that could be used to capture real-time interactions. Previous research showed inter-brain phase synchronies across a wide range of frequencies, including delta, theta, alpha, beta, and gamma, which correspond to a wide range of processes related to perception, cognition, emotion, and action. An interesting study conducted by Lindenberger and colleagues (Lindenberger et al., 2009) found phase synchronized theta and delta oscillations in pairs of guitarists playing a short melody together. The authors hypothesized that, since the reported rhythms were all in lower frequency range, the similarities in sensorimotor feedback could contribute to the inter-brain synchronization.

Even if there is not available evidence about brain synchronizations in animals, we could hypothesize that brain coupling could be to some extent present in those species that have acquired the abilities of turn-taking from maternal cares, and that show the capacity to understand others’ states. As the work of Saito and colleagues highlighted (Saito et al., 2010) the frontal areas seem to be involved in complex tasks that require mutual understanding and shared information. Some evidence suggested that a highly devel-

oped neocortex is mandatory for catching social signals, according to the social brain hypothesis (Dunbar, 1998). However, growing evidence is suggesting the presence of high-level cognitive and emotional abilities also in other mammals and birds, despite the absence of large neocortices. In the case of animals, thus, different and probably more primitive networks and processes would be engaged during mirroring and mutual synchronization.

5. DISCUSSION AND CONCLUSIONS

The present paper aimed at furnishing some hints on available objective knowledge about the emergence of cooperative behaviors in humans and non-human animals. At first, a wider definition of cooperation was suggested, from the idea of a collaborative action between two or more individuals for common behavioral effects, to a wider concept involving helping, sharing, and acting prosocially. Secondly, the construct was proposed as a continuum from more basic genetically-driven social organization, to higher and more complex actions driven by empathic concern. In fact the starting point here is that the presence of sharing behaviors can be found more easily in those species that show the tendency to bond each other. In this case it is possible to observe group organization concerning food, usage of common resources, territorial defense and protection, parental care, and control of social interactions. Nonetheless, the presence of more complex forms of cooperation have been described, besides humans, in some mammal species like mice or higher apes. In this case, helping and cooperative actions are based on the understanding of others' needs and feelings, and in some cases they seem to be driven by empathic concern. Thus, we could hypothesize that the satisfaction of such needs and feelings could become a social reward per se. Nonetheless, it is evident that in the case of humans such behaviors reach their maximum expression. In fact humans are not only a social species, not only concerned for others' wellbeing, but seem also actively in search for psychological sharing. In parallel, humans have also built a series of shared social norms that are culturally transferred and that can lead to morally-based cooperative actions and, possibly, to the construction of group-identity dynamics (for the relation between group identity and cooperation see for example Kramer & Brewer, 1984; Dawes, 1988; Bornstein & Meyrav, 1994; Brewer, 1996). This last important point should be better explored in future research in consideration of both humans and non-human animals, to study the relation between biological, social, emotional, and cultural variables. Thirdly, some different manifestations of cooperation which involve specific competen-

cies have been distinguished. It would be significant for future research to deeply analyze this issue and compare human and animal behaviors in different circumstances involving specific cognitive and affective scenarios (see for example Warneken & Tomasello, 2009b, for an exhaustive review about the distinction between sharing, helping, and informing in children and higher apes). In parallel, the same mechanisms should be also clarified within human competencies at an individual level of analysis, in consideration of subjective motivations and skills. Finally, the presence of synchronization mechanisms in bodily and cortical responsiveness has been provided. Within peripheral modulation, similarities emerged between dyadic synchronization related to maternal cares in both humans and some other mammals. For what concerns brain coupling, particular attention was given to hyperscanning, a new paradigm in social neuroscience that allows the simultaneous registration of the cortical activity from two or more participants interacting together. This tool emerged as useful and promising in the identification of functional similarities between brains in interaction. Since we don't have any evidence about such processes in animals, future research should better explore the presence of cognitive and affective mechanisms subserving such complex processes in humans and animals, within a comparative perspective. To conclude, the study of cooperative actions could also be useful in the direction of emotional rehabilitation programs involving synchronization and brain coupling in those people or patients that lack some empathic and resonance competencies.

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