# The evolution and development of human cooperation

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Humans have attained an unparalleled level of sophistication when engaging in collaborative and cooperative activities. Remarkably, the skills and motivation to engage in complex forms of collaboration and cooperation seem to emerge early on during infancy and childhood. In this paper, I extensively review the literature on the evolution and development of human cooperation, emphasizing important aspects of inter-cultural variation in collaborative and cooperative behaviour. This will not only allow us to confront the different evolutionary scenarios in which cooperation may have emerged, but will especially provide the reader with a first orientation in the abundant literature on human cooperation.

**Keywords:** Cooperation; collaboration; prosociality; altruism; fairness; punishment; reciprocity; reputation; in-group bias; norms and conformity

## 1. Introduction

In comparative psychology, the term cooperation can be used to refer to those social interactions in which actors incur in some costs to altruistically provide benefits to a partner (e.g. Kappeler & van Schaik, 2006). In a strict sense, cooperation differs from collaboration (or mutualistic cooperation), in that the latter implies individuals working together to achieve a common goal, sharing the costs and likely the benefits (de Waal, 2008; Dugatkin, 1997). Although several mammal species show some form of cooperation (e.g. Clutton-Brock, 2002; Dugatkin, 1997; Kappeler & van Schaik, 2006), the extent to which humans cooperate is probably unique. Humans cooperate with genetically unrelated strangers in large groups, divide labour, trade, provide support to sick and disabled and have complex moral systems enforced by third parties (e.g. Bowles, 2009; Boyd, Gintis & Bowles, 2010; Fehr & Gaechter, 2002).

Like other animals, humans prefer to cooperate with kin (e.g. de Bruine, 2002; Henrich & Henrich, 2007; Platek, Burch, Panyavin & Wasserman, 2002). By sharing the same genes, kin benefit from being altruistic to each other, enhanc-

*Interaction Studies* 16:3 (2015), **383–418**. DOI 10.1075/is.16.3.03ami
ISSN 1572–0373 / E-ISSN 1572–0381 

ing their fitness and passing "cooperative genes" down the lineage (e.g. Chapais, 2001; Foster, Wenseleers & Ratnieks, 2005; Hamilton, 1964). However, humans cooperate with many people other than kin. This is puzzling, because cooperation is costly, cooperative individuals should produce fewer offspring and cooperation with non-kin should thus not thrive (e.g. Dawkins, 1976). Several hypotheses have been proposed to explain how cooperation among non-kin evolved. All these hypotheses assume that cooperation can only become stable if cooperators preferentially interact with each other, so that benefits are only exchanged among cooperators and "cooperative genes" are passed down the lineage also among non-kin (see Henrich & Henrich, 2006). Below, I briefly review the main hypotheses on the evolution of cooperation among non-kin. I then discuss how cooperation develops through ontogeny (to assess the plausibility of each evolutionary scenario), and then hint to some interesting inter-cultural differences in cooperation (to better understand the extent to which biological predisposition and culture affect the emergence of cooperation).

## 2. The evolution of cooperation among non-kin

One of the first hypotheses on the evolution of cooperation among non-kin proposed that cooperation evolved from simple exchanges of altruistic acts (Trivers, 1971). In *direct reciprocity*, individuals provide benefits to each other by using tit-for-tat reciprocal strategies (i.e. cooperating at the outset and then copying the partner's behaviour in the previous round; Axelrod, 1984). When individuals interact in small groups, with visible payoffs, small delays and over long time frames, direct reciprocation of altruistic acts can lead to long-term stable cooperation (e.g. Axelrod, 1984). Indeed, tit-for-tat strategies might foster cooperation by providing limited benefits to free-riders (i.e. individuals who benefit from cooperation without contributing to it), as individuals can stop cooperating as soon as the partner defeats (Trivers, 1971). Although this hypothesis proposes a plausible scenario for the evolution of cooperation in small groups of non-kin, it suffers from several drawbacks, including the fact that individuals usually interact with multiple partners over long time frames, and might be concerned with costs and benefits on a much longer time scale than that of the immediate interaction (e.g. Fehr, 2004; Hammerstein, 2003; Noë & Hammerstein, 1994; but see Trivers, 2006).

Some authors have therefore proposed that the modern forms of human cooperation are simply the *maladaptive consequence* of altruistic tendencies evolved when humans lived in small groups, comprised mostly of kin (e.g. Burnham & Johnson, 2005; Rand & Nowak, 2013). In this setting, altruistic acts

directly benefitted kin or could be easily reciprocated, leading to stable forms of cooperation (Alexander, 1979; Hamilton, 1964; Johnson, Stopka & Knights, 2003; Nowak & Sigmund, 1998; Trivers, 1971). In the modern world, humans cooperate with non-kin they will unlikely meet again, because the proximate mechanism operates as if the ancient, small-group conditions still held (Burnham & Johnson, 2005; Delton, Krasnow, Cosmides & Tooby, 2011; Rand & Nowak, 2013).

Other authors have introduced the concept of *indirect reciprocity*, to explain why individuals extensively cooperate with non-kin also in large groups and over long time frames. In indirect reciprocity, individuals do not have a common history of previous interactions, but might nonetheless cooperate depending on the partner's reputation, i.e. on the information available on the partner's past behaviour (Alexander, 1979; Leimar & Hammerstein, 2001; Nowak & Sigmund, 1998). In indirect reciprocity, therefore, reputation serves as an efficient mechanism to reduce the risk of free-riding.

Other researchers have further developed this hypothesis, suggesting that human cooperation emerged from the unique combination of *reciprocity and culture* (Boyd & Richerson, 2009; Henrich & Henrich, 2006, 2007; Richerson & Boyd, 2005). Cultural evolution happens at faster rates than genetic evolution and allows humans to quickly adapt to complex variable environments (Boyd & Richerson, 1985; Rogers, 1995). In particular, cultural evolution might have allowed humans to increase the accuracy of reputation available on others and might have fostered imitation (e.g. of cooperative behaviours) among individuals belonging to the same group (Henrich & Boyd, 2002; Henrich & Henrich, 2006, 2007; Smith, 2003). This would have led humans to preferentially interact with people they knew something about or who belonged to the same social network. Groups creating social norms that fostered cooperation (i.e. general binding expectations about how people should behave: Chudek & Henrich, 2011) became more successful and spread (e.g. Atran et al., 2002; Diamond, 1997; Kelly, 1985; Soltis, Boyd & Richerson, 1995; Wilson, 2002). Evolution favoured individuals that rapidly acquired local norms, learning them from the most successful and skilled models (prestige-biased transmission: Henrich & Gil-White, 2001), quickly adapting to the cultural traits of the majority (conformist transmission: Boyd & Richerson, 1985; Henrich & Boyd, 1998; Kameda & Nakanishi, 2002), and preferentially interacting with people sharing the same norms (ethnicity bias: McElreath, Boyd & Richerson, 2003). Costly punishment by third parties in case of norm violations further fostered the rapid diffusion of social norms and the evolution of always stricter forms of cooperation among group members (Boyd & Richerson, 2002; Fehr & Fischbacher, 2004; Fehr, Fischbacher & Gaechter, 2002; Fehr & Gaechter, 2002; Henrich & Boyd, 2001; Henrich & Henrich, 2006; Rand, Dreber, Ellingsen, Fudenberg & Nowak, 2009).

More recently, Tomasello, Melis, Tennie, Wyman and Herrmann (2012) proposed the *interdependence hypothesis*, according to which cooperation evolved from the interaction of culture with simple forms of mutualistic collaboration (rather than reciprocation of altruistic acts). The first forms of mutualistic collaboration probably took place in a foraging context, when group-hunting allowed humans to better compete over resources (Alvard, 2012; Soltis et al., 1995). Group hunting provided incentives to all group members (e.g. sharing hunted preys), reduced individual risks by coordinating efforts (e.g. through communication) and directly punished free-riders (e.g. excluding them from the spoils; Tomasello et al., 2012). More than indirect reciprocity, therefore, collaborative foraging likely provided a context in which altruistic acts could prosper. In a first phase, collaboration became increasingly important for group members' survival and individuals became naturally interested in cooperating with the partners they depended on (Clutton-Brock, 2002; Tomasello et al., 2012). In a second phase, groups increased in size and humans developed more efficient forms to contrast free-riding (Tomasello et al., 2012). Cultural evolution allowed individuals to better identify in-group members through cultural praxis, social norms and institutions, so that only individuals sharing the same culture were considered trustworthy cooperative partners (Tomasello et al., 2012; Wyman & Rakoczy, 2011). Through cultural evolution, therefore, cooperative behaviour flourished and became a stable behaviour (Schmidt & Tomasello, 2012). Importantly, the emergence of more stable reproductive bonds (Chapais, 2008) and cooperative breeding (Hrdy, 1999, 2009) likely provided humans with a strong motivation to cooperate and collaborate (Burkart, Hrdy & van Schaik, 2009). The ability to align to others (e.g. through empathy and empathic concern: see below) likely provided humans with a strong motivation to engage in cooperative activities (Jensen et al., 2014). Combined with the cognitive challenges of collaborative foraging (e.g. coordination, joint attention, shared intentionality), this enhanced motivation possibly favoured the evolution of complex forms of cooperation which are typical of modern humans (Tomasello et al., 2012).

## 3. The development of cooperation

Although we cannot know for sure whether the first forms of cooperation emerged in a context of reciprocity or collaboration (and then quickly evolved through culture, e.g. Henrich & Henrich, 2006; Richerson & Boyd, 2005; Tomasello et al., 2012), studying how cooperative behaviour develops can be informative on the plausibility of each evolutionary scenario. If humans reciprocate from early on during infancy, for instance, and show no important

inter-cultural differences in their way to do so, it is plausible that they are born with a biological predisposition to reciprocate, which likely triggered the evolution of more complex forms of cooperation. In contrast, if humans show a preference for collaborative activities from early on and across different cultures, it is plausible that collaboration triggered more complex forms of cooperation. Furthermore, understanding when children develop cooperative behaviour can allow us contrasting the following hypotheses (also see Sebastián-Enesco, 2014): (i) humans are born with *complex and specialized cognitive and motivational skills to cooperate* (e.g. Hamlin, 2012; Wynn, 2008); (ii) humans are born with a *prosocial motivation to cooperate* with others, which gradually develops into more complex forms of cooperation (e.g. Warneken & Tomasello, 2009); or (iii) humans are simply born with the *social motivation to be* with others, which gradually develops into more complex forms of interaction and cooperation (e.g. Hay, 2009).

In the following paragraphs, we will see when humans develop the first forms of cooperative behaviour (i.e. helping, sharing and comforting others), and when reciprocity and collaboration (which might have triggered the evolution of cooperation) first emerge during development. We will then review when the cognitive and emotional foundations of cooperation emerge, and some of the mechanisms employed by children to select their partners and avoid free-riders (i.e. familiarity, fairness, reputation, in-group bias, sharing norms and punishment).

### 3.1 Helping

From early on, children help, comfort and share resources with others (see Jensen, Vaish & Schmidt, 2014; Paulus & Moore, 2012; Warneken & Tomasello, 2009, 2014, for recent reviews). Infants, for instance, provide information to others from 12 months of age, pointing to an object that was inadvertently dropped by an adult experimenter, when the latter searches for it (Liszkowski, Carpenter, Striano & Tomasello, 2006; Liszkowski, Carpenter & Tomasello, 2008). When observing people facing a problem and being unable to reach their goal (e.g., trying to access out-of-reach objects), 18-month children also provide instrumental help, even if they have no interest in the other's goal and no expectation of being rewarded (Warneken & Tomasello, 2006). However, the first instances of instrumental helping already occur at 14 months of age (Warneken & Tomasello, 2007). From two years of age, children start helping others even if the other person does not realize that a problem has occurred (Warneken, 2013), and in the absence of communicative cues (Svetlova, Nichols & Brownell, 2010). Similarly, 3-year-olds spontaneously help others to achieve their social goals (e.g., getting others' attention; Beier, Over & Carpenter, 2014).

### 3.2 Sharing

Children actively share resources, but later than they provide help (see Paulus & Moore, 2012; Warneken & Tomasello, 2014, for recent reviews). Children below the age of two share only reluctantly (Brownell, Iesue, Nichols & Svetlova, 2013; Brownell, Svetlova & Nichols, 2009; but see Hay, 1979; Rheingold, Hay & West, 1976). From two years of age, however, when presented with the choice between a tray providing food to themselves and to a partner, and a tray only providing food to themselves, children prefer to also provide food to the partner, especially after the partner explicitly communicates her desire to obtain the reward (Brownell et al., 2009). Similarly, clear affective displays also facilitate sharing. For instance, 18- and 24-month-olds donate part of their resources to an adult who requests them by making a sad face and/or using a palm-up gesture (Dunfield, Kuhlmeier, O'Connell, & Kelley, 2011; Vaish, Carpenter, & Tomasello, 2009). However, sharing is not as robust as other forms of cooperation, and is highly susceptible to the context. For instance, children's tendency to share is strongly affected by the personal relation to the partner (e.g. Birch & Billman, 1986; Fehr, Bernhard & Rockenbach, 2008; Moore, 2009) and to the costs related to sharing (Paulus & Moore, 2014; Schmidt & Sommerville, 2011; Svetlova et al., 2010). Other factors that play a role in sharing are the partner's presence (e.g. House, Henrich, Brosnan & Silk, 2012), the partner's communicative effort (e.g. Birch & Billman, 1986; Brownell, Iesue, Nichols & Svetlova, 2013), the amount of available resources (Hay, Caplan, Castle & Stimson, 1991) and their relative distribution (Paulus, Gillis, Li & Moore, 2013). In general, consistent sharing seems to emerge relatively late during development (Sebastian-Enesco, Hernandez-Lloreda & Colmenares, 2013; Wu & Su, 2014), becoming more selective during preschool years (Blake & Rand, 2010; Hay & Cook, 2007).

### 3.3 Comforting

Children also comfort others, showing a sympathetic reaction to others' distress and acting to alleviate their emotional needs. Although empathic reactions appear early in development (see below), findings on comforting are not consistent (see Paulus & Moore, 2012). Some studies have shown comforting behaviour around 18 months of age (Zahn-Waxler, Radke-Yarrow, Wagner & Chapman, 1992). In contrast, others have found evidence of helping and sharing, but not comforting, in 18- and 24-month-olds (Dunfield et al., 2011), or only after strong communicative efforts by the partner about her needs (Svetlova et al., 2010). After 24 months, children start reliably comforting others, until sharing and comforting occur with similar frequency by 3 years of age (e.g. Radke-Yarrow & Zahn-Waxler, 1976). Unsurprisingly, the personal relation to the partner strongly affects comforting,

with family members and caretakers eliciting more comforting behaviour than unfamiliar partners (Zahn-Waxler et al., 1992).

### 3.4 Reciprocity

Two- and 3-year-olds help partners independently of whether partners have previously helped them (Warneken & Tomasello, 2013a). From 3 years of age, however, children share more with partners who have shared with them (direct reciprocity) or who have shared with others (indirect reciprocity) in the past (Fishbein & Kaminski, 1985; Fujisawa, Kutsukake & Hasegawa, 2008; Olson & Spelke, 2008; Warneken & Tomasello, 2013a). Only from around 5.5 years of age, do children consistently match their partners' previous behaviour (House, Henrich, Sarnecka & Silk, 2013). These results suggest that helping and sharing emerge earlier on, and might only later be mediated by reciprocity (Warneken & Tomasello, 2013a).

### 3.5 Collaboration

Several researchers have studied whether children coordinate their actions to achieve a common goal, sharing the costs and likely the benefits of collaboration (e.g. Azmitia, 1988). Because limited motor skills likely impair infants to coordinate their actions, these tasks have only been done with children. From their second year of life, children can solve simple problems collaboratively (e.g. Ashley & Tomasello, 1998; Brownell & Carriger, 1990). Three- to 5-year-olds, for example, coordinate their roles to collaboratively obtain a reward, and profit from their previous experience in one role when roles are reversed (Fletcher, Warneken & Tomasello, 2012). Between 3 and 5 years of age, children also develop the ability to plan labour division in collaborative tasks (e.g. Warneken, Steinwender, Hamann & Tomasello, 2014). In the movie-viewer task, for instance, four children are presented with an apparatus that requires the collaborative effort of two children to work and only allows one child a time to view the film (e.g. Charlesworth & LaFrieniere, 1983). In this context, 3- to 6-year-olds usually collaborate, although resources are generally inequitably shared (reviewed in Green & Rechis, 2006). Pre-schoolers spontaneously collaborate with each other also in free play (e.g. Goncu & Kessel, 1988; Verba, 1994) and in structured learning tasks (e.g. Perlmutter, Behrend, Kuo & Muller, 1989). Through collaboration, low-performing children increase their performance, to the point that collaborative learning is generally recognized as an effective learning tool in education (e.g. Azmitia, 1988; Fawcett & Garton, 2005; Garton & Pratt, 2001). Interestingly, the chance to collaborate over a common goal makes the task more attractive for children, strongly suggesting that children find collaboration rewarding *per se* and are intrinsically motivated to act together in a

cooperative fashion (e.g. Bullinger, Zimmermann, Kaminski & Tomasello 2011; Butler & Walton 2013; Rekers, Haun & Tomasello 2011; see below).

### 3.6 Cognitive prerequisites for cooperation

Basic forms of coordination (i.e. emergent coordination) start early on, when infants show physiological adaptations like immobility and rapid heart rate decrease when being carried by their mothers (Esposito et al., 2013). But to engage in complex forms of cooperation and collaboration, individuals also need to share psychological states (i.e. shared intentionality), attention and goals, and be able to take different well-defined roles (e.g. Call, 2009; Tomasello, 2009; Trevarthen, 1979; Wyman & Rakoczy, 2011; see e.g. Knoblich, Butterfill & Sebanz, 2011). From early on, children have the cognitive skills and motivation to share psychological states with others, participate in joint action and read others' goals and intentions (see Call, 2009; Carpenter, 2009; Tomasello, Carpenter, Call, Behne & Moll, 2005; Tummolini & Castelfranchi, 2006). Already from 12 months of age, for example, infants repeatedly point to an interesting object, until the experimenter directs his attention to the same object and engages in joint action with the infant (Liszkowski, Carpenter, Henning, Striano & Tomasello, 2004; Liszkowski, Carpenter & Tomasello, 2007). From 18 months, infants recognize others' goals (Warneken & Tomasello, 2006), interpret goal-directed action (Csibra, Gergely, Biro, Koos, & Brockbank, 1999; Woodward, 1998), recognize intentionality (Behne, Carpenter, Call, & Tomasello, 2005), and correct unintended outcomes (Meltzoff, 1995). From 21 months of age, infants also read others' intentions, preferentially helping a partner who failed to reward them but had a clear intention to do that (Dunfield& Kuhlmeier, 2010). Ten-month-olds also understand when partners' actions are critical to reach common collaborative goals (Henderson, Wang, Matz & Woodward, 2013; but see Warneken, Graefenhain & Tomasello, 2012), and older children understand the commitments and obligations entailed in joint action, committing to the joint goal until it is pursued (Graefenhain, Behne, Carpenter & Tomasello 2009; Hamann, Warneken & Tomasello, 2012), and having analogue expectations from their partners (Warneken, Chen & Tomasello, 2006; Warneken & Tomasello, 2007; Warneken et al., 2012). Children also understand partners' roles during collaborative activities (e.g. Fletcher et al., 2012; Warneken et al., 2006), from 14 months in a rudimentary way (Warneken & Tomasello, 2007), suggesting that they grasp all roles from a sort of "bird's eye view" (Tomasello et al., 2012). Moreover, sharing requires inhibitory skills, as children have to inhibit a natural tendency to preserve their own resources to share them with others (Aguilar-Pardo, Martinez-Arias & Colmenares, 2013; also see Sheskin, Bloom & Wynn, 2014). Finally, flexible use of communication optimizes

performance in cooperative activities (e.g. Bullinger et al., 2011; Duguid et al., 2014; Dunfield, Kuhlmeier & Murphy, 2013; Liszkowski et al., 2008; Warneken et al., 2006). In the second year of life, explicit communication by the partner about her needs and/or desires seems necessary to trigger cooperative behaviour (e.g. Brownell et al., 2009, 2013; Svetlova et al., 2010).

### 3.7 Motivation: Empathy and empathic concern

In order to behave cooperatively, individuals need not only the cognitive skills, but also the motivation to do that. Several authors have suggested that empathic concern for others provides the motivation to cooperate (e.g. Eisenberg, Spinrad & Sadovsky, 2006; Hoffman, 2000; Jensen et al., 2014; Williams, O'Driscoll, & Moore, 2014). From early on, infants show empathic skills, i.e. an affective response arising from the apprehension or comprehension of others' emotional state (see Jensen et al., 2014). Infants are attuned to others' moods and emotions, and can interpret others' actions on the basis of their emotional displays (Hepach & Westermann, 2013). Even newborn infants respond with self-distress (e.g. reactive crying) when other infants are distressed (e.g. Sagi & Hoffman, 1976; Simmer, 1971), suggesting that empathy is innate in humans (see Jensen et al., 2014).

However, feeling what other feels does not necessarily imply caring for them, and the motivation to cooperate seems to rely on the empathic *concern* for others (i.e. sympathy), rather than just on empathy (see Jensen et al., 2014). Indeed, the empathic concern shown by children when observing others experiencing a negative situation positively correlates with their instances of comforting, helping or sharing with them (e.g. Eisenberg & Miller, 1987). After the first 12 months, in which empathic skills have not yet developed into real empathic concern for others (Hoffman, 2000; but see Roth-Hanania, Davidov & Zahn-Waxler, 2011), infants start differentiating others' distress from their own (Hoffman, 2000). Already in this phase, infants' cooperative behaviour appears to be intrinsically motivated by concern for others' welfare (Hepach, Vaish & Tomasello, 2013; see Prinz, 2007). Before the age of two, for example, infants experience positive emotions when providing benefits to others (Aknin, Hamlin & Dunn, 2012). However, it is possible that these positive emotions are simply triggered by previous experience, as infants and children are constantly rewarded by adults for helping, sharing and comforting others.

From 18 months of age, infants help more somebody for whom they had sympathetic concern (Vaish et al., 2009). Moreover, children are intrinsically motivated to see others being helped. Two-year-olds, for example, show similar sympathetic arousal when they help a person and when the person is helped by a third party, suggesting that children's helping behaviour is not motivated by mere concern for reputation and reciprocity (Hepach, Vaish & Tomasello,

2012). Moreover, children from the age of two find collaboration rewarding *per se* (Bullinger et al., 2011; Butler & Walton, 2013; Rekers et al., 2011), and require their partner's collaboration in the task even if they could do without (Warneken et al., 2006). Interestingly, cooperation levels also decrease after children receive a material reward for that (Fabes, Fultz, Eisenberg, May-Plumlee, & Christopher, 1989; Warneken & Tomasello, 2008), suggesting that children's motivation to cooperate is really intrinsic (see Hepach et al., 2012). However, other studies have shown a correlation between positive social interactions (e.g. cooperatively give objects) and negative social interactions (e.g. take objects away), until the second year of age (Hay, 2006; Hay & Castle, 2000). This suggests that children are not equipped with a real prosocial motivation to cooperate, but rather use cooperation as one strategy to socially interact with others, becoming really prosocial only after the second year of age (Hay, 1994).

### 3.8 Assessing partners: Familiarity

In cooperative behaviour, the selection of partners is crucial. Selecting a familiar partner, for instance, can be a successful strategy to avoid free-riding. Unsurprisingly, children's behaviour changes depending on the degree of familiarity with the partner (see Newcomb & Bagwell, 1995, for a review). Friends, for instance, collaborate better than acquaintances (e.g. Berndt 1981a, 1981b; Charlesworth & LaFrieniere, 1983), although in more competitive set-ups the reverse might be true, especially for males (e.g. Berndt 1981a, 1981b). The degree of familiarity with the partner also affects children's tendency to share (e.g. Birch & Billman, 1986; Fehr et al., 2008; Moore, 2009) and comfort (e.g. Zahn-Waxler et al., 1992), and the way in which resources are divided. After a collaborative effort, for instance, children from 6 years of age share equally with their friends, but according to their contribution with less familiar partners (Pataki, Shapiro & Clark, 1994).

### 3.9 Assessing partners: Fairness

The selection of partners might also depend on the way they share resources. Children attend to the outcome of resource distributions from around 10 months of age (Geraci & Surian, 2011; Meristo & Surian, 2013), showing greater attention to unfair outcomes from 15 months (Sommerville, Schmidt, Yun & Burns, 2013). Interestingly, more cooperative infants (i.e. donating a preferred toy) are more concerned about fairness than less cooperative ones (i.e. donating a not-preferred toy; Schmidt & Sommerville, 2011). Three-year-olds notice and react negatively to unfair distributions, particularly when receiving less (LoBue, Nishida, Chiong, deLoache & Haidt, 2011). They also collaborate over trials to obtain monopolizable rewards, expecting that resources will be nonetheless fairly

divided at the end (Warneken, Lohse, Melis & Tomasello, 2011). From 4–5 years of age, children start sharing with more fairness (e.g. Rochat et al., 2009), and between 5 and 7 years of age most children share with equality (e.g. Blake & Rand, 2010; Fehr et al., 2008; Graziano, Musser, Rosen, & Shaffer, 1982; Hook & Cook, 1979; McAuliffe, Jordan & Warneken, 2015; Smith, Blake & Harris, 2013). By the age of 8–9, children systematically reject unequal advantageous offers and redistribute resources in a more equal way (e.g. Bereby-Meyer & Fiks, 2013; Blake & McAuliffe, 2011; Kogut, 2012; Murnighan & Saxon,1998; Takagishi, Kameshima, Schug, Koizumi, & Yamagishi, 2010; but see Sheskin et al., 2014).

From 3 years of age, children treat resources generated collaboratively in special ways (Tomasello et al., 2012), sharing more equally after collaborative efforts (Hamann, Warneken, Greenberg & Tomasello, 2011; Warneken et al., 2011). Moreover, children take merit into account (e.g. Baumard, Mascaro & Chevallier, 2012), expecting equal distributions for equal efforts from 21 months of age (Sloane, Baillargeone & Premack, 2012; Warneken et al., 2011) and partially sharing depending on the relative contribution to the task from 3 years of age (Almas, Cappelen, Sorensen & Tungodden, 2010; Hamann, Bender & Tomasello, 2013; Melis, Altrichter & Tomasello, 2013). Some authors have therefore suggested that equality is favoured by collaborative situations, and that mutualistic collaboration may have laid the evolutionary foundation for the emergence of equality (Warneken & Tomasello, 2014).

Furthermore, children are more concerned about partiality than inequality. From 5 years of age, children prefer to use impartial procedures to share resources (Shaw & Olson, 2014), and they reject unequal offers when equal offers are possible (Wittig, Jensen & Tomasello, 2013). Although 5-year-olds propose and accept unfair offers by humans and machines, 8-year-olds reject unfair offers by humans and 12-year-olds reject all unequal offers (Bereby-Meyer & Fiks, 2013). Finally, children's dominance status and sex also affect the distribution of resources, with higher-ranking males often fighting for access to more resources, instead of sharing fairly (reviewed in Green & Rechis, 2006).

### **3.10** Assessing partners: Reputation

If partners are not familiar, cooperators might select them based on their reputation. From 3 months of age, infants already evaluate others based on their behaviour toward third parties (Hamlin & Wynn, 2011; Hamlin, Wynn & Bloom, 2007, 2010). Although 5-month-olds generally prefer individuals who cooperate with others, 8-month-olds would already show very sophisticated ways of assessing partners, preferring those acting positively toward cooperative individuals and negatively toward antisocial individuals (Hamlin, Wynn, Bloom & Mahajan,

2011). However, this series of studies has not yet been replicated in other laboratories, and has been questioned by other authors offering a different interpretation of the results (e.g. Scarf, Imuta, Colombo & Hayne, 2012a, b). For instance, infants' choices in these studies might have been driven by simple association or/and by valence matching, instead of by a sophisticated assessment of partners (Scarf et al., 2012a, 2012b). In particular, infants may associate the positive/negative valence of an event (i.e. reaching/not reaching a goal) to individuals acting in temporal proximity of the event (i.e. the actor behaving positively to cooperative individuals or negatively toward antisocial individuals). Importantly, this alternative explanation would not be ruled out by the fact that infants prefer individuals who are prosocial to victims of previous negative events: indeed, valence matching happens between temporally close events, and the prosocial individual assumes a positive valence by being temporally close to the positive event, while the previous victim assumes no valence at all, as the actions performed began too early on (Scarf et al., 2012a). Other studies have confirmed the findings from Hamlin and colleagues (2011), but only in children from around two years of age, showing that children prefer partners who were prosocial to others (Dahl, Schuck & Campos, 2013; Herrmann, Keupp, Hare, Vaish & Tomasello, 2013; Kato-Shimizu, Onishi, Kanazawa & Hinobayashi, 2013; Kenward & Dahl, 2011), and are aversive to partners who were antisocial to others (Hamlin et al., 2010; Vaish, Carpenter & Tomasello, 2010). However, other studies have failed to find differences in cooperative behaviour depending on the partner, with infants and 2.5-year-old children helping and sharing with others almost indiscriminately (Sebastian-Enesco, Hernandez-Lloreda & Colmenares, 2013; Warneken & Tomasello, 2009).

Knowing that they are judged by others, humans might be concerned by their own reputation and adjust their behaviour to signal their own fairness to potential partners (e.g. Haley & Fessler, 2005; Leimar & Hammerstein, 2001; Nowak & Sigmund, 1998; Shaw, 2013). Children, for example, share more, steal less and behave more fairly when they are observed (Engelmann, Herrmann & Tomasello 2012; Leimgruber, Shaw, Santos & Olson, 2012; Piazza, Bering & Ingram, 2011; Shaw, Montinari, Piovesan, Gino & Norton 2014), especially by in-group members (Engelmann, Over, Hermmann & Tomasello 2013). In contrast, Warneken and Tomasello (2013b) found that children do not help more when others watch or encourage them.

### **3.11** Assessing partners: The in-group bias

When others are not familiar and information on their reputation is not available, people might use other strategies to decide whether to cooperate. Humans, for instance, might have evolved a bias for indicator traits (e.g. language, race,

dress) that match their own and hint to a common membership to the same social group, whose members should share the same social norms and be more reliable partners in cooperative interactions (e.g. Ben-Ner, McCall, Stephane & Wang, 2009; Boyd & Richerson, 2009; Henrich & Henrich, 2006; McElreath et al., 2003; Panchanathan & Boyd, 2003; Wynn, 2009). From 18 months, infants increase cooperative behaviour when being mimicked (Carpenter, Uebel & Tomasello, 2013). Preschool children already show in-group preferences, including different attitudes and resource allocation, expectations of reciprocity and encoding of positive information about in-group members, even when groups are formed via random assignation (e.g. Dunham, Baron & Carey, 2011; Fehr et al., 2008; Patterson & Bigler, 2006; see Mullen, Brown & Smith, 1992, for a review). Three-year-olds understand when they share cultural common ground with others (Liebal, Carpetner & Tomasello, 2013). They actively protest violation of moral norms (i.e. norms with a wider scope, valid for all humans) for in- and out-group members, but enforce conventional norms (i.e. norms with a narrower scope, only valid for those who agree on them) for in-group members only, suggesting that they somehow hold in-group members to a higher standard (Schmidt, Rakoczy & Tomasello, 2012).

Language is probably the most powerful cue to group membership (e.g. Wynn, 2009; Cohen, 2012). From 6 months of age, infants use language and speech accent to select in-group members as cooperative partners, showing social preferences for partners with the same language or accent (e.g. Buttelmann, Zmyj, Daum & Carpenter, 2013; Cohen & Haun, 2013; Kinzler, Corriveau & Harris, 2011; Kinzler & deJesus, 2013; Kinzler, Dupoux & Spelke, 2007; Kinzler, Shutts, deJesus & Spelke, 2009; Shutts, Kinzler, McKee & Spelke, 2009). Children also encode and retrieve own- and other-race faces from memory in qualitatively different ways (Anzures, Kelly, Pascalis, Quinn, Slater & de Vivies, 2014). However, social preferences for own-race individuals only emerge around 3.5 years of age (Kinzler & Spelke, 2011), and are easily reversed when more reliable cues to detect in-group members are available (Kurzban, Tooby & Cosmides, 2001).

In-group biases are already present in preschool children, while out-group aversion develops only from school age onward (Buttelmann & Boehm, 2014; Inguglia & Musso, 2013). Negative attitudes toward out-group members are common in children (e.g. Killen & Rutland, 2011; Nesdale, 2004), and scarcity of inter-group contacts enhances the risk of prejudices and exclusion (e.g. Abrams & Killen, 2014; Bennett, 2014; Kouider, Koglin & Petermann, 2014; see Pettigrew, 1998). However, acceptance of out-group members is higher when they support in-group norms (e.g. Abrams & Rutland, 2008; Mulvey, Hitti, Rutland, Abrams & Killen, 2014). Close identification with a group enhances levels of self-esteem (e.g. Corenblum, 2014) and can boost children's motivation to learn (e.g. Master & Walton, 2013).

### 3.12 Shared norms and conformity

Children are socialized into a world of social norms, to which they are expected to and desire to conform (Haun & Tomasello, 2011; Schmidt & Tomasello, 2012; Tomasello & Vaish, 2013). This conformity to social norms is crucial to align children with the social group they belong to (see Jensen et al., 2014). From 2 years of age, children show evidence of conformist and prestige-biased transmission, following the majority (e.g. Corriveau, Fusaro & Harris, 2009; Corriveau & Harris, 2010; Haun, Rekers & Tomasello, 2012; Nielsen & Blank, 2011) or the most reliable models (e.g. Chudek, Heller, Birch & Henrich, 2012; Rakoczy, Hamann, Warneken & Tomasello, 2010; Rakoczy, Warneken & Tomasello, 2009). Interestingly, the tendency to conform is so strong that children switch to the technique used by the majority, even when their own was more efficient (Haun & Tomasello, 2011).

Children not only respect, but also create and transmit their own social norms (Göckeritz, Schmidt & Tomasello, 2014). Importantly, they actively enforce norms toward third parties (e.g. Schmidt, Rakoczy & Tomasello, 2012; Wyman, Rakoczy & Tomasello, 2009; see Rakozcky & Schmidt, 2013;Schmidt & Tomasello, 2012, for reviews), even if norms do not directly involve them or are completely arbitrary (Rossano, 2012; Schmidt & Tomasello, 2012). From 2 years of age, for instance, children intervene when someone does not conform to the norms (e.g. Rakoczy, Warneken & Tomasello, 2008). Around 3 years of age, children differentiate between moral and conventional norms (Rossano, Rakoczy & Tomasello, 2011; Schmidt et al., 2012; Vaish, Missana & Tomasello, 2011), learning the latter by observation (Schmidt, Rakoczy & Tomasello, 2011) and defending others' entitlement against unjustified interferences by second parties (Schmidt, Rakoczy & Tomasello, 2013). Four-year-olds report norm violations committed by others (Ingram & Bering, 2010) and recognize the appeasement functions that explicit apologies serve, but only 5-year-olds show more positive evaluations of norm violators expressing regret for the harm they caused (Vaish, Carpenter & Tomasello, 2011).

### 3.13 Punishment

Humans may exclude free-riders from future interactions by disrupting their reputation (Boehm, 2012; Tomasello et al., 2012), or they can enforce future cooperation by punishing them, even in the form of altruistic third-party punishment (Boyd, 2006; Boyd et al. 2010; Fehr & Fischbacher, 2004; Fehr & Gaechter, 2002; but see Dreber, Rand, Fudenberg & Nowak, 2008). Children from three years of age are willing to punish even if they need to incur in some costs for that, they protest against norm violations and are cooperative toward those who were harmed (e.g.

Kenward & Östh, 2012; Rossano et al., 2011; Vaish et al., 2011). Six-year-olds, for instance, punish others for making unfair offers to third parties, even at their own cost (McAuliffe et al., 2015). Even 8-month-old infants would selectively prefer characters being nice to prosocial individuals and not nice to antisocial individuals (Hamlin et al., 2011). However, third-party punishment is biased in favour of in-group members: 6-year-olds, for instance, punish selfish allocation of resources more when it is proposed by out-group members or if it disadvantages in-group members, although this bias reduces with age (Jordan, McAuliffe & Warneken, 2014).

## 4. Inter-cultural differences in cooperation

Most of our knowledge about cooperation comes from studies in Western large-scale industrialized societies, which can be hardly considered to be representative of all humans (Henrich, Heine & Norenzayan, 2010). Only in the last years, researchers have started analysing how humans cooperate in small-scale non-industrialized societies. These studies have provided evidence of general commonalities (e.g. humans share in all cultures), but also of important inter-cultural differences (e.g. the tendency to share and the sense of fairness strongly differ across cultures: Gintis, Bowles, Boyd & Fehr, 2003; Henrich et al., 2006, 2010; Marlowe et al. 2008). Even less is known on the way cooperation develops in other cultures. This is especially problematic, as knowing when inter-cultural differences emerge during development can reveal the relative role of genetic and cultural factors in shaping these differences (i.e. which cooperative traits are common across cultures in early ontogeny, and which ones are not; see e.g. Callaghan et al., 2011).

To date, few studies have studied inter-cultural diversity in the way children cooperate. Rochat and colleagues (2009) studied sharing in 3- and 5-year-olds from seven different cultural or socio-economic groups. When asked to distribute resources, children in all cultures tended to be more equitable when they did not benefit from the distribution, and allocated more resources to themselves when taking part in the distribution. However, the extent to which they did so depended on their cultural background, with North American children and unschooled Brazilian children living with no adult supervision allocating resources in a more selfish way as compared to Chinese, Peruvian, Fijian and schooled Brazilian children. While children across cultures became increasingly more generous with age, children from small rural communities (e.g. Peru and Fiji) already shared quite equally at three years of age. These results suggest that children from small-scale urban regions and non-industrialized villages have a higher tendency to be

cooperative and distribute resources equitably (Rochat et al., 2009). Similar results were obtained when comparing North American and Samoan 5-year-olds in the way they distributed resources among themselves, a generous puppet and a stingy puppet (Robbins & Rochat, 2011). While North Americans distributed the greatest amount to themselves, gave more resources to the generous puppet and sometimes punished the stingy one, Samoan children allocated the fewest resources to themselves, did not give more resources to the generous puppet and did not systematically punish the stingy one. These results suggest that in more collectivist cultures, like the Samoan one, children's sharing behaviour might develop toward more egalitarian forms (Robbins & Rochat, 2011). Indeed, also in rural Africa children from egalitarian hunter-gatherer groups share more frequently and with more equality than German children (Schaefer, 2014). Observations of natural sharing interactions in children confirm these findings, with children sharing more frequently and spontaneously in collectivistic cultures (e.g. Birch & Billman, 1986; French, Chen, Chung, Li, Chen & Li 2011; Rao & Stewart, 1999). Similarly, children living in more egalitarian cultures share resources after a collective effort according to equality and inter-personal harmony, rather than according to the relative contribution, as Western children instead do (e.g. Carson & Banuazizi, 2008; Schaefer, 2014). Importantly, the way in which resources are shared in small- and large-scale societies increasingly differs as children get older (House et al., 2013), when the social norms typical of their cultures have been internalized.

Inter-cultural differences have also been found in the way 5-year-olds in Western and South-East Asian cultures express empathic concern toward others' distress (Trommsdorff, Friedlmeier & Mayer, 2007). In particular, Western children show less self-focused distress and more comforting and helping behaviour than South-East Asians, possibly because Western cultures are less hierarchical (i.e. allowing children more initiative) and less inter-dependent (thus showing less self-distress in response to others' problems). Differences in developmental trajectories for cooperative behaviour have also been found between 19-month-olds from more collectivistic cultures (promoting more interdependence and less autonomy) and Western cultures (where the development of cooperation seems to rely more on empathic concern for others: Kärtner, Keller & Chaudhary, 2010).

Culture also affects the way in which roles are divided during collaborative efforts. African American siblings, for instance, collaborate by sharing activities, while European Americans divide up labour and direct each other (Budak & Chavajay, 2012). Similarly, Mayan fathers with little scholastic education collaborate with their children to solve a puzzle by sharing a common agenda, while fathers with higher education structure their contributions through a strict division of labour (Chavajay, 2008). These results suggest both important inter-cultural differences in the way collaboration works and a dangerously homologating effect of

Western education on these differences. In particular, Western schooling may be gradually transforming the collaborative social organization of indigenous groups, by promoting individual performance, division of labour and stricter hierarchical interactions during task solving (see Chavajay, 2008). Overall, these studies confirm that cooperative behaviour is the result of a complex interaction of genetic and cultural factors (e.g. Chudek & Henrich, 2011; Henrich et al., 2010). From early on, children internalize the social norms of the culture they live in, which promote different degrees of inter-dependency and different notions of how cooperation should work, leading to the emergence of different preferences and motivations when cooperating.

## 5. Conclusions

Cooperation in humans has surely attained a unique level of sophistication as compared to other species (also see the contributions by Albiach-Serrano and Braeuer). From a developmental perspective, infants are born empathic and show simple forms of coordination. Around 10 months, they already attend to the outcome of resource distributions. From one year, infants show the first instances of helping behaviour. At 24 months, they consistently comfort others and start sharing resources with them. Importantly, 2-year-olds have both the motivation and cognitive skills to cooperate. During their second year of life, they have developed empathic concern, the ability to share psychological states and attention, understand others' goals and intentions, take others' perspective and communicate. At this age, children also make complex evaluation of partners, and show conformist and prestige-biased transmission. From 2 years of age, children solve simple problems collaboratively, and start treating resources generated collaboratively in a special way. Crucially, the motivation to cooperate with others seems to be intrinsic. Consistent forms of direct and indirect reciprocity only emerge around three years of age, when children show the first instances of norm conformity and punishment of uncooperative individuals. In the following years, they develop in-group bias and then out-group bias, and a more sophisticated sense of fairness. From an inter-cultural perspective, cooperation appears to result from a complex interaction of genetic and cultural factors: differing across cultures, social norms determine different degrees of inter-dependency and different notions of cooperation, and ultimately the emergence of different preferences and motivations when cooperating.

The developmental and inter-cultural analysis of cooperation allow us assessing the plausibility of the two main evolutionary scenarios, i.e. whether cooperation emerged from the interaction of culture with either *reciprocity*

(e.g. Henrich & Henrich, 2006, 2007; Richerson & Boyd, 2005) or *collaboration* (Tomasello et al., 2012). Overall, the studies reviewed here seem to support the hypothesis that simple forms of mutualistic collaboration more likely provided the context for complex forms of cooperation to evolve. While infants engage in cooperative and collaborative behaviour from an early age, and seem to be intrinsically motivated to do that, with little substantial difference across cultures, reciprocity emerges later on during development.

The studies reviewed here also allow us better understanding whether humans are born with *complex specialized* cognitive and motivational skills to cooperate (e.g. Hamlin, 2012; Wynn, 2008), with a *prosocial* motivation to cooperate with others (e.g. Warneken & Tomasello, 2009), or with the *social* motivation to be with others (e.g. Hay, 2009), which gradually develop into more complex forms of cooperation (also see Sebastián-Enesco, 2014). Overall, we found no convincing evidence that humans are born with *complex specialized* cognitive and motivational skills to cooperate. Indeed, some studies show that very young infants already have sophisticated cooperative skills (e.g. Hamlin et al., 2007, 2010, 2011; Hamlin & Wynn, 2011), but a more parsimonious interpretation of these studies is also possible (e.g. Scarf et al., 2012a, b). In line with this, the majority of studies provide empirical support to a later emergence of complex cooperative skills, so that more research is yet needed to support Hamlin's (2012) and Wynn's (2008) claims.

At the moment, it is yet unclear whether the motivational mechanisms behind cooperation and collaboration in children are really *prosocial* (i.e. to cooperate with others: Warneken & Tomasello, 2009) or simply *social* (i.e. to be with others: Hay, 2009). Evidence supporting the first hypothesis comes mainly from three findings: (i) children spontaneously and flexibly cooperate and collaborate, (ii) they are intrinsically motivated to do so, and (iii) they partially share this motivation with our closest relatives, the great apes, suggesting that humans might have a phylogenetically inherited motivation to cooperate (see e.g. Warneken & Tomasello, 2014). However, although the first claim is rather uncontroversial, the last two are more problematic. Despite previous claims (Warneken & Tomasello, 2013b), evidence cumulates that cooperation levels drop when anonymity is clearly implemented (e.g. in adults: Haley & Fessler, 2005; Hoffman, McCabe, Shachat & Smith, 1994; Franzen & Pointner, 2012; in children: Engelmann et al., 2012, 2013; Leimgruber et al., 2012; Piazza et al., 2011; Shaw et al., 2014), or in more natural set-ups (e.g. Winking & Mizer, 2013; Xiao & Houser, 2005). Cooperating when others observe us (or in experimental set-ups, where we can assume to be observed) can involve interest in our own reputation much more than real prosocial motivation. Wynn (2009) argued that help by children is rarely useful for adults, but their tendency to be cooperative might emerge so early in development

to generate goodwill and affection in adults. Infants might start out being cooperative to conform to their parents and please them, rather than out of concern for others' welfare. From early on, children receive tons of inductions from their parents, pushing them to be cooperative in thousands of daily interactions (see Hoffman, 2000). Infants are born so helpless, that pleasing adults and having their praise (e.g. by being cooperative) might simply enhance their chances of survival. Moreover, even the existence of free-riding and in-group bias seems to contradict the existence of a pure prosocial motivation. If humans were really cooperating out of concern for others' welfare, they should do that unselectively (i.e. the in-group bias should emerge only later on during development, if ever, as a reflex of cultural influences), and instances of unfairness and parochialism should be few, which is not the case. Even more problematic is the claim that humans partially share the motivation to cooperate with great apes, as evidence of collaboration and cooperation in great apes is yet scant and often unreliable, due to serious methodological flaws (see e.g. the contribution from Albiach-Serrano; Amici et al., 2014). At the moment, therefore, no clear conclusions can be drawn on the existence of real *prosocial* motivation in young children.

In contrast, these findings seem to be in line with the more general view that children's motivation to cooperate is *social* (rather than *prosocial*), and that children engage in cooperative and collaborative behaviour simply as a reflex of their sociality (Hay, 2009; Hay & Cook, 2007). For instance, the finding that children prefer to collaborate even when they could solve the task alone can also be interpreted as children being motivated to be with others. Even the preference to cooperate with familiar partners might be seen as a preference to be with closer partners (see Paulus & Moore, 2012). This is in line with the fact that humans are equipped with complex forms of social skills from early on (e.g. Call, 2009; Carpenter, 2009), and are especially attracted to social stimuli (e.g. Cohen & Cashon, 2006; Keen, 2003). Like other social species, humans are motivated to be with their conspecifics and likely evolved the cognitive skills to relate to others both in positive ways (e.g. cooperation) and negative ways (e.g. competition). Depending on the context and partly on the cultural background, this social motivation might result in either cooperation or competition. Indeed, empirical evidence shows that the development of negative and positive social interactions (like cooperation) is strictly bounded, and real prosocial motivations only emerge later on during development (see Hay, 1994). Future studies will need to better disentangle social and prosocial motivations to cooperate during children's development. Another related aspect that remains unclear is whether all cooperative behaviours rely on the same motivation. Although children are able to help, share and comfort, the developmental trajectories of these behaviours are not identical (e.g. Dunfield et al., 2011; see Paulus & Moore, 2012). Future studies should address whether these differences

depend on the different cognitive skills that each of these forms of cooperation requires (which might develop at different stages), or whether other motivational factors rather explain these differences.

Finally, this review highlights two important aspects of research on human cooperation. Firstly, the greatest majority of the studies reviewed here have been conducted in the lab, where experiments can be planned in detail and control conditions included. However, performance can dramatically differ depending on the experimental procedures used, and between individuals tested in the lab and in everyday life (see e.g. Levitt & List 2007, 2008; cf. Green & Rechis, 2006). In particular, humans react differently in the lab, being for instance more generous than in everyday life. In the future, it will be beneficial to use a wider range of experimental approaches with a greater ecological validity, including observations of children in natural set-ups (see Guala, 2012; Winking & Mizer, 2013) and among peers (e.g. Forsman & Hummelstedt-Djedou, 2014). This will allow us drawing stronger conclusions on cooperative behaviour, while also reducing the effect of reputation-concerns, which might be triggered by the presence of adults and experimental set-ups. Secondly, inter-cultural studies reveal both similarities and differences in the way we cooperate: although all humans share, comfort and help others, the way we do that is strongly affected by the culture we belong to, and differences increase through development. These results confirm the importance of using an inter-cultural approach to study human behaviour, not only to avoid generalizations that might lead to wrong conclusions (see Henrich et al., 2010), but also to appreciate the extent to which cooperation is based on a fixed biological basis (e.g. Decety, 2011) rather than shaped by cultural factors during development. Our enviable task for the future is to develop new approaches to the study of cooperation, to better unravel its developmental and evolutionary origins.

## Acknowledgments

I would like to thank Anna Albiach-Serrano, Federico Rossano, Shona Duguid and Lucas Bietti, for providing very helpful comments on a previous version of this draft, and Carla Sebastian-Enesco for fruitful discussions and help during the organization of the workshop.

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