Abstract

The cooperative character of language is an empirical fact and one of the key tenets in linguistics. However, this cooperative character is what makes it evolutionarily suspect: under normal circumstances sharing honest information with biologically unrelated individuals and without any obvious costs is not an ESS (evolutionarily stable strategy) and is not expected to evolve. Here we approach this problem in the context of prototypical language use (also evolutionarily), that is face-to-face conversation, a multimodal interaction unfolding in real time that involves a complex interplay between embodied agents in spatial proximity. We focus our review on low-level coordinative processes – examples being proxemic alignment or postural mirroring – to a large degree continuous with what is found in non-human primates. We aim at categorisation and terminological clarification of these processes, which in turn helps us evaluate their role in initiating and maintaining cooperatively oriented communicative interaction. We conclude with suggesting ways in which such low-level coordinative processes might have formed an evolutionary basis for cooperation, with focus on the possible role of TFT (tit-for-tat) and TFT-like strategies.

Keywords

language origins, language evolution, cooperation, coordination, conversation, synchrony, mimicry, honest signalling

1. Introduction

When considered from a rigorously (neo)Darwinian perspective characteristic of modern language evolution research, conversation is problematic. Conversation involves parties sharing honest information (also) with biologically unrelated individuals, rather than using the strategies predicted by the standard signalling theory, i.e. keeping information to oneself or even manipulating the other party. Cooperation of this sort is generally not considered an evolutionarily stable strategy and is not expected to evolve under normal circumstances (Krebs and Dawkins, 1984).

Researchers into language evolution are acutely aware of this problem, by now a classic one, as well as of its importance (Tomasello, 1999, 2008; Hurford, 2007; Fitch, 2010; Dor et al., 2014). It manifests itself in two complementary versions: *why listen*, given that you stand a risk of being manipulated to the other party's advantage (Krebs and Dawkins,

1984), and *why talk*, given that others, wary of the possibility of deception, should not listen to you (Dessalles, 2014). It is true that normative mechanisms against dishonesty – such as formal obligations or reputation – help explain the stability of cooperative communication in modern humans (Gärdenfors, 2008, 2012; Nowak, 2006, Nowak and Sigmund, 2005; Sperber et al., 2010), but such mechanisms are themselves language-dependent and cannot be presupposed from the "origins" point of view. Although several explanatory frameworks have been proposed (see section 2), "the cooperative sharing of information […] remains a central puzzle in language evolution" (Fitch, 2010: 417).

However, the cooperative character of conversation is a fact (Grice, 1975; Clark, 1996; cf. also Żywiczyński and Wacewicz, 2012). We approach this paradox from the perspective of the interactional logistics of conversation. In what follows, we present an overview of the literature on low-level mechanisms of interactional coordination (*micro-coordination*), i.e. such that do not directly transmit propositional content but nevertheless facilitate smooth and focused interaction. The overview leads to a classification of these mechanisms into *synchrony*, responsible for temporal coordination of interactants' behaviours, and *mimicry*, responsible for similarity in the form of interactants' behaviours (section 3). Finally, we bring the two together by reviewing evidence for the link between low-level coordination and cooperation, and we conclude by exploring the possible mechanisms behind this link on the ultimate level (section 4).

2. Cooperation in conversation

2.1. Cooperation: definition

Numerous definitions of cooperation exist (see e.g. West et al., 2011). Our discussion here is specifically constrained by the game-theoretic perspective based on quasi-economic cost-benefit analysis. So construed, cooperation is a general problem, fundamental to behavioural ecology and the entire evolutionary paradigm. Within that perspective, some authors predicate cooperation upon the benefit to the other party rather than the possible cost[1]. However, very many authors underscore the initial cost to the actor, hence highlighting the *altruistic aspect of cooperation* (or even treating cooperation as synonymous to altruism)[2].

[1] "Cooperation: a behaviour which provides a benefit to another individual (recipient), and which is selected for because of its beneficial effect on the recipient" (West et al., 2007).

[2] "A cooperator is someone who pays a cost, c, for another individual to receive a benefit, b" (Nowak, 2006). "Cooperation occurs when an individual incurs a cost in order to provide a benefit for another person or people" (Henrich and Henrich, 2006).

This is because the altruistic component is the most problematic and thus interesting aspect of cooperation from the perspective of game theory, and evolutionary game theory specifically.

Accordingly, we limit "cooperation" to altruistic rather than "selfish" cooperation (Stevens and Hauser, 2004). Selfish cooperation or *mutualism*[3] – behaviours that generate "immediate synergistic benefits shared by cooperators that exceed the costs of providing assistance" (Clutton-Brock, 2009: 51) – are excluded because they do not present a theoretical problem from the game-theoretic perspective. As mentioned in the introduction, "true" cooperation is problematic because, unlike mutualism, it contradicts the "economicus" stance, i.e. is not accounted for by the calculation of immediate gains and losses.

The situation is complicated by the fact that in the various literatures relevant to language evolution, "cooperation" is frequently used in a much less restrictive way, closer to the rather fuzzy vernacular meaning. In this sense, it may simply indicate "collective action" of more than one individual resulting in a net benefit[4], or even coordinated joint action in general[5]. In such contexts, we prefer the looser term *collaboration*, restricting "cooperation" to phenomena that are interesting from the game-theoretic perspective because of the initial altruistic element.

2.2. Cooperation in language

As stated before, the extensively cooperative character of language is what makes it evolutionarily suspect: under normal circumstances sharing honest information with biologically unrelated individuals and without any obvious costs is not an ESS (evolutionarily stable strategy) and is not expected to evolve (e.g. Fitch, 2010; cf. Krebs and Dawkins, 1984). Resolving this apparent paradox is possible by looking into either the communicative process itself, or into more general human dispositions lying at its foundation. On the one hand, under certain narrowly defined circumstances, cheap but honest (thus, cooperative) signalling can emerge and remain stable even in a population of individuals with conflicting genetic interests (Silk et al., 2000; Lachmann et al., 2001). On the other, humans are an unusually cooperative species not just in the domain-specific

[3] Some authors prefer "mutual benefit" (West et al., 2007).
Note that like with "cooperation", we use "mutualism" in the specific sense inspired by the game-theoretic paradigm – for a broader perspective on this and similar terms, see e.g. Gontier (2016).

[4] "To co-operate is to work together for a joint benefit" (Brinck and Gärdenfors, 2003).
"Cooperation is an outcome that – despite potential costs to individuals – is <good> (…) for the members of a group (…) and whose achievement requires some sort of collective action." (Dugatkin, 1998)

[5] "Interaction is by and large cooperative, [i.e.] there is some level... at which interactants intend their actions to… *contribute to some larger joint undertaking* (having a conversation, making a hut, even having a quarrel!)" (Levinson, 2006: 45; italics: SW, PZ, AC])

context of communication but in a domain-general way, so our honest signalling does seem to be a special case of a more general disposition, grounded in a one-of-a-kind, species-specific cooperative socio-cognitive infrastructure (Tomasello, 2008).

Large bodies of recent literature explore this second route: the evolutionary mechanisms that would have produced unusual prosociality in hominin groups (see e.g. Zlatev, 2014 for review). This would have enabled stable cooperation in general, also producing the cooperative infrastructure required for honest-cum-linguistic communication. Examples include reproductive levelling and counterdominance (Knight, 1991, 1999, 2014) or cooperative breeding (Hrdy, 2009). Fitch (2010) and the proponents of the motherese conceptions (e.g. Falk, 2004) turn to kin selection (Hamilton, 1964), hypothesising that the emerging systems of honest signalling were stabilised by the genetic proximity of its first users: mothers and children. In fact, explanations of how honest signalling in humans came to be have appealed to most of the available mechanisms of the emergence of cooperation, including reciprocal altruism (Trivers, 1971; in language evolution see e.g. Ulbæk, 1998), altruistic communication as a handicap (Zahavi, 1995; in language evolution see e.g. Dessalles, 1998) or third-party sanctions as the prerequisite for honest communication (Boyd and Richerson, 1996; in language evolution see e.g. Boyd and Mathew, 2015).

2.3. Conversation

In simplest terms, conversation is the use of language in which two (dialogue) or more parties (multilogue) freely[6] take turns at talking (Levinson, 1980: 83). Its prototypical form consists in casual talk, i.e. face-to-face interaction carried out in relaxed social settings (Dunbar et al., 1997: 231-232) and not motivated by express pragmatic purpose (Eggins and Slade, 1997: 19). Most of conversational phenomena are local in scope, operating on a turn-turn basis, including the rules for changing speaker-listener roles (i.e. the turn-taking system; Sacks et al., 1974), projecting turn-types (related to the organisation of conversation into adjacency pairs, e.g. question-answer, request-acceptance, etc.; Sacks and Schegloff, 1973) or correcting misunderstanding or mishearings (i.e. the repair system; Schegloff et al., 1977). Since conversation typically takes place with participants' facing each other (Goffman, 1967), it is a socially intimate and profoundly multimodal form of communication (e.g. Bavelas et al., 1992). Although linguistic exchanges are carried out in the vocal auditory

[6] In certain, institutionalised, types of conversation this freedom is constrained with respect to e.g. the type of turn participants are allowed to take, their length and even the register of the language they use; for a more extensive explanation see Drew and Heritage (1992).

channel, the dynamics of conversation to a significant degree depends on non-verbal cues and signals, most of which are visually transmitted through eye contact (e.g. Ho et al., 2015), gestures (e.g. Clark and Lindsey, 2015; in a wide sense including orofacial gestures, cf. Wacewicz et al., 2016), facial expressions (e.g. Torreira et al., 2015) or posture (e.g. Kendon, 2010).

The intuitively appealing idea that conversation is the prototypical use of language (Levinson 1980, Dunbar et al. 1997) has found sound empirical support. From the ontogenetic perspective, conversational input (i.e. face-to-face interaction in which a child is spoken to) has been identified as the crucial factor in the child's linguistic development (e.g. Trevarthen, 1998). Numerous lines of evidence within the field of language evolution research itself suggest that conversation – understood as a medium of social interaction – is also the phylogenetically primary form of language behaviour. The exact role which proto-conversations played at early stages of language evolution is variously assessed as being related e.g. to display and courtship (Dessalles, 2007), intra-group cooperation (Gärdenfors 2003), and vocal grooming and babbling (Dunbar 1993, 1996; MacNeillage, 2008).

2.4. Levels of cooperation in conversation

The general claim that linguistic communication is essentially cooperative expresses a very sound consensus (Grice, 1975; Clark, 1996; Gärdenfors, 2004; Hurford, 2007; Fowler et al., 2008; Tomasello, 2008; cf. Żywiczyński and Wacewicz, 2012). However, unpacking this claim turns out to be surprisingly difficult. This is mostly because the parties to this consensus work from a variety of theoretical approaches within language evolution, and as a result, the term "cooperation" assumes a variety of different meanings, from the technical to the looser, more intuitive ones of collaborative effort or even coordinated joint action (section 2.1). It is critical to recognise that although such looser usage is by no means incorrect, it correspondingly dilutes the problem of the origins of cooperation and may effectively remove its rationale for theoretical interest, because from the evolutionary perspective this problem is defined as a game-theoretic one.

Secondly, cooperation in language in general, and in conversation more specifically, is a multi-level phenomenon. As one example, Hurford (2007: 270) distinguishes between what he calls *communicative* and *material* cooperation. The former is participating in the communicative act itself, in accordance with the standards; Hurford likens it to "playing by the rules" in a competitive sport such as tennis as opposed to "not showing up to the game".

Material cooperation, in turn, concerns the content of the utterances and the practical utility of such information, e.g. pointing to the location of food sources. Below, we put forward a different classification of the levels of cooperation (within our game-theoretic approach): one that is based on its relation to discourse while also tracking the type and amount of resources invested into the interaction.

2.4.1. Material cooperation

On the present definition, material cooperation is extra-discursive: it takes place over and above conversational interaction. Materially cooperating agents expend real-life resources to achieve real-life goals, such as moving a heavy sofa up the stairs, pursuing a joint project or operating a sailboat; examples closer to the human Environment of Evolutionary Adaptedness would include grooming, cooperative hunting, reciprocated foodsharing or teaching of toolmaking[7].

While it might not be unique to our species, material cooperation (between non-kin) is prevalent only in humans and is quite essential to the everyday functioning of human societies. It does not need to have a strictly linguistic character, but language clearly acts to stabilise cooperation and suppress defection, most likely through a variety of mechanisms. Particularly rich evidence comes from the game theoretic perspective (specifically, the Social Dilemma / Trust paradigm), where a very large number of studies have confirmed a clear effect of communication on the degree of cooperation, especially verbal communication relevant to the task (e.g. Kerr and Kaufman-Gilliland, 1994; Ledyard, 1995; Sally, 1995; Goren and Bornstein, 2000; Jeffreys, 2006; Brandts et al., 2015; Andrighetto et al., 2016)[8].

Language also provides an entire toolkit for establishing and maintaining complex cooperative action. The tools are not only communicative, serving to coordinate the concerted efforts of multiple individuals in real time, but also cognitive – such as shared detached symbolic representations necessary for anticipatory (or prospective) planning and establishing joint goals (see Gärdenfors, 2004). Ample experimental support also exists for the above effects[9].

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[7] See Hoppitt et al. (2008) why from an evolutionary perspective, teaching is best understood as a form of altruism, thus cooperative in the relevant sense.

[8] Some studies indicate that group size may be an important factor: e.g. in Feltovich and Grossman (2014), the effect of communication on cooperation is visible in small but not large groups.

[9] Cf. Dor and Jablonka's (2014: 26) comment on Tylén: "As Tylén et al. (2010: 3) indicate in a comprehensive review article, experimental evidence clearly shows that language facilitates social interaction in four ways, all of which are crucial for collaborative exploration: 'Language dramatically extends the possibility-space for interaction, facilitates the profiling and navigation of joint attentional scenes, enables the sharing of situation models and action plans, and mediates the cultural shaping of interacting minds."

2.4.2. Gricean cooperation

"Gricean" cooperation is content-oriented. It concerns the transmission of the "linguistic" meaning of the message, which is either formulated propositionally or can be readily re-interpreted in such a way (e.g. holophrasis). Gricean cooperation is intentional and verbal, with some role for intentional nonverbal signals that contribute to the propositional content, such as changing the truth value by winking or prosody (e.g. saying "nice weather" sarcastically), or disambiguating exophoric pronouns by pointing. This type of cooperation is basically providing truthful information geared towards optimal relevance (Sperber and Wilson, 1986). An interesting example is the use of linguistic politeness strategies whereby conversants cooperate over maintaining each other's faces (Brown and Levinson, 1978; see also Hurford, 2007: 274; Wacewicz et al., 2015).

While following the Cooperative Principle may appear to be relatively cost-free, this, in fact, is not the case. The most immediate costs are related to the cognitive effort invested in getting the message across, i.e. the careful cognitive packaging of the meaning so as to trigger the intended inferences on the part of the receiver. Somewhat less obviously, there are also the life history costs of becoming a language user. As is well known, being able to communicate verbally requires a long period of language acquisition in ontogeny as well as a number of cognitive adaptations for language-readiness that are likely reflected in the costly size increase and reorganisation of the human brain (see e.g. Bickerton, 2014; Christiansen and Chater, 2008; Donald, 1991; Schoenemann, 2009).

Finally, cooperating in a Gricean sense means paying the cost of not lying. This is because manipulative communication is always an option – and is almost always better than honest communication at maximising short-term payoff. Deciding to play by the Gricean rules, and therefore communicate truthfully, the signaller chooses a non-optimal strategy and forfeits the option to manipulate the receiver to his or her advantage for immediate benefit. Since (at least in the short term) an honest signaller has a decreased fitness compared to a manipulative one, from an economic perspective, honest communication has high alternative cost, or opportunity cost.

2.4.3. Low-level "cooperation"

In a sense, the cooperative character of conversation extends beyond the transmission of meaning. In section 3, we describe turn-taking, proxemic alignment, postural mirroring or the

matching of mannerisms as examples of the processes of low-level coordination, which are nonverbal and unintentional, and do not directly transmit propositional (or even semantic) content, but nevertheless facilitate smooth and focused interaction. This underlying layer of mechanics and structuring of interaction shows patterns of organisation that are frequently designated as cooperative, although on this level, the interpretation of "cooperation" becomes much more problematic.

For example, Levinson (2006) argues that human interaction is essentially cooperative because it involves recipient design (i.e. the producer's actions are designed to be transparent to the recipient), reciprocity (mainly related to taking reciprocal roles, such as the producer and recipient), joint attention (to be able to contribute actions interpretable in the context of joint undertaking) and other features which require the use of prosocial dispositions. This recognises as cooperative the low-level structural properties that merely enable cooperative exchanges. Still, such use of "cooperation" seems to follow from a leaner, more general definition (cf. footnote 5).

Low-level coordination, or *micro-coordination*, may indeed form a pre-requisite for cooperation in conversation, but does it instantiate "true" cooperation *itself*? That is, do low-level coordinative mechanisms fulfil the game-theoretic definition involving some cost of one participant to the benefit of the other? The alternative is, for example, a mutualistic process with "immediate synergistic benefits", in which every 'move' of each participant in the developing interaction simply reflects the naturally optimal course of behaviour[10].

The phenomenon of turn-taking in vocal communication has been specifically argued to exemplify cooperative signalling (e.g. Ghazanfar and Takahashi, 2014; Borjon and Ghazanfar, 2014; Takahashi et al., 2013). It is not clear, however, that the central 'altruistic' component is there to be found. It is possible that the turn taking organisation can be explained mutualistically rather than cooperatively (see 2.1). It may result from more fundamental constraints on efficient signal transmission and reception, or even be an emergent property in a subclass of situations of animal conflict more generally, where the strategy of each individual is still dictated by one's short term gains (cf. Colman and Browning, 2009; Franz et al., 2011). We return to these issues in section 4.

[10] Fowler et al. (2008: 266) point to the practical problems in applying the game-theoretic approach to experimental paradigms aimed at capturing cooperation on this level: "Such game-based situations are substantially different from many of the day-to-day situations in which cooperation lawfully unfolds, online, in dynamic response to information from the other individual and the environmental constraints. Studying these latter situations requires the presence of another person (and the verbal and nonverbal information they emit) and the bodily and environmental dynamics that being copresent in a situation involves. Thus, examining cooperation as an emergent, dynamical process requires embodied methods that focus on how the presence of others can extend the action possibilities (i.e., "affordance"...) for an individual."

3. Low-level coordination mechanisms

3.1. Coordination

Here understood specifically in the context of conversation, coordination can be defined as the interactive co-adjustment of "nonverbal and linguistic behaviour along many levels of social interaction [such as] facial expressions, postures, pronunciation and speech rates" (Latif et al., 2014). We simplify the "many levels" of coordinative processes in conversation into the higher-level and lower-level ones: the higher levels are representational and consist in the coordination of meaning and understanding, getting the addressee to share analogous representations (Pickering and Garrod, 2004). The lower levels are nonverbal and micro-behavioural; there, coordination is the "degree to which the behaviours in an interaction are non-random, patterned, or synchronized in both timing and form" (Bernieri and Rosenthal, 1991: 403). Although some approaches indeed subsume both those aspects, timing and form, under behavioural synchrony (e.g. Vacharkulksemsuk and Fredrickson, 2012), here we opt for a finer explanation and distinguish between synchrony proper and mimicry (see below).

The ability to coordinate one's own behaviours with those of another interactant consists of a heterogeneous class of behavioural patterns which facilitate sustaining *interactional focus*. This notion, crucial to our account, is derived from Goffman, who distinguishes two principal forms of interaction – unfocused and focused (1963). Unfocused interaction refers to contexts where individuals happen to be in the same place and time but do not sustain a single focus of attention (1963: 24). Focused interaction, on the other hand, is "concerned with clusters of individuals who extend one another a special communication license and sustain a special type of mutual activity that can exclude others who are present in the situation" (1963: 83). Accordingly, low-level coordination mechanisms serve interactants to maintain the focus of interaction and allow them to jointly carry out activities specific to a given interactional context. It is important to acknowledge the unconscious and automatic character of these forms of coordination, which is variously explained, e.g. in behavioural terms (through the postulated existence of an automatic perception-behaviour link; Chartrand and Bargh, 1999) or neurocognitive ones (with the mirror neuron system as the basis of coordinative processes; Rizzolatti and Arbib, 1998; for more details see section 4).

Adequate theories offering a unified and exhaustive systematisation of coordinative phenomena have not yet been developed. Existing ones represent a broad range of theoretical

perspectives and use an equally broad variety of partly overlapping central terms, such as *interactive alignment* (Pickering and Garrod, 2004), *accommodation* (Giles et al., 1991), *interactional synchrony* (Newtson, 1994), *mimicry* (*sensu* Chartrand and Bargh, 1999), *mutual influence* (Cappella and Panalp, 1981), *synergy* (Fusaroli et al., 2014) or *social resonance* (Duncan et al., 2007). Based on these, we distinguish between two basic classes of low-level coordinative mechanisms, on which the logistics of face-to-face conversational interaction crucially depends:

- *mimicry*, which is related to the *form* of coordinated behavioural patterns mutually adopted by interactants, e.g. in the form of spatial alignment concerning how individuals "orient and space themselves in relation to one another" (Kendon, 2010);
- *synchrony*, which primarily concerns the *timing* of individual actions in a collaborative context, e.g. turn-taking behaviours, not limited to taking turns at talking (Levinson, 2006).

3.2. Mimicry

Mimicry relies on the involuntary duplication of an event (Donald, 2005). In its non-verbal form, a fundamental type of mimicry involves phenomena where an organism seeks to adjust the form of its movements to that of its neighbours. Cross-species evidence shows that a wide range of animals, e.g. flocking birds, schooling fish, dolphins and monkeys, exhibit mimicry in this broad, basic sense (de Waal, 2009). This basic type of mimicry does not involve affect coordination and seems to depend on processing information about salient features of the environment (Couzin, 2009). Take the schooling of stickleback fish as an example: although members of a school ignore the movement decisions of a single neighbour, they are prone to reproduce the movement of the whole group (Ward et al., 2008). In this way, the tendency prompting animals to behave like their conspecifics facilitates access to decision-making capabilities that overcome individual limitations. Groups of animals have been demonstrated to employ complicated movement rules, such as "moving towards the average location of several others" (Morrell and James 2008: 193), and different strategies of aggregation based on ecological variables such as the size and density of a group. To certain extent, proxemic and postural alignment serve a related ecological purpose of organising the space in the way most conducive to accomplishing specific goals. For example, in dyadic interaction in humans, the vis-à-vis formation directs the focus of attention to participants themselves, while the "L" formation – to the topic of a conversation (Kendon, 2010). These spatial and

postural configurations have been shown to create and maintain a joint space to which interactants have equal, direct and exclusive access (the o-space) (Kendon, 1990).

A stronger type of mimicry pertains to coordination at both the bodily and the emotional level (Chartrand and van Baaren, 2009), whereby a type of interaction imposes an appropriate type of mood on its participants (Goffman, 1967, 1983). The classic example is the famous "chameleon effect", based on the observation that the matching of mannerisms such as self-touches and foot shaking increases affiliation between interactants (Chartrand and Bargh, 1999; for details see section 4); and third party observers see mannerisms similar in form as causally related (Zywiczynski et al., 2016). Other forms of such coordinative processes include aspects of facial mimicry, often exemplified with smiling and yawning behaviours (Lundqvist, 1995; Platek et al., 2003). Mutual adaptation of nonverbal behaviours in face-to face interaction begins early in human ontogeny. Infants show calming responses in reaction to maternal carrying (Esposito et al., 2013), they coordinate their movements with the rhythms of adult speech (Condon and Sander, 1974) and respond with self-distress in reaction to the distress of other infants (e.g. Simner, 1971). In their pioneering studies, Meltzoff and Moore (1977, 1983) demonstrated that newborn infants are able to engage in imitative behaviours and reproduce smiling, tongue protrusion, and mouth opening. By 9 months, infants become attuned to others' moods and can imitate emotional displays, such as joy and sadness (Jensen et al., 2014; Termine and Izard, 1988); and by 18 months, they are more cooperative when being imitated (Carpenter et al., 2013).

An important finding is that mimicry, including affect coordination, is displayed by both monkeys and non-human apes. These two taxa have been shown to follow the gaze direction of their conspecifics and to progressively adjust their attention when the latter re-orient their body posture (Kaminski et al., 2004), to be distressed by the distress of a conspecific and attempt to eliminate his pain (Preston and de Waal, 2002) and to engage in contagious laugh-like vocalizations (Provine, 2000). Another form of experience-sharing is neonatal imitation: chimpanzees (Myowa-Yamakoshi et al., 2004) and monkeys (Ferrari et al., 2006) younger than 1 week display imitative behaviours of tongue protrusion and mouth opening. These early abilities have been argued to underline a basic capacity of matching visual gestures with a proprioceptive motor scheme (Meltzoff and Moore, 1977).

Interestingly, the spontaneous coordination of bodily and behavioural patterns in human interactions has their linguistic counterpart in the mechanism of structural priming (Fusaroli et al., 2012). The main idea is that the relatively lower-level, non-representational

linguistic behaviours are repeated and imitated by the conversational partner, leading cumulatively to global convergence on the higher, representational level (Pickering and Garrod, 2004). Alignment of this kind has been observed in phonetic, lexical and sentential completion (Poesio and Rieser, 2010) as well as in syntactic constructions (Branigan et al., 2000).

3.3. Synchrony

Rhythmic coordination seems to be the most basic type of synchronisation found across animal taxa. It relies on individuals' abilities "to anticipate, attend and adapt to each other's actions in real time" (Keller et al., 2014). Isopraxism is an example of such a process well-known from the ethological literature, whereby members of a species act out the same behaviour in a rhythmic fashion (see e.g. head-nodding in lizards; MacLean, 1975). There are convincing reports that isopraxism, or mutual display, plays an important role in courtship, mainly in birds (e.g. in flamingos: Ogilvie and Ogilvie, 1986; emperor penguins: Williams, 1995; or grebes: Servedio et al., 2013). In humans, the synchronisation of rhythmic behaviours manifests itself in a variety of unconscious and conscious behaviours. The former comprises group activities, such the audience's synchronisation in swaying to music, or dyadic ones, e.g. falling into step when walking (Oulier and Kelso, 2009; Riley et al., 2011; Schmidt and Richardson, 2008). Consciously executed rhythmic synchronisation ranges from unskilled crowd activities, such as marching together or clapping, to activities requiring the acquisition of complex motoric skills, as in the case of joint musical performances or some dancing activities (Keller et al., 2014).

Turn-taking constitutes a more advanced form of reciprocal temporal adjustment of interactional roles. Although its best studied manifestation is in conversation, turn-taking is in fact the fundamental property of human joint activities, exemplified by moves in games, terms of political office, traffic at intersections or service of customers at business establishments (Sacks et al., 1974; Levinson, 2006). It is interesting to note that turn-taking, particularly in its communicative manifestations, is not unique to humans. For example, King (2004) shows that communicative exchanges among apes are characterized by co-regulation, whereby ape vocalisers can understand their mutual behaviours within a framework of their history and social context. Accordingly, facial expressions, body movements, gestures, and vocalisations are coordinated and continuously adjusted in timing to each other's actions (King and Shanker, 2003). Although such co-regulation is not equivalent to turn-taking in humans (see e.g. Tomasello et al., 2005; Tomonaga et al., 2004), there is also growing

evidence that robust forms of taking turns are phylogenetically ancient and exist in many primate taxa (Campbell's monkeys, Lemasson et al., 2010; squirrel monkeys, Masataka and Biben, 1987; Diana monkeys, Candiotti et al., 2012; Japanese macaques, Lemasson et al., 2013; marmosets, Takahashi et al., 2013 and Chow et al., 2015; bonobos, Rossano, 2013; orangutans, Rossano and Liebal, 2014; cf. Levinson, 2016; see also Tanner and Perlman, 2016, for examples of that in captive gorillas).

In line with Levinson's "interaction engine" hypothesis, this comparative evidence points to a phylogenetic continuity between primate interactional behaviour and a set of cognitive and behavioural dispositions that are crucial to linguistic communication, particularly in its prototypical use – face-to-face conversational interaction (Levinson, 2006). Linguistic turn-taking (Sacks et al., 1974) represents a highly advanced form of synchronisation, which results from two pressures – the pressure to minimize gaps between conversants' successive contributions and the pressure to avoid overlaps between such contributions. Further research, an increasing proportion of which has involved quantitative methods, has confirmed that these pressures operate similarly across languages. For example, studies employing the measure of Floor Transfer Offset (FTO), i.e. the duration between the end and beginning of two adjacent turns, indicate that FTO values are similar in different languages (e.g. Stivers et al., 2009; cf. Weilhammer and Rabold, 2003; Heldner and Edlund, 2010; Levinson and Torreira, 2015; Roberts et al., 2015). Most turn transitions, irrespective of the context, come within 500 ms from the end of the preceding turn. Levinson and Torreira (2015) stress that this time is impressively short, if we consider that it takes 600 ms to plan for the articulation of a single lexeme (Levelt et al., 1999) and as much as 1500 ms for the articulation of a simple utterance (Griffin and Bock, 2000; Gleitman et al., 2007).

Extensive research into turn-taking has shown that its rapidity and precision depends on a combination of lexico-syntactic (e.g. Ruiter et al., 2006) and prosodic signals (e.g. Couper-Kuhlen and Setling, 1996; cf. Schegloff, 1996) as well as visually transmitted cues: gesture (e.g. Kendon, 2004 or Kimbara, 2006), gaze (e.g. Ho et al., 2015) or posture (Schegloff, 1998). Within this framework, Wilson and Wilson (2005) propose that conversation is managed by a mutual entrainment of the speaker and listener, whose endogenous oscillators act as timing devices. This entails some form of cyclic patterning with the speaker influencing the timing of the listener's cognitive processes (Wilson and Wilson, 2005: 961).

4. From low-level coordination to cooperation in conversation

What is the relation between the low-level coordinative processes discussed in section 3 and cooperation in conversation? A key consideration here is that such low-level coordination, by *facilitating smooth and focused interaction*, provides a cooperative foundation in face-to-face conversation. We begin by illustrating this with available empirical data from behavioural economics, developmental psychology, Conversation Analysis, and nonverbal behaviour studies, and then we use evolutionary and game theoretic reasoning to extend this conclusion to the phylogenetic plane.

4.1. Low-level coordination and cooperation: the evidence

It is well-attested in the literature that many of the nonverbal mechanisms here subsumed under the rubric of low-level coordination exert influence on the degree of cooperation between interactants. Such reflection is present in microsociology (e.g. Goffman, 1967, 1986), where it is observed that affect coordination, e.g. by means of interaction ritual sensu Goffman, is a necessary condition for the appearance of language-based cooperation. Levinson (2006), elaborating on his influential proposal of "the human interaction engine", interprets basic conversational phenomena as themselves cooperative. For example, pre-sequences (e.g. the use of the pre-invitation "Are you free tonight?" preceding an actual invitation) or preference organisation (related to systematic differences between preferred and dispreferred responses; e.g. invitation preferentially followed by acceptance and dispreferentially by rejection), as he argues, depend on the cooperative design of participation structure, which allows "each [interactant] to assume the other has constructed his or her actions to be interpretable to the intended participant" (Levinson, 2006: 52; cf. Atkinson and Drew, 1979: 253; Pomerantz 1984).

Developmentally, the tendency for synchrony and mimicry to enhance cooperative and altruistic behaviour has an early ontogenetic start (Malloch and Trevarthen, 2009). For example, a study with 14-month-old infants reported that after bouncing to music in synchrony with the experimenters, they showed an increased tendency to help the experimenter collect accidentally dropped objects (Cirelli et al., 2014). By 18 months, infants are more cooperative when being imitated (Carpenter et al., 2013). In line with this, Contaldo and colleagues (2016) found that an early intervention designed to activate the neural circuits involved in "being imitated" might also improve prosocial orientation in children with autism spectrum disorder.

This is consistent with findings in behavioural economics using the Social Dilemma or related paradigms. For example, research has shown effects of low-level nonverbal phenomena, such as mutual eye gaze or gentle touch, on prosociality in public goods games (Kurzban, 2001). Bicchieri et al. (2010) found increased reciprocation in a Trust game in face-to-face communication relative to computer-mediated communication. Studies on human social exchanges suggest that mutual accommodative behaviours are at work, facilitating cohesion and cooperation between the participants (Valdesolo et al., 2010). A positive influence of low-level interpersonal coordination on cooperation has been confirmed experimentally, e.g. mimicry has been found to have an effect on helping behaviour and general prosocial behaviour, even extending beyond the person mimicked (van Baaren et al., 2004). A similar link has been confirmed between synchrony in a more general sense, e.g. in walking or singing, on prosocial performance in a public goods game (Wiltermuth and Heath, 2009).

Support for this line of thinking also comes from experiments used in the study of cooperative tasks, e.g. measuring the continuous bodily coordination of people solving a cooperative "puzzle task". Richardson and colleagues (2007) showed that in spontaneous story-telling eye movement coordination is sensitive to cognitive factors: the gaze patterns of the participants were more coupled when they had listened to the same background information than when they had not. There is also evidence for the symmetricity of this effect: movement coordination occurring spontaneously during conversation was found to promote cognitive coordination and thus aided cooperative communication (Shockley et al., 2003). Consistent with these findings, Tolston and colleagues (2014) observed that constraining hand movement within cooperatively communicating dyads affects interpersonal and cognitive coordination.

4.2. Low-level coordination and cooperation: the ultimate level

What mechanisms may be responsible for the link between low-level coordination and progressively higher levels of cooperation in conversation? In the absence of genetic relatedness or factors that are themselves fully or partly dependent on symbolic communication (such as reputation or explicit norms against cheating, see sections 1. and 2.2), most accounts of cooperation appeal to the mechanism of *direct reciprocity*.

The emergence and stability of cooperative behaviour via reciprocity is typically modelled with iterated prisoner's dilemma (PD), and evolutionary game theory points to "tit-

for-tat" as the most effective pro-cooperative strategy (TFT; see Axelrod, 1984)[11]. TFT consists in cooperating on the first move and then doing whatever the other player does in response: if the other player reciprocates, then a TFT player continues to cooperate; if the other player defects, a TFT player also defects. The effectiveness of TFT results from its simplicity and hence salience, which makes it easily recognisable (in fact the simplicity of TFT makes it the only cooperation-promoting strategy in a repeated prisoner's dilemma games played by children; Blake et al., 2015), as well as its non-exploitability – but for the first move, it is impossible to take advantage of a TFT player.

Explaining how cooperation can be promoted in real-life situations, Axelrod points to two factors. Firstly, a crucial element is the social structure that allows TFT to accomplish evolutionary stability. The problem is captured by John Maynard-Smith's famous question of how cooperation can get a foothold in a world of "meanies" dominated by self-interest and defection. This is possible if cooperators, who may form a negligible part of the whole population, are not negligible to each other by clustering together (Axelrod, 1984). In other words, TFT-emergent cooperation will become dominant and resistant to invasion if the cooperators in a population are able to recognise each other. Secondly, stable cooperative strategies tend to "enlarge the shadow of the future," (Axelrod, 1984: 126-133; cf. Mithen, 2005: 213-214, in the language evolution context) meaning that initial cooperation incurring little cost promotes subsequent cooperation incurring progressively larger costs. When cooperation depends on a history of previous cooperative interactions, such a history itself becomes a capital, while defection, which results in dissipating this capital, becomes costly.

To sum up, conditions conducive to the emergence and stabilisation of cooperation are as follows. Firstly, individuals cooperate selectively: they prefer partners whom they can reliably identify as likely to reciprocate cooperation (e.g. via affiliation). This would partly appeal to the mechanism of spatial or network selection (Nowak 2006). Secondly, cooperation starts small and builds a progressive positive "feedback loop" through continually renewed and gradually increasing investments. Below, we discuss how low-level coordination phenomena are relevant to those two points: low-level cues are reliable, may inform about the disposition to cooperate, and may serve as an initial small investment through which cooperation may progressively develop.

[11] For our purposes, TFT is used broadly to indicate a family of strategies, including the standard TFT and TFT-like strategies (e.g. generous TFT). Also note that WSLS strategies (Imfoh et al., 2007) have been shown to be more robust that TFT at maintaining cooperation, but TFT appears to be the most effective in establishing cooperation in a generally non-cooperative population (Nowak 2006).

4.2.1. Low-level nonverbal cues are reliable

The first precondition for low-level, nonverbal behaviours to stabilise cooperation is the reliability component. As a whole, low-level behaviours are indeed difficult to fake because of their involuntary character (e.g. Chartrand and Jefferis, 2003). One specific example refers to the behaviours that are tightly linked to emotions and emotional expressions (e.g. Boone and Buck, 2003). Evolutionarily speaking, affect displays are signals, i.e. they have been adaptively designed to communicate information (or influence the behaviour of the reactor; Krebs and Dawkins, 1984), but on the proximate level they are largely beyond voluntary control, and therefore relatively trustworthy (cf. Okanoya 2002). Many other nonverbal behaviours are not signals but cues (Maynard-Smith and Harper, 2003), for which providing information is not their evolved function but rather a side effect – a kind of "information leakage". In their case, too, the relative lack of intentional control restricts their use for deception and so translates into higher reliability. Wacewicz and Żywiczyński (2012) suggest that such cues may have played a role in stabilising honest communication at the very early stages of language emergence, when linguistically-based mechanisms against cheating – such as explicit norms or reputation – had not yet been in place. The proposal is that because flexible verbal messages co-occur with inflexible nonverbal cues, the latter may have helped assess the reliability of the former.

The coordination of such low-level cues between the interactants has likewise been documented to be largely unconscious, rapid and automatic (e.g. Bargh and Chartrand, 1999; Bargh et al., 1996; Dijksterhuis and Van Knippenberg, 1998; see also section 3.1). Although little is known about the mechanisms behind this automaticity, some have argued that unconscious coordinative responses may be the result of inherent biological and behavioural rhythms and a temporal coupling of the conversants' low-level perceptual cues (e.g., Richardson and Dale, 2005). Interlocutors engaged in conversation perceive the behaviour of others and react using anticipatory or predictive strategies (Knoblich and Jordan, 2003). To this extent, the non-consciousness of coordination fits with the idea of an automatic perception-behaviour link leading people to spontaneously behave as they perceive. Like the production of low-level cues, also their coordination is thus relatively inflexible and near-impossible to fabricate via a consciously applied strategy.

4.2.2. Low-level coordination reliably indexes similarity and affiliation

In addition to the relation between low-level coordination and direct (i.e. behavioural) measures of cooperativeness, it is interesting to pay attention to a number of variables such as "trust", "liking" and "rapport" that can be considered psychological proxies for cooperation. On the proximate level, the degree of such subjectively perceived affiliation may constitute a mechanism for tracking the likelihood of the other party reciprocating a cooperative investment: within a particular dyad (cf. the "shadow of the future", 4.2.) as well as in the context of a wider social circle (in-group status; cf. Lakin et al., 2003; Marsh et al., 2009). In other words, low-level coordination could have acted as an index of potential cooperativeness, telling the cooperators with whom to associate and whom to avoid; cf. Kurzban (2001): "One possibility is that relatively low-level <social psychophysical> cues, information in the perceptual array that affords meaningful and consequential social inferences, might also act as inputs to information-processing devices that are engaged when one is making decisions about whether or not to cooperate with others."

Ample evidence for the link in question comes from experimental studies in social psychology, in particular the recent tradition that appreciates the profoundly multimodal nature of most human interaction, including conversation. For example, mimicry of mannerisms such as foot-shaking leads to increased rapport (Chartrand and Bargh, 1999; van Baaren et al., 2004; Ashton-James et al., 2007); in the reverse direction, having a conscious or non-conscious affiliative goal influences the degree of mimicking the fellow interactant (Lakin and Chartrand, 2003). Similarly, there is a relation between gaze coordination and the sense of affiliation (Khoramshahi et al., 2016).

Both conscious and nonconscious synchronised activities promote social bonding (McNeill, 1995) as well as prosociality by: viewing fellow interactants as more similar to oneself (Cross et al., 2016; Lakens and Stel, 2011; Miles et al., 2009), being well disposed toward each other (Dijksterhuis and Bargh, 2001) and more inclined to behave altruistically toward them (Valdesolo and DeSteno, 2011). Neural evidence suggests that synchronous behaviour may activate self-other overlap at the neural level, with a corresponding enhancement of closeness and affiliation (Tognoli et al., 2007). The degree to which people synchronise their movements has been found to depend on the nature of conversation (affiliative vs argumentative, Paxton and Dale, 2013). In the reverse direction, synchronised movement increases reported affiliation (Hove, 2008; Hove and Risen, 2009), even when actual interaction is replaced by computer-generated patterns (Launay et al., 2012). In non-human primates, chimpanzees, macaques and baboons have been reported to show contagious yawning (Anderson et al., 2004; Palagi et al., 2009; Paukner and Anderson,

2006), which along with the coordination of affiliative facial expressions in chimpanzees is connected to familiarity and social closeness (Campbell and de Waal, 2011). Chimpanzees have been also shown to rhythmically coordinate affiliative facial expressions to signal group identity (Shepherd et al., 2012).

4.2.3. Low-level coordination as a form of cooperative investment

An additional interesting possibility is related to the conceptualisation of low-level coordination as already instantiating cooperation. The participation in the communicative act itself, and *actively* maintaining focused interaction, implies at least minimal investment of limited resources – such as time, attention and energy – from both interactants. This can be compared to *grooming* (Dunbar, 1996), which is a social activity not explicable by the calculation of immediate gains and losses of either participant, but rather needs to be construed as a form of *social investment*.

Dunbar's own work on geladas shows that females come to aid of their grooming partners harassed by a dominant male (1984, 1988, cf. 1996: 20-21). The long-standing character of bonds established and maintained by grooming has been shown to exist among various primate taxa (e.g. in chimpanzees, Goodall 1986, de Waal 2007; baboons, Smuts 1985; macaques, Dunbar 1988) as well as non-primate taxa (e.g. horses, Kimura 1998; or vampire bats, Wilkinson, 1986). As already noted, there is "a correlation between the amount of time a pair of animals spend grooming and their willingness to support each other in agonistic interactions" (Dunbar 1988: 253). Very interesting is the case of vervets' reactions to calls for help issued by their group members: vervets show a much stronger interest in the call when it comes from an individual with whom they groomed during the past two hours (Cheney & Seyfarth 1992; cf. Dunbar 1995: 23-24). Grooming also performs other functions related to social cohesion and affiliation – e.g. conciliation (de Waal 1989), releasing tension (Schino et al. 1988) or payment for sex (de Waal 2007). Clearly, in some of these contexts, grooming should be conceptualised as social investment: a groomer incurs a cost by spending a limited resource (time) on grooming a particular individual rather than grooming somebody else or engaging in other fitness-related activities such as foraging. Viewed from this perspective, mutual grooming – or mutual co-investment – establishes a social-emotional platform that facilitates cooperation in the strong sense, i.e. such that involves acts of altruism as in the case of defending a grooming partner. Thus, using Axelrod's terms, we could argue

that the prosocial role of grooming consists in extending "shadow of the future" and making future cooperation more likely.

Similarly, initiating and remaining in a focused interaction requires each participant to choose to co-regulate their actions with the other participant (rather than choosing some alternative course of action). The key element here is the fact that focused interaction, rather than being a default, needs intentional effort to maintain. This requires the allocation of resources such as energy and time – when the participant opts to remain in the focused interaction rather than choosing some other, potentially more ecologically profitable course of action. Such an expenditure of resources, however small, can in principle be conceptualised as a cooperative investment. In this way, micro-coordinating mutual actions constitutes the minimal amount of investment that could feed into the proposed 'shadow of the future' mechanism (Axelrod, 1984).

5. Conclusion

Human language is unique in nature as a cheap but honest cooperative signalling system. Available evidence from the linguistic and psychological study of conversation suggests that this cooperative character rests on a scaffolding of lower-level mechanisms, which in turn show continuity with those found in non-human animals. In this paper, we have provided a review of low-level coordinative mechanisms (formal: mimicry, and temporal: synchrony), and we pointed to several properties that are of interest from the point of view of evolutionary game theory. Specifically, low-level coordination phenomena are difficult to fake (reliability), they may carry information about the disposition to cooperate (indexing affiliation and group allegiance), and they may serve as an initial small investment through which cooperation may progressively build up toward higher levels of mutual investment. Further research will shed light on which specific low-level coordinative mechanisms are conducive to increased cooperation between interactants, as well as what psychological mechanisms mediate this link on the proximate level. Importantly, such research needs to be integrated into wider theoretical frameworks, informed by several theoretical approaches to the phenomenon of cooperation.

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