



LUND UNIVERSITY

The co-evolution of human intersubjectivity, morality and language

Zlatev, Jordan

Published in:
The Social Origins of Language

2014

[Link to publication](#)

Citation for published version (APA):

Zlatev, J. (2014). The co-evolution of human intersubjectivity, morality and language. In D. Dor, C. Knight, & D. Lewis (Eds.), *The Social Origins of Language* (pp. 249-266). Oxford University Press.

Total number of authors:

1

General rights

Unless other specific re-use rights are stated the following general rights apply:

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Read more about Creative commons licenses: <https://creativecommons.org/licenses/>

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

LUND UNIVERSITY

PO Box 117
221 00 Lund
+46 46-222 00 00

THE CO-EVOLUTION OF HUMAN INTERSUBJECTIVITY, MORALITY AND LANGUAGE

Jordan Zlatev

Centre for Languages and Literature (CLL)

Centre for Cognitive Semiotics (CCS)

Lund University, Sweden

Abstract

The chapter argues that language, which rests on the *sharing* of linguistic norms, honest information, and moral norms, evolved through a co-evolutionary process with a pivotal role for intersubjectivity. Mainstream evolutionary models, based only on individual-level and gene-level selection, are argued to be incapable to account for such sharing of care, values and information, thus implying the need to evoke multi-level selection, including (cultural) group selection. Four of the most influential current theories of the evolution of human-scale sociality, those of Dunbar, Deacon, Tomasello and Hrdy, are compared and evaluated on the basis of their answers to five questions: (1) *Why we and not others?* (2) *How: by what mechanisms?* (3) *When?* (4) *In what kind of social settings?* (5) *What are the implications for ontogeny?* The conclusions are that the theories are to a large degree complementary, and that they all assume, explicitly or not, a role for group selection. Hrdy's theory, focusing on the evolution of alloparenting, is argued to provide the best explanation for the onset of the evolution of human intersubjectivity, and can furthermore offer a Darwinian framework for Tomasello's theory of shared intentionality. Deacon's theory deals rather with the evolution of morality and its co-evolution with "symbolic reference", but these are necessarily antecedent to the primary evolution of human intersubjectivity. Dunbar's theory on the transition from "musical" vocal-grooming to vocal "gossip" can be seen as providing a partial explanation for evolution of *spoken* language, most likely with *Homo heidelbergensis* 0.5 MYA, but presupposes the capacities accounted for by the other models.

Keywords

alloparenting; altruism; cultural group selection; intersubjectivity; language; morality; multi-level selection; norms; sharing

1. Introduction

Language crucially involves two kinds of *sharing* between the members of a community: (a) of lexical meanings, grammatical rules/constructions and conventions of use, all of which are necessary for successful symbolic communication, and (b) using these for honestly communicating factual knowledge and for constructing fictive beliefs. Due to (a), human languages can conveniently be defined as “socially shared symbolic systems” (Nelson and Shaw 2002) and due to (b), *cooperation* is a central property of language use, which on its part is essential for the conventions of (a) to be established (Clark 1996; Tomasello 2008). If evolution is fundamentally based on the natural selection of individuals, or of their genes (Dawkins 1976), the evolution of both kinds of sharing appears anomalous. On the basis of such assumptions, Fitch (2010: 417) concludes: “The cooperative sharing of information thus remains a central puzzle in language evolution”.

The central proposal of this chapter is that a solution to this “puzzle” can be found by linking the evolution of language, and its two kinds of sharing outlined above, to that of two other (interconnected) features of human sociality, which likewise have appeared as anomalous for a gene-centred perspective on evolution. The first is *intersubjectivity*, a suite of capacities such as joint attention, joint actions and empathy involving “the sharing of affective, perceptual and reflective experiences between two or more subjects” (Zlatev 2008: 215). The second is *morality*, understood as “a sense of right and wrong that is born out of group-wide systems of conflict management based on shared values” (Falck and de Waal

2000b: 69). These definitions, offered mostly for the sake of successful communication with the reader than as an attempt to capture the “essences” of these two complex multi-faceted phenomena, show their main differences: while intersubjectivity is essentially a dyadic, subject-to-subject relation and does not presuppose a group-wide system of “shared values”, morality does presuppose this, and is clearly normative, defining “right and wrong”. Neither of the two is equivalent to *altruism*, either in the evolutionary sense of involving a fitness cost to the donor and a fitness benefit for a recipient, or in the psychological sense of a genuine, “other-oriented, altruistic motivation” (Eisenberg 2000: 677), (see Sober and Wilson 1998, 2000 for a thorough discussion of these two related, though distinct notions). Intersubjectivity can also be used “selfishly” for the purpose of manipulating others, and morality (commonly) involves the punishment of those who transgress the moral precepts. Still, both intersubjectivity and morality are essentially super-individual phenomena, involving at least in part a degree of (“genuine”) psychological altruism. Hence, unsurprisingly, both have been difficult to reconcile with individual-fitness accounts of evolution, assuming that we need “to teach generosity and altruism, since we are born selfish” (Dawkins 1976: 2). In Section 2, I outline a general argument that the co-evolution of intersubjectivity, language and morality in human beings (and their communities), require a *multi-level selection* (MLS) theory of evolution (Sober and Wilson 1998, 2000; O’Gorman, Sheldon and Wilson 2008), according to which, evolution operates (at least) on the levels of genes, cells, organisms, and groups, implying a trade-off (or arms race) between “selfish” individual-selected traits, and “altruistic” group-level selected traits. Furthermore, I show that MLS coheres with the theory of *cultural group selection* (Richerson and Boyd 2005), and gene-culture co-evolution, providing together a basic framework for addressing the co-evolutionary thesis in the title of the chapter.

Then, in Section 3, I proceed by focusing on four currently influential theories of the evolution of “human sociality”, the first three of which explicitly consider this in relation to the evolution of language, those of Dunbar (1996), Deacon (1997), Tomasello (2008) and Hrdy (2009). I compare and evaluate these theories on the basis of five criteria, showing *complementary* strong and weak points, opening the possibility for a composite account. Without attempting to elaborate such a composite theory for reasons of time and space, I sketch the outlines of a possible one based on a co-evolutionary scenario between intersubjectivity, morality and language, and a multi-level selection approach to human social-cognitive evolution.

2. How can we explain the evolution of human-specific sociality?

2.1 Beyond ape intersubjectivity and morality

Human beings are, of course, not the only social animals on the planet. Since Darwin (1882 [1871]), in attempting to uncover what is special about us as a species, it has become necessary to compare specific human traits with analogous (or perhaps homologous) ones in other species, and in particular with species with which we are most closely related. De Waal and colleagues (e.g. de Waal 1996; 2007; Flack and de Waal 2000a; Preston and de Waal 2002) have persuasively argued that intersubjectivity (with a focus on empathy), should be viewed phylogenetically (and ontogenetically) as consisting of several layers or levels, with mammalian roots in basic processes of maternal care and “emotional contagion”. More cognitively demanding processes of “feeling into” (*Einfühlung*) another’s mental state – and on occasions acting sympathetically – are testified by numerous cases of “targeted helping” and “consolation” behaviour in chimpanzees and other great apes, but not in monkeys

(Preston and de Waal 2002). Yet, as numerous experimental studies carried out foremost by Tomasello and colleagues have shown, chimpanzees mostly succeed in understanding the intentions of another conspecific or human partner in *competitive* contexts, i.e. when they were motivated to consider the perspectives, goals and knowledge states of the other in order to maximize their own profits (Hare et al. 2000; Hare, Call and Tomasello 2001; Hare, Call and Tomasello 2006; Melis, Call and Tomasello 2006; Kaminski, Call and Tomasello 2008). This suggests strongly that at least one extra “layer” of empathy has been selected for in hominid evolution, after the last common ancestor of our species, four-five million years ago.

With respect to morality, Flack and de Waal (2000a: 3) argue that non-human primates, and especially apes, “have similar methods for resolving, managing, and preventing conflicts of interest within their groups. Such methods, which include reciprocity and food sharing, reconciliation, consolation, conflict intervention, and mediation, are the very building blocks of moral systems”. However, as other contributions to the same volume devoted to the “evolutionary origins of morality” make clear (e.g. Boehm 2000; Knauft 2000; Thierry 2000), capacities such as these “building blocks” are rather to be viewed as precursors or pre-adaptations of true moral systems. The latter require collectively shared norms, which in all human societies are reflected, if not explicitly expressed by language. In the often quoted words of Goodall (1982), chimpanzee societies are characterized by “order without law”, i.e. not just lack of legal systems (which are absent in many traditional societies), but of shared moral ones, as shown by an observation of in-group cannibalism, occurring when the victims were unprotected by close relatives or allies, without this leading to group sanctions to the perpetrators.

In sum, while current comparative psychological and evolutionary research has done much to counter-act age-old dualisms with asymmetrical value such as human vs. animal, culture vs. nature, reason vs. emotion, human beings remain a very “peculiar” kind of social animal. As Falck and de Waal (2000a: 22, Table 1), admit: “It is particularly in these areas – empathy, internalization of rules, sense of justice, and community concern – that humans seem to have gone considerably further than most other animals”.

The question remains: why and how have we “gone considerably further” in these respects in hominid evolution? The simple answer: “language”, will not suffice since (a) we are brought back to the question of why and how language evolved, and (b) the answer to this latter question is to be sought in a framework according to which language is fundamentally a socially shared phenomenon, as outlined in the introduction (and as assumed by the present volume as a whole). Thus, in attempting to tackle the evolution of human sociality (including intersubjectivity and morality) and language, we are led to a chicken-and-egg problem (Zlatev 2008). This in itself suggests the venue of addressing it: a co-evolutionary account, based on the “common denominator” of language, intersubjectivity and morality: *sharing*. But sharing (of information) presupposes at least a degree of (psychological) altruism, running against the stream of mainstream evolutionary reasoning (cf. Section 2.2). As argued by Tomasello (2008: 191): “If human cooperative communication had arisen initially to enable more complex forms of competition and deception, then we would not expect to see a common cognitive infrastructure with collaborative activity, nor would we expect to see as its most basic motivation the desire to help others by providing them with the information they need.”

2.2 The limits of individual-level selection

Darwin (1982 [1971]) was aware of the limits of individual-level natural selection to account for cases of altruism, such as the risks taken by group members to defend other member, and proposed “group selection”, with competition *between* rather than within groups, as the mechanism through which altruistic traits evolved. Since the 1960s, when the notion of group selection fell out of favour in evolutionary biology due to a number of influential articles claiming that it is both non-parsimonious as an explanation and inefficient as a mechanism compared to individual selection (Maynard Smith 1964; Hamilton 1964), there have been repeated attempts to account for the evolution of (apparently) altruistic behaviour through gene-level and individual-level selection. The most straightforward is *mutualism*: the actor/donor gains a fitness benefit by teaming up with the recipient, for example for obtaining food, or minimizing the risk of predation. Cases of such mutualism can easily be found in the animal kingdom, but are of course not a matter of altruism but of co-selfishness. Hamilton (1964) proposed the influential notion of *kin selection*, also known as “inclusive fitness”, and the famous rule for the conditions for the evolution of altruistic behaviour: $rB > C$ (since then known as “Hamilton’s Rule”), i.e. if the cost for donor C is smaller than the benefit B for a recipient, standing in degree of genetic relatedness r , then such behaviour would be optimizing fitness on the genetic level. Kin selection would thus appear to explain phenomena such as parental care, or even self-sacrifice for close relatives, and “nepotism” more generally, but cannot be extended to cooperation between the members of large social groups, many of which are not closely related (Boyd and Richerson 2009, see below).

In another influential paper Trivers (1971), argued that *reciprocity* is an essential component for the evolution of cooperation, or what Trivers called “reciprocal altruism”: the

donor takes on a cost for performing an action that benefits a recipient, assuming that the recipient will reciprocate in the future. This may operate in very small groups, where reciprocating ultimately gives benefits to each member, but in larger groups, the system is vulnerable to “defectors” or “free-riders” who reap the benefits of others’ altruistic acts, but do not reciprocate. Thus, a sizable literature has been devoted to various mechanisms, under the general heading of *indirect reciprocity*, which may curtail the negative effect of free-riders. Two of these are “image scoring”, according to which so-called bystanders (third-party observers of the interaction) elevate the social reputation of individuals who help a needy recipient and decrease the social reputation of individuals who do not (Nowak and Sigmund 1998) and “social standing”, where bystanders decrease the social reputation only of individuals who fail to help a recipient in good social standing (Leimar and Hammerstein 2001). Related to these is the proposal of Zahavi (2003) that altruism functions as a “handicap”, similar to the peacock’s tail, signalling high individual fitness and thus gaining in mating opportunities. Such models have been applied to empirical cases of cooperation in animal species far removed from us phylogenetically, such as sticklebacks (*Gasterosteus aculeatus*) and guppies (*Poecilia reticulata*) where two or more animals leave the larger social group to gain information about an approaching predator, thus each assuming costs in the form of increased predation risk (Dugatkin 2008). If the inspecting fish co-operate by keeping a similar distance to the predator, the strategy is most efficient. At the same time, by observing their behaviour bystanders can judge their “reputations”. This process has been suggested to affect future willingness to cooperate and to mate. It can be noticed, that such explanations rely heavily on notions of individually remembered “reputations” and collectively shared “social standings” – which imply fairly advanced skills in memory and communication.

Ecologically, they require rather small and/or compact groups: “The payoff for exhibiting cooperative behaviour ... will be realized only if bystanders are present in sufficient numbers to ensure that added benefits are available to balance the extra investment (Earley 2010: 2680). The combination of these conditions is questionable for any animal species, and Falck and de Waal (2000a: 4) state: “It is not yet clear whether systems of indirect reciprocity exist in non-human primate social groups”.

A final piece in the toolbox of factors that appears to be necessary for (extensive) social cooperation, are *systems of sanction*, punishing defectors/free-riders in one way or another. But if such punishment is enforced by individual members, that itself implies a cost (that could be as high as death), there is the problem of “second-order free-riders”, who may be good co-operators but bad punishers. Thus, the evolution of sanctions for group-exploiting free-riders (as opposed to spontaneous retaliation for transgressions on near kin or close friends) is itself a problem. Panchanathan and Boyd (2004) have proposed that it can be solved by “collective action”, implying group-wide norms on what is wrong and right, which appears to cross over to morality, as defined earlier in this section.

2.3 Cultural group selection and multi-level selection (MLS) theory

Reviewing some of the same literature summarized above, but with focus on the evolution of *human* altruism/cooperation Boyd and Richerson (2009: 3283) conclude that “evolutionary thinkers typically explain human cooperation as the resulting from the ‘three Rs’: reputation, reciprocation and retribution” and that “it seems probable that the three Rs can explain why cooperation is evolutionarily stable.” However, they point out, these three factors are not sufficient to explain why it *evolves*:

The problem is that the three Rs can stabilize *any* behaviour. If everybody agrees that individuals must do *X*, and punish those who do not do *X*, then *X* will be evolutionarily stable as long as the costs of being punished exceed the costs of doing *X*. It is irrelevant whether *X* benefits the group or is socially destructive. It will pay to do *X*. Thus, the three Rs can explain how cooperative behaviours like participating in group defense can be favoured by evolution, but they can also explain anything else. (ibid: 3283)

The only way that human-scale cooperation and (psychological) altruism can evolve, argue Boyd and Richerson (2009) is through multi-level selection, with a crucial role for cultural adaptation and group selection. Their proposal can be broken down schematically in a four-step process. First, advanced social learning made cumulative cultural evolution possible, and increased heritable variation between groups. Second, the “three Rs” can stabilize different kinds of social behaviours, leading to pronounced differences between groups. Third, competition between groups would favour those with higher cooperative tendencies. Finally, selection within these most successful groups “favoured genes that gave rise to new, more pro-social motives. Moral systems enforced by systems of sanctions and rewards increased the reproductive success of individuals who functioned well in such environments, and this in turn led to the evolution of other regarding motives like empathy and social emotions like shame” (Boyd and Richerson 2009: 3281-82). A major advantage of such an account is that it shows not only how “functional” altruism and coercive social rules can evolve, but also psychological, or “genuine” altruism, characterized by Boehm (2000: 213) as “behavior that is

based on genes which are selected at the between-group level and that is motivated by feelings of concern for non-kinsmen”. That such “felt” altruism, or empathy, which is not *only* culturally learned (*pace* Dawkins 1976), is the “proximal cause” of pro-social acts in many cases, for a majority of subjects, has been demonstrated convincingly by thorough experimental methods (Bateson 1991, 2000).

This process of gene-culture co-evolution is quite consistent with Sober and Wilson’s (1998, 2000a) general theory of multi-level selection (MLS), which reverses the gene-and-individual centred focus of the traditional accounts. From the perspective MLS theory, kin selection is a special case of group selection, applying to cases when the group members are closely related. Likewise, models of indirect reciprocity require incentives such as “reputations” and “status”, as described above, but “the evolution of an incentive system is itself a multi-level selection problem” (Sober and Wilson 2000b: 260). Finally, while MLS is more general than the cultural group selection model proposed by Boyd and Richerson, it can accommodate the special character of human cooperation and altruism: “culture allows a form of selection to occur whose elements may be found in the absence of culture. Bees ‘police’ the behavior of other bees. What is uniquely human is the harnessing of socially shared values” (Sober and Wilson 2000a: 195).

Combining the accounts reviewed so far in this section (i.e. those of de Waal, Boyd and Richerson and Sober and Wilson) leads to the conclusion that the human-specific levels of intersubjectivity, culture and morality co-evolved during the last million years of hominid evolution through multi-level selection. What about language? Paraphrasing Sober and Wilson from the final quotation, while some of the “elements” necessary for the stabilization of cooperation systems can perhaps be found in other species, e.g. the learning of

“reputations” through “image scoring”, it is difficult to imagine how systems of “shared values” and “collective action” (i.e. fully-fledged moral systems) can be established and maintained without the presence of symbolic communication. This is especially so given that early human social groups were characterized by “fission-fusion” membership and large home ranges, an assumption based both on the character of chimpanzee social groups, and on those of extant hunter-gatherers (Knauff 2000). In the words of Boehm (2000: 156), “an ability to communicate with displacement is critical because such communities must continuously track everyone’s behavior and group members are often dispersed”. Thus, in order to effectively establish reputations, a communication system with displaced reference would have been required (i.e. “gossip”). Such a system, amounting at least to “protolanguage” would have been even more necessary to be able to reach consensus on issues of guilt and retribution. The absence of such a system was what allowed the cannibalistic chimpanzees reported by Goodall (1982) to go unpunished.

Therefore, we are led to the conclusion that human intersubjectivity, morality and language must have co-evolved, as stated in the title of this chapter. This has also been suggested by Knauff (2000: 135), calling for a “bolder and more revolutionary argument that considers the suite of human cultural socialization, complex symbolic communication, and morality as key features in human evolution since the emergence of *Homo erectus* perhaps two million years ago”. What this section has presented is some general support for such an argument, along with the thesis that the evolution of this suite of features requires multi-level selection, including cultural group selection. In the following section, I attempt to make this argument more concrete by considering four independent current theories of the evolution of

human social-cognitive uniqueness, showing how they focus on particular aspects of this more general suite.

3. Four theories of the evolution of human sociality

During the past two decades a number of theories on the evolution of specifically-human sociality have been proposed that focus on specific factors more or less directly related to the evolution of language. The following four theories, listed chronologically, are perhaps the most influential ones. Dunbar (1996) has argued that life in larger groups necessitated a novel mechanism for social bonding, and hence at first *vocal grooming* and then *gossip* emerged in the *Homo* lineage. Deacon (1997) has instead suggested that a *social contract* regulating sex (“marriage”) in multi male/multi-female groups is what propelled our ancestors to higher levels of sociality and symbolic reference. Tomasello (2008) has advocated that a cognitive adaptation for *shared intentionality* and a motivational one for *pro-sociality* emerged first, providing an “infrastructure” for the subsequent evolution of language. Finally, Hrdy (2009) has argued that a transition in reproductive and rearing strategy to *alloparenting*, or cooperative breeding, radically altered our ancestors’ interpersonal relations, and thus provided the basis for adaptations in intersubjectivity and language. The goal of this section is to compare and evaluate these proposals along the following set of criteria, formulated as five questions:

1. *Why us and not others?* Does the theory provide an explanation of why a higher level of sociality (and language) evolved in the *Homo* genus, rather than other animals?

2. *How?* What kind of evolutionary mechanism for the evolution of human-specific sociality is provided or implied?
3. *When?* Is the timing proposed by the theory consistent with relevant anatomical changes (e.g. bipedalism, reduced canines, reduced sexual dimorphism), attested in the archaeological record?
4. *How large social groups?* Is the theory consistent with anthropological evidence from extant hunter-gatherer societies (as well as technologically advanced ones)?
5. *Development?* Is the theory consistent with evidence on how the features claimed to be unique for human sociality develop in children?

Three of these criteria/questions resemble three of Tinbergen's famous "four questions of ethology" (cf. Tinbergen 2010): Questions 1 and 2 correspond to the "ultimate mechanisms" of *evolution* and *function*, respectively, and Question 5 to the "proximate mechanism" of *ontogeny*. I do not deal with the complex issue of *causation*, though this was touched upon in the previous section in arguing that psychological altruism is at least a component of human sociality. Rather, I compare the theories with respect to their proposed evolutionary timelines and how well this matches archaeological evidence (Question 3), and furthermore, whether their predictions are consistent with the sizes of present-day social groups, especially among hunter-gatherers (Question 4).

3.1 Why us and not others?

Dunbar frames his theory as focusing on the evolution of language. The answer to the *why* question is the following scenario: physical grooming is an important mechanism of social

bonding and coalition-building in primates, but it is relatively inefficient, and therefore sets limits on the sizes of primate groups. With life in open territory, larger groups are required (for minimizing risk of predation, extended foraging and territory defence), but that has negative side-effects in terms of intra-group conflicts. This tension was resolved by the emergence of “vocal grooming” (chousing), and eventually “gossip”. In brief: “language evolved to service social bonds in a more generic sense by providing a substitute for social grooming” (Dunbar 2009: 14). To the question: “Why do only humans have language?” Dunbar replies: “No one else has evolved group sizes large enough to require more than grooming for social bonding” (ibid: 30). This, however, is hardly a sufficient explanation. The ecological living conditions of gelada baboons are similar to those envisioned by Dunbar for early humans, and – in partial support for his theory – gelada also live in large terrestrial groups or herds of 200-300 individuals. Interestingly, gelada have evolved enhanced vocal signalling for keeping contact primarily with members of the same “harem” (a one-male reproductive unit), but not a communication system allowing them to “gossip”. This shows that the above mentioned dilemma can be resolved by other means than language and/or large-scale cooperation, e.g. by harem-based social structure and non-symbolic vocalizations.

Deacon's explanation for what led to the uniqueness of human sociality (and cognition) is that our ancestors happened to live in the following very unusual conditions: multi-male/multi-female social groups (for the sake of protection and group hunting), having immature infants with slowly maturing brains (in part due to bipedalism), which required extensive maternal care and paternal provisioning. Together, these conditions constituted an “evolutionary bottleneck” in which the only groups that survived were those that established a sex contract (“marriage”) that required symbolic marking of the social rights and obligations

of sex-partners, and the means to make sure that these are followed. Or as stated by Deacon (1997: 401): “The need to mark these reciprocally altruistic relationships arose as an evolutionary adaptation to the extreme instability of the combination of group hunting/scavenging and male provisioning of mates and offspring”. Thus, Deacon supposes that what spearheaded the process was the evolution of morality and “symbolic reference”, rather than intersubjectivity (social bonding, empathy). Deacon does not consider whether the problem of ensuring (relative) sexual fidelity and for male provisioning could not have been at least curtailed by an adaption for strong emotional attachments between sex-partners (“love”), lasting on average 4-5 years: the time when lactating mothers and children are most vulnerable (Fisher 1992).

Tomasello has for some time argued that the evolution of language must have been preceded by human-specific adaptations for social/cultural life. In an earlier scenario (Tomasello 1999), this prerequisite was the understanding of others as intentional agents. When empirical evidence disproved this (cf. Section 2.1), the theory became somewhat less mentalist and more social (Tomasello et al. 2005; 2008). Two key adaptations are proposed to have occurred in the hominin line: (a) a capacity for *shared intentionality*, needed for performing actions jointly (e.g. not just for coordinating, but for planning a hunt) and (b) a *pro-social motivation* to share, above all, information. However, almost nothing is offered in terms of explaining *why* these capacities would have evolved apart from suggesting that (a) “evolved in the context of mutualistic collaborative activities” (Tomasello 2008: 170), while for (b) it is necessary “at some late point to invoke processes of social identification and conformity to account for the sharing motive” (ibid: 171).

In contrast to Tomasello, *Hrdy* proposes a very specific answer to the *why* question: what started the cascade of processes that led to increased brain size, human-specific cognitive abilities and ultimately language was a switch in reproductive and rearing strategy: “Without doubt, highly complex coevolutionary processes were involved in the evolution of expanded lifespans, prolonged childhoods, and bigger brains. What I want to stress here, however, is that *cooperative breeding was the pre-existing condition* that permitted the evolution of these traits in the hominin line” (Hrdy 2009: 277, my emphasis). Indeed, it is only in our species among the Great Apes that child care is extensively shared among group members. While in orangutans, gorillas, chimpanzees and even bonobos, mothers are the only ones to hold and nurse infants due to fear of kidnapping from other females, or infanticide by males, other alloparenting primates like marmosets and tamarins are “unusually altruistic, displaying a curiously human impulse to give” (ibid: 96). Thus, the evolution of particularly human intersubjectivity is seen as “an unprecedented convergence – the evolution of cooperative breeding in a primate already possessing the cognitive capacities [...] typical of all Great Apes” (ibid: 280). Hrdy (2009) repeatedly addresses the issue “why us and not them”, but unlike Dunbar and Deacon does not appeal to changes in ecological conditions. While not stated explicitly, the answer seems to be that different species of primates (that survived) found their respective “evolutionary stable strategies” (ESS). Our ancestors did not *have* to make the transition to alloparenting – a very unusual system for mammals (about 3% of mammal species are characterized by cooperative breeding). We simply are the lucky descendants of those who chanced on this route less-travelled, which turned to be a “winning strategy”. As argued below this logic implies a process of group selection.

3.2 By what kind of evolutionary mechanism?

Dunbar bases his theory on fairly robust correlations between group size and brain volume in modern human groups (both technologically advanced and traditional) and extant apes and monkeys, and interpolating the likely group sizes of hominin groups on the basis of cranial volume. He proposes that neocortex size increased in response to increases in group sizes (the so-called “social brain hypothesis”): “Since maintaining coherent groups is cognitively demanding, brain size (or more specifically neocortex volume) will evolve to match the cognitive demands of the species’ *optimal group size*” (Sutcliffe, Dunbar, Binder and Arrow 2012: 151, my emphasis). Dunbar does not explicitly address the kind of selection mechanisms through which such evolution could have taken place, but references to “mating opportunities” suggest that a standard type of individual selection is assumed: individuals with larger brains, larger number of friends and better vocal grooming reproduced more successfully. However, this is problematic, since “optimal group size” is not a property that is determined by individual brains, and the communicative signals, even if initially non-symbolic, would need to be shared with both kin and non-kin members of the group. On the other hand, it is conceivable how group selection would have allowed evolution to converge on “optimal” groups, both in terms of size, and the adequate means to bond their members, with within-group selection favouring those most adept for living in such groups. In other words: a multi-level selection process. One could attempt to explain this as a result of “selection at the individual level that prefers individuals who tend to aggregate in groups of the size that they are equipped to handle” (Kenny Smith, personal communication), but this would seem to imply a higher degree of universality of group sizes than is warranted (cf. Section 3.4).

Deacon also correlates the evolution of “symbolic reference” with increase in brain size, and (according to his estimates) above all the prefrontal cortex, responsible for much of “higher” social cognition and “executive function”, i.e. voluntarily planned actions. Since at the root of the adaptation proposed by *Deacon* is not pair-bonding *per se* (which could perhaps be accounted for by direct reciprocity, and resulting in an adaptation for emotional attachment, love), but symbolically mediated social norms, beneficial for the social group as whole, a process of group selection is clearly required: groups that found a way to ensure sex-based division of labour and paternal provisioning out-competed those which did not. To the extent that the sex-contract was a cultural invention – which given its symbolic nature would seem to be the case – it could also spread through cultural transmission, implying a process of cultural group selection, as outlined in Section 2.3.

As with the *why* question, *Tomasello* gives only the most general answers to the question of *how* (cognitive) shared intentionality and (motivational) pro-sociality would have evolved: at a first stage, some unspecified collaborative activities in which mutualism would have operated for the evolution of shared intentionality, and at a later stage, a process of cultural group selection for the evolution of pro-social motivation. Why the process is divided in this way is not made clear. One may note that the postulation that the motivational/emotional aspects of human intersubjectivity evolved through *cultural* group selection implies that altruistic impulses evolved at a secondary stage, first after advances in cognition (presumably accompanied with brain expansion) and extended cultural transmission were underway.

For *Hrdy*, the order suggested by *Tomasello* is very much reversed, since the transition to alloparenting spearheaded the process, and along with it, the nurturing tendencies of

mothers were extended to other members of the group, including fathers but not limited to them. It can be noted that alloparenting relaxes the need for paternal provisioning of their own progeny, allowing food and child-care to be more equally distributed within the group than in Deacon's scenario (cf. Sections 3.1, 3.4). Alloparenting was a winning strategy for our ancestors since it allowed for unusually fast rates of reproduction, despite large-brained, slowly maturing and "costly" babies: "Mothers can overshoot their capacities to provide, and fathers can vary, because both sexes evolved in a highly fluid system where alloparents often provided the compensatory assistance" (Hrdy 2009: 167). Hrdy argues that this process can be accounted for by an evolutionary model that generalizes Hamilton's Rule $rB > C$ (cf. Section 2.2) where r does *not* refer only to genetic relatedness (and hence standard kin selection) since "once the neural and physiological underpinnings for helping behavior were in place, helpers did not need to be close kin" (ibid: 188). Since kin selection is a special form of group selection (cf. Section 2.3), this "generalized kin selection" even more clearly involves multi-level selection, with selection between groups favouring those which have adapted the "winning strategy".

3.3 When?

On the issue of timing, Dunbar points to the relatively scarce (and still disputed) fossil evidence on larger thoracic vertebral canal (MacLauron and Hewitt 1999) and hypoglossal canal – both of which have been proposed as indexes of increased control over vocalization – first in *Homo heidelbergensis*. Together with re-estimated group sizes of hominins, somewhat decreased compared to the original proposal, he concludes: "Thus, the 0.5 MYA rubicon may mark the appearance of some form of intensely music-like exchanges, with full grammatical

language (i.e. language as we know it today) emerging only later – perhaps with the appearance of anatomically modern humans around 200 KYA” (Dunbar 2009: 29). However, 0.5 MYA is a rather late date for the onset of the process leading to human-specific sociality, given the many earlier adaptations, from *Ardipithecus ramidus* at 4.4 MYA (involving reduced canines, reduced sexual dimorphism and partial bipedalism) to *Homo ergaster/erectus* at 1.8 MYA, with basically modern human body anatomy, Achulean bifacial hand-axe technology, and gradual colonization of most of Asia and Europe (Donald 1991).

Similarly to Dunbar, *Deacon* appeals to novel ecological conditions of “life on the savannah” for what started the process, but in contrast places the beginning of the transition to more than 3 MYA with *australopithecines*. Since for Deacon the transition should begin with “symbolism” (rather than “music-like exchanges”, as for Dunbar), this is a remarkably early date, without any clear support in the archaeological record.

Interestingly, *Hrdy* places the onset of evolution of human-specific sociality between these “late” and “early” dates: with *Homo ergaster/erectus*, based on evidence for changes in diet (including meat), sexual division of labour, larger brains and longer life-spans. To the extent that *erectus* had made the transition to alloparenting, she argues that the species should be considered “emotionally modern” (Hrdy 2009: 31). But if so, this was hardly an abrupt transition, especially since the traces of a process of “self-domestication” can be found in *Ardipithecus ramidus*, with reduced sexual dimorphism and partial bipedalism, as mentioned earlier. This, however, would suggest a co-evolutionary scenario of more immature infants, prolonged childhood, more need for shared care and provisioning, in which alloparenting was not the single initial factor, as suggested by Hrdy, but was itself facilitated by increased neotony (i.e. very immature babies). For example, in birds, cooperative breeding

(alloparenting) has been found to be more likely to evolve in taxa where chicks are helpless rather than in those where they are soon able to survive on their own (Cockburn 2006).

Finally, *Tomasello*, as mentioned earlier, prefers not to “speculate” on the issue of timing.

3.4 How large social groups?

Dunbar has made much of group sizes, noting that present day human social groups fall into three categories — small, medium and large, equivalent to “bands”, “cultural lineage groups” and “tribes” — with respective size ranges of 30–50, 100–200 and 500–2500 members each.

The number that matches best with his estimates for “optimal group size” given human brain size has been approximately 150, and he has tended to overemphasize this so-called “Dunbar’s number”. In Western societies, it has been shown that “the range in network size is vast, with 90% of the adult population knowing anywhere between 250 and 1,710 other, and half knowing between 400 and 800” (Wellman 2012: 174). On the other hand, most other anthropologists emphasize the “band” of 30-50 people as the most significant group for hunter-gatherers, and it is likely that in such “societies of intimates” (Givon 1979) that the initial adaptations for human intersubjectivity first occurred.

Deacon focuses, as pointed out above, on the family as the primary locus of sharing. This is troublesome, since in hunter-gatherers the distribution of food is not limited to the “nuclear families”, but to the whole group, and beyond (Weissner 2002). Paternal provisioning is far from being a universal phenomenon, since as Hrdy (2009: 162) emphasizes: “Across cultures and between individuals, more variation exists in the form and extent of paternal investment in humans than in all other primates combined”.

Tomasello makes a few references to hunter-gatherer practices of sharing resources with the whole group, but does not make it clear why and how this would be related to either mutualism or cultural group selection (cf. Section 3.2).

Hrdy is the one who extensively bases her theory on the social practices of extant hunter-gatherer groups. It is of course always controversial when extant hunter-gathering societies are alluded as evidence for evolutionary scenarios, and Hrdy is duly cautious, reminding that these should not be viewed as “living fossils”, but rather as the closest models for what the lives of our pre-agricultural ancestors could have been like. It is significant that in culturally, geographically and environmentally highly distinct hunter-gathering societies such as Aka, Efe, !Kung San (Central Africa), Himba (Western Africa), Yanomamo (Venezuela) and Agta (Philippines) care is shared between mothers and alloparents, and in some cases fathers. It should be noted that this is related to, but distinct from the so-called “grandmother hypothesis”, according to which women live longer than female apes after ceasing to ovulate, due to their positive role on the survival of grandchildren (Hawks 2004). Hrdy observes that human longevity increased for both men and women, and while (maternal) grandmothers typically function as alloparents, other group members do as well: “Efe babies average 14 different caretakers in the first days of life” (Hrdy 2009: 79).

3.5 Development

Since the four theories focus on different aspects of the suite of features defining uniquely human sociality, including intersubjectivity, morality and language, it is impossible to straightforwardly compare them with respect to developmental evidence. For Dunbar, that would involve the development of vocalization (e.g. babbling), language (“gossip”) and what

he refers to as “levels of intentionality”, by which he means progressively deeper embedding of mental predicates (Dunbar 2009, see below). For Deacon, it would be the development of “symbolic reference”, and perhaps moral sense. Tomasello’s and Hrdy’s accounts are more easily comparable, since they both assume that what initially evolved was pre-linguistic forms of intersubjectivity, though as pointed out above, Tomasello focuses (initially) on cognitive features, while Hrdy on emotional ones. Given these reservations, we can briefly look at what kind of developmental evidence can be adduced in support for each theory.

Dunbar’s theory claims that human sociality evolved for the management of intra-group social relations, and the result of this were above all expanded neo-cortex and improved vocalization. This would imply that to the extent that human infants differ from those of the apes, this should be a side effect of their larger brains, adapted for vocal grooming and higher levels of intentionality. In children, human-specific vocalizations indeed start early in the first year, followed by the emergence of language in the second year of life, while neo-cortex undergoes extensive expansion first in late childhood (6-11 years), reflected in tests requiring third-order to fifth-order intentionality, e.g. “*I think that you believe that I suppose that we understand that Jane wants...*” (Dunbar 2009: 30).

The thrust of *Deacon’s* explanation is on the evolution of symbols for social roles such as kin terms. While children in Western societies learn some kin terms (*mother, father, brother, sister*) early, it takes quite some time for them to master the complex semantics of kin terms for more distant relations (Haviland and Clark 1974), though corresponding studies for children in traditional societies remain to be carried out.

Tomasello’s theory that human sociality evolved through selection for basic pro-social capacities (sharing impulses, joint attention, informative pointing etc.), finds considerable

support in findings that such capacities both develop before language, and are human-specific (Tomasello et al. 2005). While some of these claims have been contested (Leavens et al. 2009), it is hard to interpret the evidence of prolonged childhood compared to apes, and the fact that e.g. chimpanzees fail in tasks that require understanding cooperative intentions (cf. Section 2.1) as not reflecting evolutionary selection.

Hrdy's theory is strongly inspired by an updated version of attachment theory (Bowlby 1988), where mothers may be special but not unique, and the “infant intersubjectivity” approach in developmental psychology (Trevarthen 1979; Bråten 2007). Growing up in the context of alloparenting, according to Hrdy, the child develops an enhanced understanding of perspective and self-awareness: “A baby thus had far more incentive to monitor his mother’s whereabouts and to maintain visual and vocal contact with her, as well as far more motivation to pay attention to her state of mind, and to the willingness of others who might be available to care for him when his mother was disinclined” (Hrdy 2009: 114). Evolutionarily, the model explicitly assumes a “self-reinforcing evolutionary process of parents and alloparents who are more sensitive to infantile signals and babies who are better at emitting them” (ibid: 220).

In sum, it is characteristic that Dunbar and Deacon pay relatively little heed to developmental evidence, while Tomasello and Hrdy do so extensively. It can be argued that this reflects differences in what Dunbar and Deacon, on the one hand, and Tomasello and Hrdy on the other, believe that the “ultimate” evolutionary mechanisms (Sections 3.1 and 3.2) operated on: While Deacon and Dunbar consider the evolution of human sociality to be based primarily on the selection of adults, and Tomasello focuses on children, Hrdy seeks the “niche” for the evolution of human intersubjectivity in the interactions between mothers, children and alloparents.

3.6 Summary

As shown, the evolutionary theories reviewed in this section all address the five questions, with the exception of Tomasello, who is largely silent on *why* and *when*. Their answers to these questions are quite different, which is hardly surprising given that they hypothesize different *starting points* for the evolution of human-specific sociality: vocal grooming (Dunbar), symbolic reference (Deacon), shared intentionality (Tomasello), and infant-alloparent intersubjectivity (Hrdy). Concerning the *why* question, Dunbar and Deacon both appeal to specific ecological conditions, and the need to resolve conflicting tensions. Their accounts for how these tensions were resolved can be seen as complementary rather than contradicting: human language is both symbolic and predominantly vocal in its service of social functions such as bonding, gossip, and the maintenance of shared moral norms. However, both Dunbar and Deacon seem to attribute too much importance to language-like communication between adults at the *onset* of the trajectory leading to human-specific sociality, while Hrdy's argument that "cooperative breeding was the pre-existing condition" for this trajectory is persuasive. Furthermore, alloparenting can be seen as the "missing piece" in Tomasello's account, since it would provide the context in which shared intentionality could evolve. However, as pointed out in Section 3.2, that would imply that motivational and emotional aspects of sharing (care, food, protection) should be given priority to cognitive ones.

Concerning *how*, it was argued that all four theories rely, explicitly or implicitly on multi-level selection, including group selection, and in the case of traits subject to cultural transmission ("marriage" and perhaps other social norms such as "egalitarianism", cf. Boehm

2000), on *cultural* group selection (cf. Section 2.3). This conclusion is likely to be controversial, since the notion of group selection continues to be hotly debated (cf. commentaries to Sober and Wilson 2000a). However, its outright rejection is no longer possible, as even former opponents seem to be converging toward the notion of multi-level selection (Wilson and Wilson 2007).

The differences between the theories, and their complementary nature, become again apparent when we consider that they could in fact be plotted along a *single timeline*, by adjusting their individual claims. If we accept that “alloparenting came first” as suggested above, then it can be hypothesized to have begun even *before* the major changes that happened with *Homo erectus*, and have in fact been one of the crucial factors that led to them, perhaps even contributing to the establishment of habitual bipedalism. Then, Deacon’s “sex contract” and the co-evolution of morality and “symbolic reference” could be linked to *erectus*, with larger, more coherent and technologically advanced social groups, needed for e.g. long-distance migration. The fact that fossilizing adaptations for speech (enlarged thoracic vertebral canal and hypoglossal canal) are not observed until 0.5 MYA are not problematic for this proposal, if we accept that the origins of sign-use were initially not in the vocal-auditory, but in the bodily-visual channel (Donald 1991; Zlatev 2008). Non-symbolic vocalization would at first have had mostly affiliative functions (as in gelada), but could have with time been “reinterpreted” symbolically, given the tight synchronization of multimodal, hand-mouth, communication (Brown 2012). This would naturally have set selection pressures for anatomical changes leading to enhanced vocal control. Thus, the origin of multi-modal language can be linked to *Homo heidelbergensis*, and modern-like language with *Homo*

sapiens, with language and culture-specific grammars emerging through processes of cultural evolution.

Concerning the *size* of the relevant social groups in which these evolutionary processes apply, we can again obtain something of a compromise, if we take aboard a model of “concentric circles” for different social networks such as that suggested by Dunbar (cf. Section 3.4), to which Sutcliff et al. (2012) add two even smaller circles: the “support clique” of 4-5 individuals and the “sympathy group” of 12-15. These five levels can be characterized with progressively higher reliance on symbolic means for establishing group identity, shared moral values and hence trust and cooperation. The innermost circles, involving immediate family and close friends, are thus the sphere where cooperation/altruism is based most directly on empathy, while identifying and cooperating with the “clan” of 150 or so people, and the “tribe” of 500, not to mention still larger circles like “nation”, clearly require moral rules, symbolically mediated “shared values” and language. On this reasoning, the middle circle of the “band” with 30-50 members seems again to play a key role, since this appears as the first generalization “up” from family and friends (which are groups of intimates with correlates even in ape societies, cf. Section 2.1). Since this corresponds to the type of group in which alloparenting is assumed to have evolved (and still functions in hunter-gatherers today), this gives further support to Hrdy’s theory that the band corresponds most closely to the social niche in which human-specific intersubjectivity first arose, prior to language.

Finally, in terms of *development*, human sociality can be similarly seen to extend in concentric, Russian-doll-like layers. Bråten and Trevarthen (Bråten 2007: 3) distinguish, schematically, between three such layers: (1) *primary intersubjectivity*, from the first months of life onwards, based on “direct sympathy with actual others’ expressions of feelings in

intimate reciprocal subject-subject contact”, (2) *secondary intersubjectivity*, from 9 months, involving “objects of joint attention and emotional referencing are brought into play within trusting relations of companionship [...] sometimes inviting imitative learning” and (3) *tertiary intersubjectivity*, based on “symbolic conversation with actual or virtual companions”. These developmental layers correspond to some extent to the spatial layers discussed above: the first in which the child interacts with mother and alloparents, the second extending to a somewhat wider circle of intimates, including peers, and the third to a virtually open circle, since sharing has become symbolically mediated. While ontogeny does not in general recapitulate phylogeny, there are good reasons to expect a degree of parallelism (Zlatev 2003). Thus, this offers additional support for the proposal of Hrdy that human-specific traits of intersubjectivity evolved first on the level of “direct sympathy” between child and alloparents, and was subsequently extended to shared intentionality which is not yet dependent on language (as proposed by Tomasello), and finally to language-mediated intersubjectivity, involving morality.

4. Conclusions

We, human beings, are not only special in the animal world for our ability to share languages and to use them cooperatively, but also for the degree to which we (tend to) share material resources and child-care, and communal values of right and wrong. The argument of this chapter has been that these different kinds of sharing co-evolved. The precise nature of this co-evolutionary process needs to be further investigated, but the discussions of the previous two sections lead to the following conclusions.

The first one is that more “mainstream” models of evolution based only on individual-level and gene-level selection are insufficient, and that in order to account for the possibility of human-scale sharing of care, values and information, i.e. of intersubjectivity, morality and language, requires models of multi-level selection, including (cultural) group selection. This conclusion is further bolstered by the fact that four of the most influential theories “on the market” explicitly or implicitly presuppose such a model, as argued on Section 3.2.

The second major conclusion is that the four theories were found to be to some extent complementary, rather than in contradiction – especially if they are interpreted somewhat “revisionistically”, as proposed in Section 3.5. Specifically, Hrdy’s theory focusing on the evolution of alloparenting was shown to provide the best explanation for the onset of the evolution of human intersubjectivity (as a kind of blend of Great Ape cognition and tamarin-like altruism), and it was suggested that this could have started along with the transition to bipedalism more than 4 MYA. In this perspective, Tomasello’s theory of shared intentionality and pro-social motivation can be placed within a Darwinian framework, after reversing its (tentative) proposal for the order in which these two aspects of intersubjectivity evolved. Deacon’s “sex contract” can be seen as an important factor (though most likely not as the sole one) for the evolution of morality, understood as a “system of conflict management based on shared values”, and his proposal that this co-evolved with “symbolic reference”, thus providing an impetus for the evolution of language, is compelling. It was further suggested that this most likely coincided with the emergence of *Homo erectus* (cf. Knauff 2000), and that sign-use was initially multi-modal, but not predominantly vocal, i.e. a form of bodily mimesis (Donald 1991; Zlatev 2008). Finally, Dunbar’s theory, specifically on the transition from “musical” vocal-grooming to vocal “gossip” can be seen as providing a partial

explanation for evolution of *spoken* language, most likely with *Homo heidelbergensis* 0.5 MYA. It is characteristic that cultural evolution becomes cumulative first after that, with inevitable effects on group differentiation and cultural group selection, as explained in Section 2.3.

Thus, the co-evolutionary scenario of intersubjectivity, morality and language that we are led to is, in brief, that intersubjectivity (in an alloparenting context) spearheaded the way, followed by morality and language which evolved co-temporally, in spirals of increasing complexity. However, this linear ordering cannot be strictly maintained, since as morality and language spread culturally, to quote again Boyd and Richerson (2009: 3281-82), they “increased the reproductive success of individuals who functioned well in such environments, and this in turn led to the evolution of other regarding motives like empathy and social emotions like shame”, as well as of increasing the reproductive success of individuals who were competent language users, we may add.

Still, there is an important difference between moral systems and language as super-individual, social phenomena, and the “moral sense” and “linguistic competence” of individuals. (Confusing language as a social institution and as individual competence is the main fault of the Chomskyan paradigm in linguistics). As we are well aware, there is large individual variation in the latter respects, and there are no clear correlations between levels of “moral development” and “linguistic development”, either on individual or societal levels. Thus, even if intersubjectivity, morality and language co-evolved, as here argued, it is possible to disentangle them, and to envision a society with “high” prescriptive morality, but in which “regarding motives like empathy and social emotions like shame” are not selected for, but rather the contrary.

Toward the end of her book, Hrdy (2009) alarmingly suggests that current Western societies might be of this type. On the one hand, while resolutely democratic, they are becoming increasingly individualist, consumption-oriented, and alienated: moving further and further away from the conditions necessary both for the evolution of intersubjectivity, and for its development in each successive generation. On the other hand, due to technological and medical advances “an ever-increasing proportion of the species fails to encounter those conditions but nevertheless survives to reproduce” (ibid: 293). The possible outcome is spelled out in the following memorable passage: “If empathy and understanding develop under particular rearing conditions, and if an ever-increasing proportion of the species fails to encounter those conditions but nevertheless survives to reproduce, it won’t matter how valuable the underpinnings for collaboration were in the past. Compassion and the quest for emotional connection will fade away as surely as sight in cave-dwelling fish.” (ibid: 293) Even if this is a pessimistic assessment of our present situation, it is worth taking seriously. Biological evolution does not plan ahead, but on a cultural and societal level, we are still (hopefully) capable of influencing our future.

Acknowledgments

I would like to thank Kenny Smith and two anonymous reviewers for comments on a previous version of this text. The Centre for Cognitive Semiotics (CCS) at Lund University, funded by *Riksbankens Jubileumsfond* (RJ), and the research project ‘Precursors of Sign Use in Intersubjectivity and Imitation’ (PSUII), funded by *Vetenskapsrådet* (VR), provided most of

the ideal and material environment necessary for conducting this research. I am grateful to my colleagues for all the idea-sharing, without this necessarily implying agreement.

References

- Batson, C. D (1991). *The Altruism Question: Toward a Social-Psychological Answer*. Hillsdale, NJ: Lawrence Erlbaum.
- Batson, C. D. (2000). Onto Others: A service... and a disservice. *Journal of Consciousness Studies* 7, 1/2: 207-210.
- Boehm, C. (2000). Conflict and the evolution of social control. *Journal of Consciousness Studies* 7, 1/2: 79-102.
- Bowlby, J. (1988). *A Secure Basis: Parent-Child Attachment and Healthy Human Development*. New York: Basic Books.
- Boyd, R. and Richerson, P.J (2009). Culture and the evolution of human cooperation. *Philosophical Transactions of the Royal Society B* 364: 3281–3288.
- Bråten, S. (2007). Introduction. In S. Bråten (ed.), *On Being Moved: From Mirror Neurons to Empathy*, 1-17. Amsterdam/Philadelphia: Benjamins.
- Brown, J.E. (2012). *The Evolution of Symbolic Communication: An Embodied Perspective*. PhD thesis, University of Edinburgh.
- Clark, H. (1996). *Using Language*. Cambridge: Cambridge University Press.
- Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society of London Biology* 273: 1375-83.
- Darwin, C. (1982 [1871]). *The Descent of Man, and Selection in Relation to Sex*. Princeton:

Princeton University Press.

Dawkins, R. (1976). *The Selfish Gene*. New York: Oxford University Press.

de Waal, F.B.M. (1996). *Good Natured: The Origins of Right and Wrong in Humans and Other Animals*. Cambridge, MA: Cambridge University Press.

de Waal, F.B.M. (2007). The ‘Russian doll’ model of empathy and imitation. In S. Bråten (ed.), *On Being Moved: From Mirror Neurons to Empathy*. Amsterdam/Philadelphia: Benjamins, 35-48.

Deacon, T. (1997). *The Symbolic Species: The Co-evolution of Language and the Brain*. New York: Norton.

Donald, M. (1991). *Origins of the Modern Mind: Three Stages in the Evolution of Culture and Cognition*. Cambridge, Mass.: Harvard University Press.

Dugatkin, L. A. (2008). *Principles of Animal Behavior*. New York, NY: Norton.

Dunbar, R. (1996). *Grooming, Gossip and the Evolution of Language*. Cambridge, Mass.: Harvard University Press.

Dunbar, R. (2004). *The Human Story: A New History of Mankind’s Evolution*. London: Faber and Faber.

Dunbar, R. (2009). Why only humans have language. In R. Botha and C. Knight (eds.) *The Prehistory of Language*. Oxford: Oxford University Press, 12-35.

Early, R. L. (2010). Social eavesdropping and the evolution of conditional cooperation and cheating strategies. *Philosophical Transaction of the Royal Society Biology* 365: 2675–2686.

Eisenberg, N. (2000). Empathy and sympathy. In M. Lewis and J.M. Haviland-Jones (eds.), *Handbook of Emotion* (2nd ed), 677-691. New York: Guilford Press.

- Falck, J.C. and de Waal, F.B.M. (2000a). 'Any animal whatever': Darwinian building blocks of morality in monkeys and apes. *Journal of Consciousness Studies* 7, 1/2: 1-30.
- Falck, J.C. and de Waal, F.B.M. (2000b). Being nice is not a building block of morality. *Journal of Consciousness Studies* 7, 1/2: 67-78.
- Fisher, H. (1992). *Anatomy of Love: A Natural History of Mating, Marriage, and Why We Stray*. New York: Random House.
- Fitch, T. (2010). *The Evolution of Language*. Oxford: Oxford University Press.
- Givón, T. (1979). *On Understanding Grammar*. New York: Academic Press.
- Goodall, J. (1982). Order without law. *Journal of Social and Biological Structures* 5: 349-352.
- Hamilton, W. D. (1964). The genetical evolution of social behaviour. *Journal of Theoretical Biology* 7 (1): 1-16.
- Hare, B., Call, J., and Tomasello, M. (2001). Do chimpanzees know what conspecifics know? *Animal Behaviour* 61(1): 139-151.
- Hare, B., Call, J., and Tomasello, M. (2006). Chimpanzees deceive a human competitor by hiding. *Cognition* 101(3): 495-514.
- Hare, B., Call, J., Agnetta, B., and Tomasello, M. (2000). Chimpanzees know what conspecifics do and do not see. *Animal Behaviour* 59(4): 771-785.
- Haviland, S. E. and Clark, E. V. (1974). 'This man's father is my father's son': a study of the acquisition of English kin terms. *Journal of Child Language* 1: 23-47.
- Hawkes, K. (2004). The grandmother effect. *Nature* 428: 128-129.
- Hrdy, S.B. (2009). *Mothers and Others: The Evolutionary Origins of Mutual Understanding*. Cambridge, Mass.: Harvard University Press.

- Kaminski, J., Call, J., and Tomasello, M. (2008). Chimpanzees know what others know, but not what they believe. *Cognition* 109: 224–234.
- Knauff, B.M. (2000). Sex, symbols and sociality in the evolution of human morality. *Journal of Consciousness Studies* 7, 1/2: 130-138.
- Leavens, D., Racine, T. and Hopkins, D. (2009). The ontogeny and phylogeny of non-verbal deixis. In R. Botha and C. Knight (eds.) *The Prehistory of Language*. Oxford: Oxford University Press, 142-165.
- Leimar, O. and Hammerstein, P. (2001). Evolution of cooperation through indirect reciprocity. *Proceedings of the Royal Society London Biology* 268: 745–753.
- MacLauron, A. and Hewitt, G. (1999). The evolution of human speech: the role of enhanced breathing control. *American Journal of Physical Anthropology* 109: 341-363.
- Maynard Smith, J. (1964). Group selection and kin selection. *Nature* 201 (4924): 1145–1147.
- Melis, A., Call, J., and Tomasello, M. (2006). Chimpanzees (*Pan troglodytes*) conceal visual and auditory information from others. *Journal of Comparative Psychology* 120(2): 154–162.
- Nelson, K. and Shaw, L. K. (2002). Developing a socially shared symbolic system. In J. Byrnes and E. Amseli (eds.) *Language, Literacy and Cognitive Development*, 27-57. Mahwah, N.J.: Erlbaum.
- Nowak, M. A. and Sigmund, K. (1998). Evolution of indirect reciprocity by image scoring. *Nature* 393: 573–576.
- O’Gorman, R., Wilson, D. S. and Sheldon, K. M. (2008). For the good of the group? Exploring group-level evolutionary adaptations using multilevel selection theory. *Group Dynamics-Theory Research and Practice* 12 (1): 17–26.

- Panchanathan K. and Boyd, R. (2004). Indirect reciprocity can stabilize cooperation without the second-order free rider problem. *Nature* 432: 499–502
- Preston S.D. and de Waal F.B.M. (2002). Empathy: Its ultimate and proximate bases. *Behavioral and Brain Sciences* 25: 1-72.
- Richerson, P. J., and Boyd, R. (2005). *Not by Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press.
- Sober, E., and Wilson, D. S. (1998). *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Cambridge, MA: Harvard University Press.
- Sober, E., and Wilson, D. S. (2000a). Summary of *Unto Others: The Evolution and Psychology of Unselfish Behavior*. *Journal of Consciousness Studies* 7, 1/2: 185-206.
- Sober, E., and Wilson, D. S. (2000b). Morality and ‘Unto Others’. *Journal of Consciousness Studies* 7, 1/2: 257-268.
- Sutcliffe, A., Dunbar, R., Binder, J. and Arrow, H. (2012). Relationships and the social brain: Integrating psychological and evolutionary perspectives. *British Journal of Psychology* 103: 149–168.
- Thierry, B. (2000). Darwinian elements of morality are not elements of morality. *Journal of Consciousness Studies* 7, 1/2: 60-62.
- Tinbergen, N. (2010). On aims and methods of Ethology. *Zeitschrift für Tierpsychologie* 20 (4): 410.
- Tomasello, M. (1999). *Cultural Origins of Human Cognition*. Cambridge, Mass.: MIT Press.
- Tomasello, M. (2008). *Origins of Human Communication*. Cambridge, Mass.: MIT Press.

- Tomasello, M. Carpenter, J. Call, T. Behne and H. Moll (2005). Understanding and sharing intentions: The origins of cultural cognition. *Behavioral and Brain Sciences* 28: 675-691.
- Trevarthen, C. (1979). Communication and cooperation in early infancy. A description of primary intersubjectivity. In M. Bullowa (ed.), *Before Speech: The Beginning of Human Communication*. London: Cambridge University Press, 321-347.
- Trivers, R.L. (1971). The evolution of reciprocal altruism. *Quarterly Review of Biology* 46: 35–57.
- Weissner, P. (2002). Taking the risk out of risky transactions: A forager's dilemma. In Frank. K. Salter (ed.), *Risky Transactions: Trust, Kinship and Ethnicity*. New York: Berghahn Books, 21-43.
- Wellman, B. (2012). Is Dunbar's number up? *British Journal of Psychology* 103: 174–176.
- Wilson, D. S., and Wilson, E. O. (2007). Rethinking the theoretical foundation of sociobiology. *Quarterly Review of Biology*, 82: 327–348.
- Zahavi, A. (2003). Indirect selection and individual selection in sociobiology: my personal views on theories of social behaviour. *Animal Behavior* 65, 859–863.
- Zlatev, J. (2003). Meaning = Life (+ Culture). An outline of a unified biocultural theory of meaning. *Evolution of Communication*, 4 (2): 253-296.
- Zlatev, J. (2008). The coevolution of intersubjectivity and bodily mimesis. In J. Zlatev, T. Racine, C. Sinha and E. Itkonen. (eds.) In *The Shared Mind: Perspectives on Intersubjectivity*. Amsterdam: Benjamins, 215-244.