

The co-evolution of language and emotions

Eva Jablonka^{1,*}, Simona Ginsburg³ and Daniel Dor²

¹The Cohn Institute, and ²Department of Communication, Tel-Aviv University, Israel ³The Open University, Raanana, Israel

We argue that language evolution started like the evolution of reading and writing, through cultural evolutionary processes. Genuinely new behavioural patterns emerged from collective exploratory processes that individuals could learn because of their brain plasticity. Those cultural–linguistic innovative practices that were consistently socially and culturally selected drove a process of genetic accommodation of both general and language-specific aspects of cognition. We focus on the affective facet of this culture-driven cognitive evolution, and argue that the evolution of human emotions co-evolved with that of language. We suggest that complex tool manufacture and alloparenting played an important role in the evolution of emotions, by leading to increased executive control and intersubjective sensitivity. This process, which can be interpreted as a special case of self-domestication, culminated in the construction of human-specific social emotions, which facilitated information-sharing. Once in place, language enhanced the inhibitory control of emotions, enabled the development of novel emotions and emotional capacities, and led to a human mentality that departs in fundamental ways from that of other apes. We end by suggesting experimental approaches that can help in evaluating some of these proposals and hence lead to better understanding of the evolutionary biology of language and emotions.

Keywords: gene-culture co-evolution; genetic assimilation; language evolution; plasticity; self-domestication; social emotions

1. INTRODUCTION

PHILOSOPHICAL TRANSACTIONS

THE ROYAL

SOCIETY

There is a lacuna in the study of language evolution: although there are many studies exploring the evolution of the language capacity in humans, and there is much research on the human moral and social emotions, there is relatively little discussion of the interrelations between the evolution of language and that of the emotions. In this paper, we explore some aspects of this interrelation within a framework of gene-culture co-evolution. We see language as an integrated part of an evolved, sophisticated and adaptive social and mental suite, which involved the co-evolution of culture and genes. This view, which is opposed to some influential positions [1,2], is developed in §2 of the paper. We stress the complementary processes of the adjustment of language to general cognition and that of general cognition to culturally evolving language. We suggest that although many of the cognitive adaptations that enable language are domain general, some language-specific adaptations may also have been genetically accommodated.

In §3, we follow and develop proposals suggesting that for language to evolve, certain emotional preconditions must have been in place. We propose that the human technological and social practices that are considered to be important for the evolution of human cognition, in particular, tool-making and alloparenting, required emotional control and increased social sensibility, and led to the development of the social emotions of pride, shame, guilt and embarrassment. These social emotions are thought to regulate cooperative alliances, and to establish and consolidate group organization—social functions that are crucial for the stabilization of cooperation, including linguistic information sharing. The socially moderating effect of this emotional evolution can be thought of as part of a process of human-specific self-domestication, which is more targeted than that of other domesticates.

We explore the effects of language on the range and control of emotions in §4. We suggest that the imagination-instructing facet of modern language enhanced the need to exercise and extend emotional control. This need for controlling emotions could have encouraged the usage of arbitrary linguistic signs that carry no associative experiential connotations. However, in addition to inhibitory control, language enormously expanded the experiential world of individuals, and led to the expansion of their emotional world. The range of social emotions began to include emotions related to truth, to humour and to individual and social identity and agency. Language was also used to anchor and define emotions on the one hand, as well as to excite and dampen them on the other, through the use of metaphors based on the expression of emotions.

Since the relationship between the evolution of language and the evolution of emotions has not been sufficiently researched, our suggestions are inevitably speculative. In §5, we therefore suggest some experiments which could help to evaluate some of them.

^{*} Author for correspondence (jablonka@post.tau.ac.il).

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2. EVOLUTIONARY DYNAMICS

Our starting point is Dor's theoretical characterization of language as an imagination-instructing communication system [3]. According to this view, language is used by communicators to instruct the imagination of their interlocutors: the communicator produces a code, a plan, a skeletal list of the basic co-ordinates of an experience, which the interlocutor uses as a scaffold for the construction of a parallel experience in his or her own mind. Dor's stress on the social aspects of this culturally evolving system of communication follows the Vygotskian understanding of language as a socially learned tool of communication [4,5], and, like Tomasello's framework [6,7], emphasizes the dynamic cultural-innovation and cultural-learning processes involved in language evolution.

The focus on culturally learned aspects of language raises questions about the relationship between the evolution of languages (a cultural process) and the evolution of speakers (a cognitive-genetic process). We adopt an evo-devo perspective that emphasizes processes of developmental plasticity, particularly processes of open-ended plasticity, which underlie the ontogenetic recruitment and reorganization of pre-existing neural structures enabling the production of novel adaptive behaviours [8]. A good example of adaptive, cognitive plasticity is the linguistic behaviour of the bonobo Kanzi [9]. Although there is a controversy about the precise significance of his linguistic achievements, there is no doubt that Kanzi's communicative ability, based on the learned use of the communication system invented by the humans around him, goes well beyond the communication among bonobos in the wild: symbolic communication, which Kanzi masters to the extent of a 2.5 year old child, is not part of the behavioural repertoire of his species. Another well-researched and uncontested case of adaptive open-ended communicative plasticity in humans is the reorganization of the human brain involved in literacy, which shows how the redeployment of pre-existing neural structures enables humans to read and write, a culturally selected and developmentally constructed ability, which was not itself genetically selected [10,11]. A recent striking example of adaptive plasticity is the echolocation technology invented by blind people, through which they can discriminate among distant objects. This new capacity is based on brain plasticity, which has enabled them to develop a novel sensory-motor ability [12].

We suggest that just as literacy has done during historical time, early language evolution involved socially learned and constructed alterations, adjustments and improvements in communication signs and structures, which came together through historical-cultural evolution. Although it is impossible to reconstruct the actual stages in the evolution of early human protolanguages, the cases of literacy, and of socio-political systems in some Austronesian societies, suggest that they involved incremental innovations and complexifications, and occasional losses [13]. During this process, individual speakers were solving-deliberately or accidentally-new communicative problems. They invented signs for things that had not yet been named, gave new meaning to existing signs, arranged signs in new ways to express new relations and found new ways to reduce ambiguity. Based on what we know of other cultural communication systems, we assume that during their long history proto-languages diversified, increased in size and efficiency, and developed an internal structure.

Assuming that the process of language evolution was ongoing, and that the pressure to add to and to sophisticate language was, on the average, consistent, then heritable changes at any level, including the genetic level, that helped individuals meet the increasing demands of cultural proto-language learning, would have been selected. In other words, human linguistic culture, which is the accumulated result of collective activities over many generations, constructed a new social and developmental linguistic niche in which heritable, epigenetic and genetic variations that fitted the consistent features of this niche were selected [14].

The idea that the evolution of the language capacity involved changes in linguistic communication and cognition that were initially brought about by cultural changes, and were subsequently stabilized through the selection of supporting genetic variants, was first suggested by Waddington. Waddington [15] argued that the evolution of language, like that of many complex adaptive traits, was driven by genetic assimilation. Genetic assimilation is a process whereby selection for the developmental capacity to respond adaptively to a new persistent environmental stimulus (for example, a new chemical, a heat shock, or a new predator) leads to the construction of a genetic constitution that facilitates such an ontogenetic adjustment. It is based on pre-existing heritable differences among individuals in their responsiveness to changed conditions. For example, individuals who can learn more readily how to avoid a new type of predator would have a selective advantage, and hence, over time, the genetic constitution of such individuals would become more common. Eventually, the behavioural trait, which was originally learned after many trials, appears with a briefer induction and far less learning; in extreme cases, it appears after just a single exposure to the stimulus. The trait is then said to be genetically assimilated. According to Waddington, 'If there were selection for the ability to use language, then there would be selection for the capacity to acquire the use of language, in interaction with a language-using environment; and the result of selection for epigenetic [developmental] responses can be, as we have seen, a gradual accumulation of so many genes with effects tending in this direction that the character gradually becomes genetically assimilated' ([15, p. 306] our italics). Waddington pointed out that the extent of genetic assimilation may vary, and, in the case of language, as in many other cases (for example, song-learning in many song bird species), learning would still be necessary although with fewer trials than in the original population and circumstances. Such partial genetic assimilation constructs biases and propensities, which are sometimes quite slight, and are always learning-dependent. In addition, when some aspects of the environmental conditions are rapidly changing, the evolution of improved responsiveness can lead to sensitivity to a greater range of environmental contexts. West-Eberhard [8] calls the evolutionary processes that lead to the extension of responsiveness and increase in flexibility, as well as the stabilization and streamlining of existing responses, 'genetic accommodation'.

Later scholars who came from several different theoretical camps, using a variety of approaches, adopted and developed Waddington's idea that the evolution of language involved complex interactions between genes and culture [16-22]. Two extreme ends of the spectrum of views about the nature of the faculties that became assimilated during language evolution are represented by Pinker & Bloom on the one hand, and Deacon on the other. Pinker and Bloom [16] suggested that specific syntactic properties-as they are defined in the generative literature-may have appeared as communicative conventions during the social evolution of language, and these conventions became genetically assimilated. Deacon [19] and more recently Christiansen & Chater [22] have argued that languages are simply too varied, too different from each other, for any particular property of any of them to have been universally internalized in an identical way by all humans. They therefore concluded that only properties of general cognition could be genetically assimilated, especially, according to Deacon, the capacity for symbolic thinking.

In spite of the differences between these positions, both sides stress the constraints imposed on language by the structure of human cognition. They agree that elements of language were indeed invented, but the elements that survived and were eventually established were those that became adapted to the general or specific pre-existing structures of our minds and brains. Our position, in contrast, highlights the adaptations of *cognition to language*: we argue that although general human learning capacities may have ruled out the regular acquisition of some linguistic features, the structure of human brains and minds were never the primary 'attractors' (the set towards which a dynamical system evolves over time) around which human language development was organized. The primary attractors were the languages of the communities, the products of innovative collective inventions and socialdevelopmental processes, which 'stretched' the plastic cognitive capacities of individuals in novel directions. Our suggestion that language was not only shaped by, but also shaped general cognition, making it more 'linguistic', is based on the profound and reciprocal relations between language and culturally constructed modes of cognition, as documented, for example, by Everett [23] among the Pirahã, as well as on evidence suggesting that the culturally invented practice of literacy affects categorical thinking [24,25]. However, such bi-directional interactions leave open the question as to the nature of cognitive features that had become genetically accommodated: the accommodated changes that were driven by the cultural evolution of language may have been domain-general, for example, improved general memory or better analogical reasoning, or they could have been language-specific.

Our position on this issue is intermediate between that of Pinker and Bloom, who suggest that genetic assimilation led to a syntax-specific linguistic structures, and Deacon, and Christiansen and Chater, who argue that *only* domain general structures were genetically accommodated. It has been convincingly argued that the variability exhibited by languages precludes genetic assimilation of syntactic structures [26,27]. However, the partial assimilation of broad, but nevertheless language-specific predispositions, such as language-specific discrimination and production of sounds and gestures and early and rapid language-specific learning, have not been excluded, and the question is therefore still open. We interpret the persistent developmental, structural and semantic features of language as the result of the genetic accommodation of both domain-general aspects of cognition (e.g. enhanced general memory, improved associative learning, symbolic representation, heightened social emotions), and some language-specific capacities. We suggest that these language-specific capacities included sensorimotor aspects of language production and comprehension: for example, the ability to better distinguish linguistic sounds or gestures from other types of sounds and gestures; more refined phonetic and phonological analysis of auditory signs and gestural analogues; an improved semantic-linguistic memory, which enabled the memorizing of conventional communicative signs, and through this enabled sign-based recall of episodic experiences; an earlier and more facile learning of language in infants. If this interpretation is valid, we expect that future research will unravel some human-specific genetic variations that have distinct effects on these language-specific components [14].

Whatever the nature of the assimilated adaptations, the co-evolutionary genetic assimilation process that increased the robustness and speed of languagelearning, could have led to the sophistication and expansion of linguistic achievements. By making some learned acts easier, more things can be learned with the same cognitive resources, and the result is an increase of learned behavioural outputs, a process that has been termed the 'assimilate-stretch' principle [28]. Moreover, acquiring the ability to accomplish one thing (using language), scaffolds the learning of other things (reading and writing).

In addition to the increased channelling of some aspects of early development brought about through partial genetic assimilation, culture-gene co-evolution led to positive selection for increased plasticity. Once human cultural evolution began to accelerate and languages began to change rapidly, there would have been strong selection for general and language-specific increases in brain plasticity. Since the one thing that is consistently stable in a rapidly changing culture is the culture's context-dependent flexibility (which the cultural evolutionary process itself creates), there is persistent selection for increasingly flexible and sophisticated ways of learning, including language-learning. As increased flexibility is selected, more learning opportunities, both those afforded by the assimilate-stretch principle and those driven by an increase in cognitive resources (for example, through increase in brain size) are opened up. Such selection produced one of the positive feedbacks that created the human cultural ratchet [6,7].

Many other general cognitive capacities were genetically accommodated during language evolution, including better skills for social engagement, more extensive associative learning, the ability for causal and analogical reasoning, and the capacity for hierarchical organization and embedding of actions necessary for complex tool-making and for managing complex social interactions. We believe that social emotions were very important in this process, facilitating, accompanying and reinforcing language evolution.

3. CO-EVOLVING FACTORS: TOOL-MAKING, ALLOPARENTING AND THE SOCIAL EMOTIONS

There are many speculations about the culturalgenetic evolution of language, but most evolutionary linguists agree that it involved a fairly protracted process of proto-language evolution [29,30], followed by either gradual or saltatory change into the symbolic-syntactic language observed in Homo sapiens. It is also generally agreed that a sophisticated level of information sharing like that seen in linguistic communication requires a high level of cooperation and collaboration [31], and there are many suggestions as to the conditions that fostered cooperation and its affective correlates [6,32-34]. The cognitive requirements, in particular those associated with cooperative hunting and complex tool-making, were also emphasized, and are seen as important facilitating and co-evolving facets of language evolution. Here, we want to emphasize the emotional rather than cognitive requirements, and stress the importance of alloparenting in addition to technological challenges.

(a) Tool-making

Sterelny [35] stresses the major importance in the evolution of human cognition, including language, of extractive foraging, which was already evident over 1.7 Mya, in the early Acheulean industry associated with Homo erectus. He suggests that those foraging practices indicate that 'apprentice learning' of tasks such as tool-making involved passive and possibly even active pedagogy [36], and argues that the motor control involved in learning and teaching tool manufacture is the platform for the evolution of increasingly complex communication. Corballis [37], too, emphasizes the role of motor control, arguing that the evolution of language may have had its origins in the control of manual and orofacial gestures (and only later of vocalizations). He proposed that the voluntary motor control that was necessary for toolmaking made gestural communication easy, and this was generalized to oral movements, which then led to speech. Other, non-mutually exclusive ideas are that motor imitation, necessary for the manufacturing of complex Acheulean tools, was a prerequisite for the evolution of syntactic language: the hierarchical recursive organization that enables the stepwise combination of motor units necessary to manufacture complex tools is the suggested basis of hierarchical and recursive syntax, in which communication signs are embedded and combined into larger semantic representations (see, for example, [38–41]).

The faculties and features required in the manufacture of Acheulean tools thus go well beyond the template-matching seen in the manufacture of tools by Caledonian crows [42]. It required, in addition to focused attention and causal reasoning, other faculties and features, such as the recognition of functions and goals, pedagogy and tolerance, and the high degree of executive control that is manifest as patience and tenacity, which are necessary for following a consecutive sequence of steps before a goal is reached (reviewed in [43]). It is probable that the cognitive and emotional faculties that were required for multi-stage tool-making in these early hominins also had profound effects on their communication abilities.

(b) Alloparenting

In her important book, Mothers and others, Hrdy [44] suggests that it was another aspect of human social life-alloparenting-that promoted the emergence of language. Humans are the only species of higher apes that practises alloparenting, the care of the young by individuals other than the mother, and Hrdy argues convincingly that alloparenting by fathers, grandparents, other kin, or friends may already have evolved in early hominins, around 1.6 Mya. It has obvious reproductive advantages: help from alloparents, especially supplementary feeding, enables human mothers to reproduce faster than any great ape, in spite of having offspring that are more dependent and slower to mature. Although the context in which alloparenting in hominins evolved is not clear, in other primate species, such as tamarins and marmosets, its evolution seems to be associated with ecological conditions that make females remain in their natal groups, close to matrilineal kin, within relaxed and flexible female dominance hierarchies. It is therefore reasonable to suggest that in erectile hominins, constraints on female dispersal in conditions that necessitated collective foraging, produced situations in which mothers would get help from relatives and close friends [44].

Hrdy proposes that in highly intelligent and cooperative apes, as our ancestors were likely to have been, alloparenting promoted not only further economic cooperation, but also trust and empathic bonding within the group. An alloparented infant interacts and bonds with males and females, with individuals of different ages, temperaments, inclinations and skills, from whom it learns and whom it learns to please. On the alloparents' side, there is the need to coordinate their caring activities, to devote more of their time to caring, and to be tolerant towards and empathic with infants who are not their own, and to whose care they are not as hormonally primed as the mother. Alloparents therefore need to have both a greater motivation to care and a greater control of their emotions than their non-alloparenting ancestors did. Both the infant and the alloparent need to learn to read the minds of others. Such enhanced mentalizing would be both a product and a cause of social selection for intra-group cooperation and information sharing [44].

(c) The evolution of social sensibility

The patience and tolerance demanded by alloparenting and tool-making may have been beneficial in many situations. Initially, the executive control and patience involved in tool-making and that involved in alloparenting may have been based on different cognitive and hormonal conditions. But since both practices were probably associated with passive and active pedagogy, and since executive control contributes to the learning of *any* sophisticated multi-step skill, such as coordinated hunting and gathering activities, and the collectively organized consumption of the food at the home-base [31], its generalization was advantageous for hominins.

Hrdy stresses the overlaps among empathy, theory of mind and intersubjectivity in humans, and suggests that our alloparented hominin ancestors not only attributed intentions and mental states to others (beginning with their parents and alloparents), but also cared about what they thought about them. Infants younger than 12 months manifest embarrassment, which is not related to actual punishment, but to the failure to meet the expectations of caretakers [45]. Caring about the opinion of a widening range of others-alloparents, teachers, collaborators-led to the social emotions, to embarrassment, shame, guilt and pride. These emotions were socially constructed from their emotional precursors: the first three are believed to be associated with feelings accompanying subordination and appeasement, and pride with prestige attainment [46]. Shame and embarrassment are thought to establish and maintain social hierarchies by appeasing dominant individuals (e.g. alloparents, teachers), and to reduce aggressive reactions by showing submission. Pride, on the other hand, is a signal of achievement and success, which is directed towards the self, reinforcing one's motivation, and it is used as a signal to others.

Evolutionary psychologists highlight two general functions of the social emotions: the regulation of cooperative alliances, and the establishment and consolidation of group organization [46,47]. The disposition to feel and display social emotions may therefore be assumed to have been a selective advantage in hominins who were increasingly dependent on cooperation. However, in spite of the universal occurrence of the social emotions, it is unlikely that each of them is underlain by a distinct social-emotional 'module'. Social emotions have very varied modes of expression and interpretation across cultures, something that is expected when people need to respond to changing cultural norms through cultural learning. When learning of specific social norms is combined with some docility, mind reading, patience and heightened attention to members of one's group, the social emotions of embarrassment, shame, guilt and pride are inevitable. Consequently, there is no reason to assume genetic selection of distinct emotional modules for each of these emotions. It is more probable that there has been selection for an increased (general) sensibility to social situations that affect one's social standing.

The one human-specific expression of emotions in humans, the blush, may have been the product of the evolution of such general social sensibility. Darwin argued that the blush is the only universal and uniquely human expression of emotions [48]. Given its universal social importance, it is likely to have evolved in pre-*sapiens* ancestors, in Archaic humans, and possibly earlier. The blush is associated with all four basic social emotions, and is manifest in diverse social contexts [49]. We suggest that a heightened emotional responsiveness to social cues—a responsiveness which itself acts as a social signal to oneself, and sometimes to others, and is based on a distinction between the self and an internalized notion of group-decreed norms—is the basis of all four social emotions. The interpretation of the approving or disapproving 'social gaze' renders the social emotion positive or negative, with the gradations and hues of the emotion depending on the particular social context. In view of the attested variability, on every level, of the social emotions associated with blushing [49], and the selective advantages of flexibility in a changing cultural world, we suggest that what evolved genetically was the plastic social–emotional predisposition to blush in response to social scrutiny, rather than several distinct social–emotional modules.

(d) Human-specific self-domestication?

The affability and cooperativeness of humans led to the recurring idea that humans evolved through a process of 'self-domestication' (reviewed in [50]). The self-domestication hypothesis is based on the notion that social selection in humans led to 'tameness' and 'docility' akin to those seen in domesticated mammals such as dogs, cats, silver foxes and cattle. In these domesticates, tameness and docility were imposed by human selection, and resulted in remarkable parallel evolution [51]. A recent report adds weight to the proposal that self-domestication is possible in primates and that it is indeed similar in its effects to human imposed domestication: the profile of domesticationassociated gene expression in bonobos and artificially domesticated mammals is similar (though limited), suggesting that bonobos may have, indeed, undergone a form of self-domestication [52; F. Albert 2012, personal communication]. The same data, however, show that humans probably do not share the gene expression patterns of other domesticates, which may argue against human self-domestication. However, a simple parallelism between humans and other domesticates, even the bonobo, is probably not to be expected. Each domestication event was the result of unique selection pressures, leading to a unique gene expression profile. Docility in humans is probably the result of the selection for increased control of the emotions, for patience, for fine motor control, for delayed gratification, for increased empathy and mind reading, and for interest in social relations and social status. The blush and the emotions associated with it reflect the internalization of this social awareness, and is a strong indicator of socially constructed self-consciousness.

4. HOW LANGUAGE CHANGED HUMAN EMOTIONS

In addition to its many effects on cognition, instructive linguistic communication, even in its early stages, must have entailed a greatly reinforced control of motor actions and of the emotional drives that elicit motor activity. As we have already suggested, in pre-linguistic hominins, selection for emotional control was enhanced by the motor control necessary for complex tool-making, by tutoring, by alloparenting, and by other factors, such as the suspension of greedy behaviour during hunting and gathering, when individuals had to take food to the home-base rather than eat it while foraging. However, the evolution of linguistic signs greatly enhanced the need to exercise and extend this emotional control: when told about a predator that is far away, individuals had to be able to control their fear and their wish to run away. Volitional imagining, which is a crucial facet of linguistic communication, therefore entails an inhibitory control of actions and the emotions that trigger them. This inhibition of emotions is at the root of the distinction humans make between thought and feelings. We therefore see this dichotomy as an evolved phenomenon, specific to humans.

The importance of inhibition suggests that the arbitrariness of linguistic signs may not be just an inevitable by-product of the cultural evolution of language, what Tomasello [6] calls 'the drift to the arbitrary'; it may also be a product of positive cultural selection. Since instructive communication involves symbolscollectively agreed-upon communication signs that scaffold imagination-it could be advantageous for the signs themselves (unlike iconic representational signs, such as onomatopoeic words) not to carry any inherent emotional baggage. Using the abstract word 'lion', rather than the sound of a roaring lion, allowed the instructive symbol to move between contexts, and enabled the individual to perform combinations and operations with other symbols that would otherwise be difficult because of the emotional associations of iconic signs. Experiments with apes that can count and perform arithmetic operations show that they do better with abstract symbols than with concrete items, such as balls and bananas, which they associate with emotionally laden play or eating activities [54-56]. In humans there may therefore have been positive (though of course, not deliberate) cultural selection during the later stages of the evolution of language for arbitrary, invented, communication signs, because they reduced the need for inhibitory control.

Linguistic communication affected much more than inhibitory control. It also created new experiences and emotions. The range of an individual's experiences increased, because through language and imagination the individual could share the experiences of others. Language was employed for creating empathy and communality of feeling among individuals through metaphors, especially metaphors related to the states of the body. (For a cognitive view of metaphors, see [57]; the view that metaphors evoke pre-linguistic experiences is expounded in [58].) Metaphors such as 'my blood froze', or 'my heart pounded' enable the imagining of bodily experiences that are common to all people, and thus they facilitate empathy. Moreover, once instructive communication was in place, the all-important issues of truth and falsity emerged: truth and falsity are properties of the relationship between a message and the world. Feelings of suspicion and doubt appeared alongside new types of feelings of certainty. Humour, which is strongly related to surprising changes of perspective and counterfactual situations, probably began to assume social importance, increasing social bonding through a kind of affective-cognitive grooming [59], and encouraging the use of analogy and imagination [60,61]. Crucially, language reinforces social norms and the 'we'

perspective, improves group decisions and upgrades individual decision-making [62]. It also enhances the generation of communal feelings through emotional contagion during rituals, which generate emotions specifically related to the collective 'we': solidarity, moral outrage, collective pride, new types of fear and anger, and so on. Social emotions, which from the outset were constructed by cultural traditions, became more varied and context-dependent. For modern humans, E. F. Barrett and her colleagues have convincingly argued that even emotion-words such as 'afraid' or 'angry' act as 'place holders', categorizing and crystallizing the fuzzy feelings associated with particular behaviours [63–65].

5. SUMMARY AND IMPLICATIONS

Our view of language as a part of a sophisticated suite of mental adaptations highlights the intimate interactions between language and emotions. It stresses the role of cultural innovation and cultural learning in the evolution of language. It implies that the different facets of language, including the ability for recursion, evolved gradually and incrementally, within the entwined contexts of tool-making, collaborative social practices and communication. We therefore disagree with the suggestion of Hauser *et al.* [66] that a fully formed recursive ability, which had evolved in another context, was grafted onto an evolving cognitive-sensorimotor human representation and communication system, transforming it in one dramatic thrust into full-blown syntactic language.

We argued that not only were the social emotions a precondition for the evolution of instructive communication and controllable imagination, but also suggested that their co-development and co-evolution with language led to new repertoires of emotions. Our view thus agrees with and extends Tomasello's suggestion that human cooperation has some unique features [32], and suggests that one of the contributing factors making human cooperation and aggression unique is the language-based control of emotions. However, the ability to control emotions can lead not only to inhibitory effects but also to excitatory ones: language can be mobilized for generating aggression. Furthermore, because words and phrases construct and stabilize human mental emotional categories, language makes it much easier to manipulate emotions for both aggressive and cooperative ends. In humans, cooperation and aggression are therefore, at least partially, symbol-bound and symbol-controlled, and, in this respect, are qualitatively different from cooperation and aggression in other animals.

Very little attention has been given to the relationship between the evolution of language and the emotions, and the evolutionary scenario we have drawn is speculative. It is therefore important to suggest some ways of evaluating our proposals. One research avenue would be to compare fMRI patterns of activation in language-trained chimpanzees, young children at an equivalent linguistic stage, and encultured chimpanzees that have not been linguistically trained. Comparisons based on the responses of individuals in the different groups to linguistic and non-linguistic signs, could reveal which areas in the language-trained chimpanzees have been recruited for the new task of symbolic communication and whether some areas are the same as those used by children. The results may point to brain regions that have been developmentally recruited and then evolutionarily expanded and stabilized during human linguistic evolution.

A second type of experiment would investigate the role of transgenerational and epigenetic effects promoting alloparenting. If in early hominins, related females, as well as male and female young of different ages, stayed close together, then exposure to infant-caring may have induced and promoted both the inclination to care and the learning of caring behaviours. It has been shown by cross-fostering experiments between polygynous meadow voles, which do not practise alloparental care, and prairie voles, which do, that male meadow voles can become caring fathers if they are exposed as neonates to the alloparental caring-style of prairie voles. This suggests that altering the social/ familial environment could trigger a developmental change in caring style, which could be the basis of further evolution of the trait [28]. It would be interesting to see if similar effects can be observed in primates: fostering experiments, in which tamarins or marmosets (which are alloparenting New World monkeys) adopt young from non-alloparenting but closely related species, and observations of the behaviour of the fostered males when they become parents, might shed light on this possibility.

In a third study, alloparenting and non-alloparenting primates would be exposed, at different developmental periods, to the hormone oxytocin, which is involved in eliciting care and bonding [67]. Identifying probable target genes whose activity is induced by the hormones that are involved in caring would contribute to our understanding of the development of alloparenting behaviour.

The suggested experiments could provide data that might help us to evaluate some aspects of the proposal we have made regarding the interactions between language and emotions. Since human language evolution has been multidimensional, involving different levels of selection, different inheritance systems and complex interactions among different facets of cognition, a synthetic approach as that suggested in this paper can contribute to our understanding of the biology and evolution of human cognition.

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