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Review

What makes us... apes? The emotional “building blocks” of intersubjectivity in hominids

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Running head: Emotions and intersubjectivity in hominids

Highlights

1. Intersubjectivity has often been lauded as one of the defining features that separates humans and other extant hominids.
2. Intersubjectivity and empathy are different, yet related, phenomena.
3. The study of emotions and empathy-related abilities can provide insights into the ontogeny and evolution of intersubjectivity.

Intersubjectivity, which refers to the capacity to create shared value or connection between individuals, is a complex and multi-faceted phenomenon involving both cognitive and affective components. Intersubjectivity has often been lauded as one of the defining features that separates the social minds and existence of humans and non-human animals. Despite the apparently profound importance of inter-subjectivity for the socio-cognitive functioning of our species, we know surprisingly little about its evolution, nor how its evolution relates to the evolution of other related phenomena, such as empathy. In this review, we embrace the “bottom-up” perspective to consider recent theoretical and empirical advances in the fields of non-human animal cognition and emotion and what they can tell us about how complex socio-emotional capacities evolve. In particular, we focus on great ape species. Given their close phylogenetic relationship to us, great apes (the non-human, extant hominids) offer a unique lens to identify which of our capacities may be evolutionarily derived or phylogenetically shared.

KEY WORDS: intersubjectivity, empathy, emotions, mimicry, consolation, *Homo sapiens*, great apes.

WHAT MAKES US HUMAN?

In the ongoing search for the capacity that sets humans apart from other animal species, numerous behavioural and cognitive traits have been selected as potential candidates, without providing any definitive answers. While the “top-down approach” of seeking to identify a “uniquely human capacity” has motivated considerable progress in the human evolutionary sciences, it is nevertheless anthropocentric and can suffer from numerous limitations (see de Waal & Ferrari 2010) for discussion). Take for example, the Ape Language Studies, first started in the 1930s that focussed on trying to teach great apes human language (Tomasello 2017). While such studies have provided important insights into the cognitive and linguistic capacities of great apes, they have also highlighted the substantial theoretical, methodological and moreover ethical flaws imbued by trying to superimpose human forms of intelligence onto other species.

The “Cognitive Revolution”, the intellectual movement started in the 1950s in the United States, aimed at legitimating the study of the cognitive processes of the human mind; by consequence, the scientific study of “other minds” also opened up, leading to the birth of the new domains of evolutionary and comparative cognitive sciences. Moving beyond the era of behaviourism, biologists and psychologists started to look inside the “black box” of the animal mind, something previously considered scientifically inscrutable. Instead of finding a clear-cut separation between human and non-human animal cognition, these studies showed that the border between “us and them” is often nebulous, in line with the Darwinian principle of evolutionary continuity (Darwin 1872). This new body of research led to a fundamental shift in the theoretical paradigm that constitutes today the scaffolding of the scientific endeavour aimed at discovering the presence, development and evolution of animal mental capacities. Rather than taking a top-down approach, there was a wide reversal to adopt a “bottom-up” perspective (de Waal & Ferrari 2010) focussed on

understanding the evolutionary drivers, conditions and underlying mechanisms, which may result in the evolution of complex abilities in one or more species (Fitch et al. 2010). Thanks to this approach, it is possible to reconstruct the phylogenetic basis of certain cognitive traits, exactly in the same way as it is possible to reconstruct the evolutionary history of certain physical traits. In a provocative way, we could state that today behavioural biologists and comparative cognitivists are interested in finding what “makes us animals” rather than “what makes us human”.

With its strong focus on cognition, the influential era of Cognitivism has resulted in a growth in knowledge in the mental faculties of animals. By contrast, there has been a notable paucity of attention towards the emotional or affective processes driving animal behaviour, something not helped by a more general and long-held view that animal emotions are inaccessible to scientific study and even taboo (see de Waal 2011; Panksepp & Watt 2011). This reflects a more general bias in human and evolutionary sciences favouring research on cognition over emotion. Nevertheless, while cognition has dominated, there is now a growing shift across disciplines that acknowledge the role of emotion and its interaction with cognition (Dukes et al. 2021).

Neurobiological studies have indicated that emotions crucially influence higher order cognitive behaviours, such as decision making (Bechara et al. 2000; Bar-On et al. 2003; Rilling et al. 2008). Moreover, limbic structures that include ancient and basal structures participate in a wide array of emotional and motivational systems, such as anxiety regulation and fear conditioning but also episodic and spatial memory and other processes (Damasio 1998; LeDoux 2000; Heimer & Van Hoesen 2006; Fanselow & Dong 2010). Hence, emotions have become more relevant to the investigation of the evolution of human and non-human cognitive abilities.

Indeed, there is momentum towards the view that, with the advent of new technologies, animal emotions can be systematically studied and compared by examining their measurable behavioural or physiological components (Davila Ross et al. 2008; Massen et al. 2019; Kret et al. 2020). The increasing recognition of the role that emotion plays in shaping and understanding human and

animal cognition and psychology has even led some scholars to argue that we are now entering a new scholarly period of ‘affectivism’ (Dukes et al. 2021).

In this review, we embrace these new avenues of research to consider recent theoretical and empirical advances in the fields of animal cognition and emotion and what they can tell us about how complex socio-emotional capacities evolve. In particular, we focus on the evolutionary basis of intersubjectivity, which refers to the capacity to create shared value or connection between individuals (Rochat et al. 2009). Intersubjectivity, a complex and multi-faceted phenomenon involving both cognitive and affective components, has often been lauded as one of the defining features that separates the social minds and existence of humans and non-human animals. Despite the apparently profound importance of inter-subjectivity for the socio-cognitive functioning of our species, we know surprisingly little about its evolution, nor how its evolution relates to the evolution of other related phenomena, such as empathy. In order to assist us with understanding this, we focus on insights gained from our closest living relatives, the great apes. Given their close phylogenetic relationship to us, great apes (the non-human, extant hominids) offer a unique lens to identify which of our capacities may be evolutionarily derived or phylogenetically shared.

Through considering evidence for the affective skills underpinning intersubjectivity and relatedly, empathy, in humans and our closest relatives, this chapter seeks to provide new insights and avenues of investigation into the evolutionary basis of our deepest forms of social connection.

WHAT IS INTERSUBJECTIVITY?

In its broad sense, the term intersubjectivity refers to a suite of capacities involving “the sharing of affective, perceptual and reflective experiences between two or more subjects” (Zlatev 2008). Rochat et al. (2009) argue that inter-subjectivity refers to the notion of ‘shared values’; or the way that one individual understands or relates to another. In this respect, intersubjectivity is how two

individual “exist and interact” in an emotional and cognitive “we-centric” space” (Zlatev 2008). This definition encompasses several nested layers of cognitive complexity, spanning mutual sensory engagement and mutual intention reading that are likely to have emerged across multiple evolutionary and developmental timepoints. The basic layers are usually united under the label of “primary intersubjectivity”, which can be defined as the capacity of adjusting one’s own sensory orientation toward the orientation of another subject (Trevarthen & Aitken 2001). In humans, it is argued that this kind of social orientation and attunement is already evident from birth (Trevarthen 1998), through the earlier onset of processes such as imitation and mirroring which enable a ‘basic sense of social connectedness and mutual acknowledgement with others’ (Rochat et al. 2009).

While primary intersubjectivity is considered to be a dyadic phenomenon, “secondary intersubjectivity” is characterised by joint attention towards an entity that is external to the two interacting subjects, thus making it a cognitive, referential triadic phenomenon (Tomasello et al. 2005). In human infants, secondary intersubjectivity is externally evident around the age of nine months (Trevarthen & Hubley 1978), although its developmental trajectory is thought to begin much earlier (Deák et al. 2013). By 9 months, human infants start actively engaging in joint attention: they share attention with others about external referents including objects and events, they recognize their names, understand other’s needs, goals and desires and engage in increasingly sophisticated linguistic and communicative interactions, just to cite some examples (Rochat & Striano 1999). The ability of infants to share attention with someone else in reference to a third entity requires them to be sensitive to the other’s “sensory perspective” and to be able to experience a sense of “togetherness” (Tomasello et al., 1993). Rochat et al. (2009) theorise that humans also show a third form of intersubjectivity, that starts developing around the age of 20 months, and that deals with emergence of values, meanings and norms that are jointly represented, negotiated and constructed with others.

Various psychologists have considered that, even in its primary form, intersubjectivity is uniquely human (e.g. Tomasello et al. 2005). This view comes in part from suggestions that non-human

primates do not seem to be able to hold eye-to-eye contact, although they pay attention to conspecifics' faces (Moll et al. 2021). However, there is growing evidence that numerous primates, including chimpanzees, possess some skills that may underpin forms of social referencing and joint attention (Russell et al. 1997; Bard et al. in press). This includes following the gaze of others towards a particular location as well as various forms of attention-getting by human carers in order to gain out of reach objects (Hopkins et al. 2007; Leavens & Bard 2011; Carpenter & Call 2013). However, whether or not great apes are able and willing to harness these socio-cognitive skills to engage in more sophisticated forms of inter-subjective connectedness, including joint attention, remains unexplored.

Another crucial but unresolved issue in our understanding of intersubjectivity in other animals is the impact of the socio-ecological and cultural rearing environment (Leavens et al. 2019; Bard et al. in press). Thus far, research on joint attention and other forms of intersubjectivity in non-human primates has been primarily conducted on captive individuals, including those reared in human-centric environments, known as enculturated. Evidence suggests that, unless rearing and social conditions are effectively accounted for, such artificial rearing environments may constrain the evolutionary validity of corresponding conclusions, particularly where those conclusions are based upon direct comparisons with humans. There is evidence for instance that enculturated chimpanzees, i.e. those raised in a human socio-cultural environment, are more likely to engage in joint attention events with human experimenters, than chimpanzees reared by their own mothers (Carpenter & Tomasello 1995). In addition, while captive chimpanzees engage in referential pointing (Leavens & Bard 2011), a form of intersubjective engagement, evidence in the wild still remains equivocal. These findings suggest that the socio-ecological and cultural environment play a crucial role in shaping the onset of intersubjectivity in other primates as well as humans (Leavens & Bard 2011).

Relatedly, current understanding of the evolutionary basis of intersubjectivity is also limited by strong biases towards visual forms of connection (Bard 2017; Botero 2016). Specifically, limiting the notion of primary intersubjectivity to the mutual exchange of visual contacts could lead scholars to miss detecting other types of interactions requiring intersubjective skills. According to this view, mutual attunement among great apes may primarily occur through physical, rather than through visual contact (Bard 2017; Botero 2016).

It is worth noting that a similar form of reciprocal engagement is observed in certain human cultures, where social interactions are mostly based on body contact and touch (Keller 2007).

Hence, the possibility to theorise and examine the existence of intersubjectivity in non-human primates is linked to the very definition we give to this phenomenon. If we apply an anthropocentric, “top-down approach” by adopting a restrictive definition of intersubjectivity that has been set by using humans as the reference point, we should not be surprised that only humans appear to have human-like intersubjective abilities. On the other hand, if we apply a “bottom-up approach” with a broader definition of intersubjectivity, to include other types of interactional features, we could discover that some traits are shared (at least) with our closest living relatives. We advocate to adopt this second approach as we believe that the comparative study of intersubjectivity and its constituents is of major interest for reconstructing the development and evolution of socio-emotional and cognitive skills in non-human and human primates.

INTERSUBJECTIVITY AND EMPATHY

Intersubjectivity and empathy are distinct yet highly related phenomena (Rochat et al. 2009). Broadly speaking, empathy refers to the capacity to share and understand others’ emotions and thoughts thus is specifically other-oriented (Preston & de Waal 2002) (Figure 1). According to the ‘Russian Doll’ model, proposed by Preston and de Waal (2002), empathy can be viewed both phylogenetically and ontogenetically as a set of concentric spheres, each representing specific

empathy-related skills. The inner core of empathy consists in more basic and evolutionarily ancient processes that are unified under the label of “affective empathy”, whose evolutionary roots can be traced back at least to the origin of mammalian maternal care (Decety 2011). Evidence of empathic capacities in some birds has however challenged that empathy is a mammalian phenomenon, and may instead reflect broader mechanisms that have evolved in species where dependence on social, pair and parental bonds is particularly strong and enduring (Horn et al. 2016).

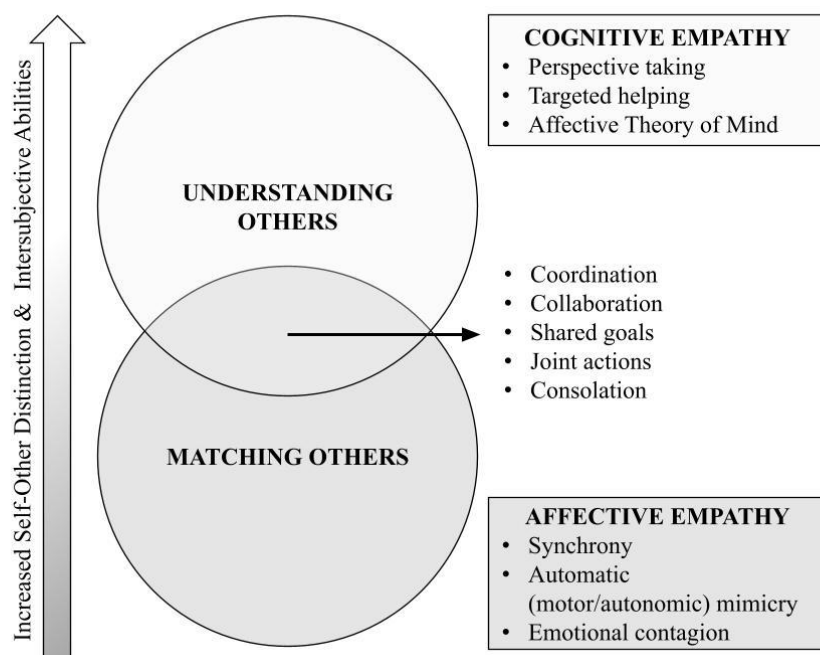


Figure 1

A proposed mechanism of affective empathy is emotional contagion, which consists in automatic contagion of (apparently similar) emotional states from one individual to another (de Waal, 2008). Emotional contagion may be based on the Perception-Action Mechanism (PAM) (Preston & de Waal 2002) and on the Mirror Neuron System (MNS). Both models foresee that a motor resonance is translated into emotional resonance when the observed motor sequence bears information on the affective state of the subject enacting such sequence (de Waal & Preston 2017; Rizzolatti & Caruana 2017). However, the PAM takes into account the individual experience (Preston & de

Waal 2017) and the MNS focuses more on the target of an emotionally-charged motor pattern (Rizzolatti & Caruana 2017). The motor-emotional resonance especially applies to facial expressions, clear manifestations of basic emotions to the external world. Both PAM and MNS models help explain how an emotion - or at least the same emotion - can spread across subjects. The resulting process can be briefly summarised as follows: (i) the subject A experiences a state of sadness; (ii) the subject A shows the facial expression linked to sadness (in humans: inner corners of eyebrows raised, eyelids loose, lip corners pulled down); (iii) the subject B perceives A's sad facial expression (perception); (iv) the subject B replicates A's sad facial expression (action); (v) the subject B experiences a state of sadness. Emotional contagion can occur not only via motor mimicry but also via autonomic mimicry, when a physiological state can be perceived and replicated by others (e.g. sweating, pupil dilation; Prochazkova and Kret, 2017).

Moving towards the more external spheres of the Russian-Doll model, we shift from feeling to understanding others' emotions (cognitive empathy) which requires high orders of self-other differentiation, including perspective-taking and mental state attribution (affective Theory of Mind) (Sebastian et al. 2012).

Alternative to the Russian Doll model, Yamamoto (2017) has proposed a non-linear, combination model of empathy, composed of three organising factors: matching with others, understanding of others, and prosociality. These three components are intertwined but also independent to one another, and different combinations of such components can lead to different empathy related phenomena (e.g. targeted helping and consolation). Decety et al. (2016) have provided yet another model of empathy that is particularly interesting for the study of empathy in non-humans and its link to intersubjectivity. According to this model, empathy is an induction process reflecting the innate ability to perceive and be sensitive to the emotional states of others. It would only require the basic capacity to discriminate between self-generated versus externally-generated stimulation. In this perspective, feeling and understanding others' emotions result from a biological capacity for empathy, rather than the other way around.

Crucially, all the previous models converge in indicating that although it may involve them, empathy is not contingent on complex cognitive abilities. Hence such models allow the inclusion of non-humans in the study of empathy. Indeed, affective and cognitive components of empathy can be dissociated (Decety 2011), thus meaning that these phenomena can be investigated separately. Self-other distinction in the emotional sphere and the capacity of establishing a sense of togetherness – in one word intersubjectivity – are essential for unconsciously sharing and consciously understanding others' emotions and therefore expressing empathy. In the next sections, we will present some evidence supporting the view that it is possible to investigate primary and secondary intersubjective abilities by studying empathy-related phenomena in extant hominids, which include modern humans and great apes.

THE PRIMARY “WE”: EXCHANGING EMOTIONS

Although most studies on intersubjectivity focus on cognitive mechanisms, early forms of dyadic “we-centric” cooperative interactions are likely to rely heavily on emotional engagement as well as emotion regulation (Bard et al. 2014a). In both humans and chimpanzees (*Pan troglodytes*), dyadic social attunement starts developing in the first three months of life along with the establishment of mother-infant bond (e.g., van Lawick-Goodall 1968; Bard 1994; Adamson 1996). Until now, mother-infant attunement has not been investigated so far in other hominids although there is evidence of facial mimicry, a form of social attunement, in macaque monkeys suggesting an evolutionary ancient basis.

Regarding secondary intersubjectivity, despite the apparent importance of joint attention for human cognition and interconnectedness, there has been surprisingly little research about joint attention in other primates. In chimpanzees and bonobos, the few studies conducted have reached different conclusions and have shown the importance of the early rearing environment in shaping “human-like” joint attentional skills (Bard 1994; Carpenter & Tomasello 1995; Boesch 2005; Warnecken et

al. 2006; Pika & Zuberbühler 2008; Heesen et al. 2020). Further investigation is necessary to verify the differences across humans, chimpanzees and other hominids.

An untapped but potentially promising context to explore evidence for intersubjectivity in primates is through the study of play. Play is a widespread behaviour across mammals, and it is particularly common in primates, and its universality makes it a robust comparative tool. The finding that social play – and not solitary play – is significantly and positively related to the neocortex ratio in primates strongly supports the hypothesis that play is important for the development of social cognition (Lewis 2001). Social play is a suitable context to check for inter-individual dyadic attunement and commitment as during a play session individuals communicate to achieve shared goals (Heesen et al. 2021) which are to prolong the duration of the playful interaction and to avoid the risk of escalation into aggression (Bekoff 1984; Waller & Dunbar 2005; Cordoni & Palagi 2011; Cordoni et al. in press).

Rapid Facial Mimicry (RFM; Palagi et al. 2020a) represents a phenomenon through which individuals may implicitly share the same emotional state as indicated in the replication of the facial expression of another subject within 1sec (500 msec in humans; Hess & Fischer 2013). In both humans and great apes, RFM is present during play. In chimpanzees and juvenile lowland gorillas, RFM can prolong the play session and is more frequent between strongly bonded subjects (Palagi et al. 2020a). Emotional attunement via RFM is also seen outside the play context. For example, in bonobos RFM increases the duration of socio-sexual contacts between females (Palagi et al. 2020b) whereas between human mothers and infants facial mimicry (also referred to as neonatal imitation) is considered a spontaneous positive feedback mechanism that is pivotal in enhancing the emotional connection between the mother and her baby (Murray et al. 2016). Myowa-Yamakoshi et al. (2004) studied neonatal imitation in two infant chimpanzees (*Pan troglodytes*) that had been reared from birth by their biological mothers. They obtained results similar to those obtained with human babies (Meltzoff & Moore 1977). Both infant chimpanzees imitated human facial gestures such as tongue protrusion and mouth opening within the first weeks of life. These behaviours demonstrate human

and chimpanzee newborns' ability and motivation to engage with others. Moreover, chimpanzees' ability to replicate human facial actions disappeared after 2 months, similarly to what has been reported for human infants.

Yawn contagion represents another promising behavioural phenomenon to study the evolutionary basis of intersubjectivity. Yawn contagion is considered a form of behavioural (and possibly emotional) matching possibly based on the PAM (de Waal & Preston 2017). Yawn contagion occurs when a subject yawns in response to the yawn emitted by another subject (releasing stimulus, sensu Tinbergen & Perdeck 1950). Yawn contagion in primates has been linked to inter-individual synchronization and, possibly, emotional contagion (de Waal & Preston 2017; Prochazkova & Kret 2017; but see Massen & Gallup 2017). Yawn contagion has been found in all the hominin species: chimpanzees (Anderson et al. 2004; Campbell & de Waal 2011; Campbell & Cox 2019), bonobos (Demuru & Palagi 2012; Tan et al. 2017; Norscia et al. 2022; but see: Amici et al. 2014) and humans (*Homo sapiens*; Provine & Hamernik 1986). As it occurs for RFM, yawn contagion may follow an empathic gradient though this has been contested (Massen & Gallup 2017). Indeed, this phenomenon reaches the highest frequencies between closely related or familiar subjects, in certain cohorts of humans (Norscia & Palagi 2011; Norscia et al. 2016, 2021), chimpanzees (Campbell & de Waal 2011), and possibly bonobos (Demuru & Palagi 2012; but see Amici et al. 2014; Tan et al. 2017; Norscia et al. 2022). Two studies failed to find yawn contagion in lowland gorillas (*Gorilla gorilla*; Amici et al. 2014; Palagi et al. 2019). However, yawn contagion was found in orangutans (*Pongo spp.*; van Berlo et al. 2020), a great ape species which separated earlier than gorillas from the human line (Groves 2018). Lowland gorillas live in one-male groups and show low affiliation levels between adults (Palagi et al. 2019), whereas orangutans do not form social groups but they may have been more social in the past when food resources were more abundant (Harrison & Chivers 2007). No social bias was found in the distribution of yawn contagion across dyads in orangutans – which show dispersed sociality – and in different groups of bonobos (Amici et al. 2014; Tan et al. 2017; Norscia et al. 2022) which live in tolerant and

xenophilic social groups (Furuichi 2011). In orangutans, the effect of social bond may have a reduced adaptive significance because individuals do not form social bonds or alliances. In bonobos, the effect of social bond may have acquired a low adaptive significance for the opposite reason, that is because they can show affiliative behaviours even towards unfamiliar conspecifics (Tan & Hare 2013). The opposite cases of bonobos and orangutans converge in indicating that the familiarity bias may be related to inter-individual cohesion and type of sociality, which suggests that yawning may have been co-opted during evolution as a signal leading to emotional sharing under certain social conditions.

FROM TWO TO THREE: TRAJECTORIES TOWARDS SECONDARY INTERSUBJECTIVITY

Human infants are seen to progress through several stages of attentional engagement towards full capacity for inter-subjectivity (Rochat et al. 2009). This starts at the dyadic stage, i.e., interaction with and responsiveness to another individual; moving to triadic, i.e., shared goals and perceptions with other individuals regarding outside entities; and finally to collaborative, i.e., shared goals and intentions including coordinated action plans, with complementary and potentially reversible roles (Tomasello et al. 2005). As stated above, secondary intersubjectivity includes a third entity that two subjects pay attention to and/or get engaged on, it adds the ‘aboutness’ to social connection and social value. In humans, this kind of engagement is said to be expressed from around the age of 9 months (Adamson 1996) and in chimpanzees up to 12 months of life even though it is debated whether intersubjectivity can be found beyond humans (Bard et al. 2014a, 2014b).

Above, we have discussed how the study of play and yawn contagion can represent promising avenues for studying the basis of dyadic and even triadic engagement in great apes. Another type of interaction that is worth investigating for understanding secondary intersubjectivity could be found in the social dynamics following an aggressive encounter. Specifically, we refer here to unsolicited triadic contacts that occur when an uninvolved third party spontaneously offers an affiliative

behaviour to either the aggressor or the victim (de Waal & Aureli 1996). Unsolicited triadic contacts require that the conflict between two individuals is processed by a third, uninvolved subject and that the third party takes agency in resolving the conflict. Agency plays an essential role for understanding how individuals can interpret their physical environment and social world, also in the light of intersubjective abilities. Indeed, recent neuroscientific studies showed that primates taking part in social interactions activate different cortical areas than individuals that just observe social interactions (Freiwald 2020). This differentiated and distributed primate brain circuitry supports social interaction analysis and - via such circuitry - observed pairwise interactions can generate social dynamics involving other group members (Freiwald 2020), for example expanding the intersubjective space to third parties.

When the spontaneous triadic contact by a third-party works at reducing the emotional arousal in the contacted individual, additional cognitive mechanisms may be involved (de Waal & Preston 2017) because an individual should be able to process the affective response of a group mate toward a third entity (Walle et al. 2017a, 2017b), that is the conflict. A triadic contact towards the victim of an aggression can be called “consolation” when it is spontaneously offered by the bystander, where the primary function seems to be to reduce the victim’s anxiety (e.g., scratching), and when the third party shares a strong social bond with the victim (Clay & de Waal 2013a, 2013b). All these elements show that also in this context the familiarity bias plays an important role in triggering this intersubjective, empathy-driven social contact. We suggest that the investigation of post-conflict management be revived, with a focus not just on functions but also on the cognitive mechanisms underlying the dynamics that can be observed after an aggression.

CONCLUSIONS

In conclusion, various studies have accumulated to support the existence of elements of primary, and possibly secondary, intersubjective skills in great apes and potentially other primates. Although there is little comparative research that has explicitly focussed on inter-subjectivity, examples on

joint attention, facial mimicry, neonatal imitation, play and post-conflict third party affiliation all provide relevant contexts in which forms of primary and potentially secondary intersubjectivity can be examined. These examples do not exhaust the topic, but highlight that a bottom-up approach to the study of intersubjectivity can lead to the identification of “building blocks” of emotional interconnection in non-humans. Such building blocks can add up to more complex forms of affective intersubjectivity in hominids and help shed light on the emergence of cognitively complex empathic behaviours in humans. This would provide an in-depth understanding on how intersubjective emotional communication is deeply rooted in our nature of apes and has helped us relate to the physical and social world, since when we left our relatives in the forest several million years ago.

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