Emotions through the eyes of our closest living relatives: exploring attentional and behavioral mechanisms

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Chapter 8

General discussion

Detecting and correctly recognizing emotional expressions is pivotal to social life, as these expressions guide our thoughts and behaviors, and enable us to understand others' feelings and intentions. They are at the basis for complex phenomena such as empathy (De Waal & Preston, 2017; Koski & Sterck, 2010) and cooperation (Boone & Buck, 2003), which have long been considered to be uniquely human. However, when and why did our high sensitivity to emotions evolve, and are the processes that govern emotion perception truly unique to our species? Do emotions mean anything to other animals? One way to go about answering these questions is to reconstruct the lives of our ancestors, but this is difficult. The fossil record of early humans is sparse (Andrews, 2020) and fossilization of brain tissue is extremely rare. Nevertheless, our closest living relatives, the great apes, offer us an invaluable window into the past, allowing us to indirectly infer the social and cognitive characteristics of extinct humans and other apes (e.g., Wilson, 2021).

Studying great apes can not only inform us about our evolutionary past but can also provide a stepping stone towards understanding the evolutionary pressures that shaped the expression and processing of emotions throughout the animal kingdom. Here, it is important to remember that the social and cognitive abilities of hominids are just *examples* that are part of a diverse collection of exceptional skills that organisms can develop to deal with the social and physical demands of their specific environments (i.e., "There is not 'one cognition'", Bräuer et al. (2020)). That said, directly comparing different species is challenging. Preferably, we would measure emotion perception using the same method for all species involved, without neglecting species-specific characteristics that may impact the expression of emotion perception (for instance, if one species expresses emotions mainly through facial expressions and another species expresses them mainly through vocal signals, using the same testing method may not be optimal). Based on the literature on cognition and behavior in great apes, it is reasonable to assume that there is at least some continuity between how humans and great apes express and perceive emotions (Kret et al., 2020; Nieuwburg et al., 2021). Following this assumption, the studies reported in this dissertation focused on several unconscious and automatic mechanisms underlying emotion perception that can be studied similarly across humans and great apes: *attention*, *spontaneous mimicry*, and *implicit associations*.

The goal of this dissertation was to take a closer look at the differences and similarities in emotion perception in humans, bonobos, and orangutans. Specifically, we examined emotional modulation of *attention* (Figure 1i) and *spontaneous mimicry* (Figure 1ii), and developed a method that could potentially probe *implicit* *associations* in primates and other animals (Figure 1iii). In this final chapter, I will focus on integrating the key findings from each chapter and discuss the implications of the results. At the end of the dissertation, I will point towards new and unanswered questions that can help us move forward in understanding the continuity between human and animal emotions.

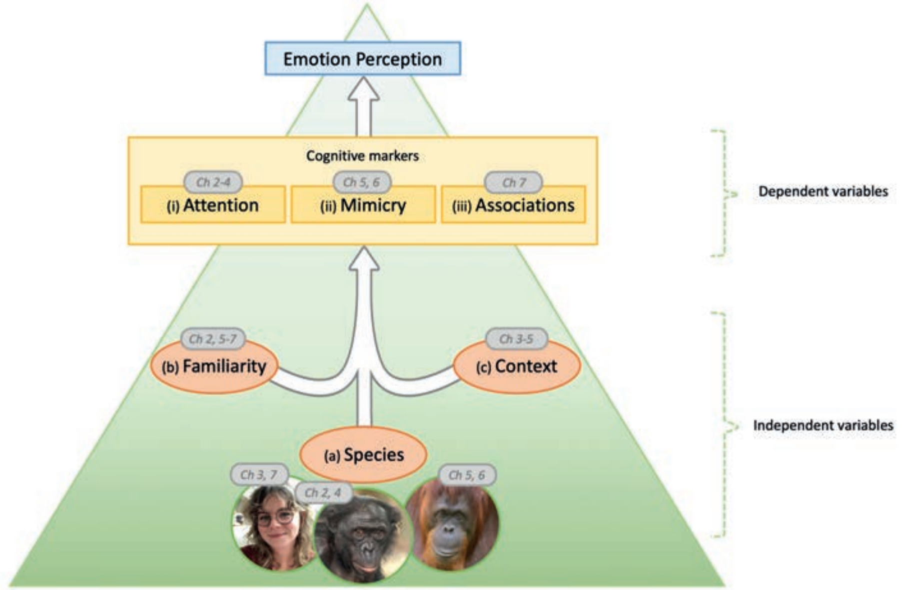

Figure 1. Schematic overview of the research topic. Emotion perception is a multifaceted phenomenon that is governed by many different cognitive mechanisms. Often, these mechanisms operate on an implicit level; automatically and unconsciously. To study emotion perception across species, I investigated its underlying implicit mechanisms or *cognitive markers*. The focus of this dissertation lies on *(i) attention, (ii) mimicry,* and *(iii) implicit associations*. Moreover, I investigated the effects of *species (a), familiarity (b),* and *context (c)* on these markers across six chapters (grey circles) in this dissertation.

Summary of key findings

In **Chapter 2**, I compared an attentional bias for emotions (Figure 1i) between bonobos and humans and examined whether this bias is affected *by familiarity with* or *the species of* the expressor (Figure 1a, b) across a series of three experiments using the dot-probe task. In Experiment 1, bonobos were presented with emotional and neutral scenes of familiar and unfamiliar conspecifics, and we found that the attention of bonobos was automatically tuned to emotions of unfamiliar conspecifics. In Experiment 2, we examined whether this emotion-biased attention in bonobos also occurred when bonobos were exposed to human facial expressions of emotions, again of familiar individuals (caretakers) or unfamiliar individuals. Bonobos did not show an attentional bias towards human expressions of emotions, even though in a control experiment using the same stimuli, humans did show this bias. Nevertheless, low power may explain the null findings in bonobos. In Experiment 3 using a heterogeneous human sample, we found that in contrast to bonobos, humans showed an attentional bias towards emotions of familiar, socially-close conspecifics. The findings of this study underline that an attentional bias for emotions is driven by factors that hold motivational relevance to the observer (i.e., socially-relevant characteristics such as the species of the expressor and social closeness) (Brosch et al., 2013). Importantly, it indicates continuity between the attentional mechanism (i.e., selective attention) underlying emotion processing in humans and bonobos, but also that attention to emotions may be most sensitive when the expressors of these emotions are conspecifics.

As we did not study whether humans have an attentional bias for emotions of bonobos, we attempted to close this knowledge gap in the study described in **Chapter 3** (Figure 1i). Moreover, most research into emotion-biased attention in humans has used isolated facial expressions of emotion, thereby not fully appreciating the role that whole-body emotional expressions play in recognizing emotional expressions, as these whole-body expressions embedded in a scene can provide more context (Figure 1a, c) (Kret et al., 2013a). Additionally, many studies have looked only at specific age classes or homogeneous populations such as university students, which are not good examples for generalizing about humans (Henrich et al., 2010). We partially tackled these issues by examining how a more heterogeneous (i.e., non-university) group of human adults and children rate emotional *scenes* of humans as well as bonobos on valence and arousal, and by measuring their attentional bias towards these scenes. Overall, humans perceived emotional scenes of other humans to be similar to scenes of bonobos in terms of valence (positivity or negativity) and arousal (intensity). However, children misinterpreted the bared-teeth display as a positive expression.Humans also showed an attentional bias towards emotional scenes of both species, but the bias was strongest for human emotional scenes. These findings could suggest a shared evolutionary origin for emotional expressions and their perception (Kret et al., 2020), but also show that in humans, a learning component may be important for understanding emotional expressions by other species such as bonobos.

As a next step, we examined whether an attentional bias towards emotions in bonobos and humans does not only occur initially when early attentional mechanisms (e.g., covert attention) are recruited but also when emotional scenes are presented for a longer duration (**Chapter 4**). Bonobos and humans were presented with emotional and neutral scenes of conspecifics and heterospecifics (Figure 1i, a, c). Each emotional and neutral stimulus combination was shown for three seconds, thereby recruiting not only initial, more reflexive attentional mechanisms, but also more voluntarily controlled attention. We found that humans overall showed a more pronounced emotion bias than bonobos, i.e., humans looked longer to emotional scenes of different categories (play, grooming and embracing, sex, distress, and yawning), whereas bonobos only looked longer to scenes of distressed bonobos or bonobos having sex. For both species, distress was the most salient emotional category, holding attention the longest. Moreover, we extended our previous findings (Chapter 2) indicating a lack of attentional bias to human emotional expressions in bonobos. Conversely, humans looked longer at grooming and playing bonobos: two categories also rated most positively in the study of Chapter 3. In general, humans and bonobos appeared to be most sensitive to the emotions of individuals of their own species. Additionally, humans appeared sensitive to the emotions of bonobos, but bonobos not to the emotions of humans.

In **Chapter 5**, I moved away from attention and focused on another unconscious process at stake during social interactions: spontaneous mimicry (Figure 1ii). Specifically, we investigated contagious yawning and self-scratching in relation to social closeness and context in orangutans: our most distantly related relatives within the great ape family (Figure 1a-c). Nine orangutans were observed for a period of four months, and all occurrences of yawning and self-scratching and the context within which they occurred were recorded. There was only sufficient data on self-scratching, as yawn occurrences are generally rarer. The results showed that in orangutans, self-scratching was indeed contagious, and most strongly so during situations where there was tension, and between individuals with a relatively weak social bond. The novelty of the findings is that this study presents a potential case of *negative* emotion contagion, rather than the more typically presented positive emotion contagion.

In **Chapter 6**, I reported on an experiment on contagious yawning in orangutans (Figure 1ii). Orangutans were presented with videos of real, unfamiliar orangutans, familiar orangutans (conspecifics that were also housed in Apenheul), and a 3D avatar orangutan (Figure 1a, b). The orangutans in the videos either yawned or showed a neutral expression, allowing us to investigate whether yawns occur more frequently in response to other yawns compared to neutral videos. For the first time, orangutans were shown to yawn contagiously, but only in response to yawn videos of *real* orangutans. The avatar did not elicit more yawns, and there was no difference between yawns in response to familiar or unfamiliar orangutans. These results are interesting for several reasons: i) orangutans show contagious yawning despite their more semi-solitary nature (previously, contagious yawning was only found in highly social species (e.g., Norscia et al., 2020)), ii) the yawning avatar did not elicit more yawns, even though a previous study found a contagious yawning effect in response to a virtual representation of a chimpanzee (Campbell et al., 2009), and iii) familiarity did not modulate the occurrence of yawn contagion, even though this is expected if contagious yawning serves some social function or is linked to emotion contagion (Palagi et al., 2020). Overall, the findings of Chapters 5 and 6 indicated that orangutans, despite being classified as the least-social great ape, are susceptible to yawn and self-scratch contagion.

Finally, in **Chapter 7**, I elaborate on a fully pictorial version of the *Implicit Association Test* (PIAT) that we created to eventually test implicit attitudes in great apes (Figure 1iii). The PIAT was designed to be intuitive and require minimal instructions (as the apes cannot be instructed). In this study, we validated the PIAT in children and adults and compared how it performed in relation to the classic IAT using words in an online study with mainly university students. Participants were tested on their implicit attitudes towards individuals of Dutch or Moroccan descent (Figure 1a, b). We chose these specific categories because a race bias is one of the most established IAT effects, thus testing for it was useful for examining the validity of the PIAT. We established that a pictorial version of the IAT can tap into the same implicit attitudes as the original word-IAT in human adults and children. Though we have not yet had the opportunity to test its utility in great apes, I hope that others may find the PIAT useful for inter-species or inter-cultural research.

Theoretical implications

The results in this dissertation converge to two main conclusions. Firstly, the mechanisms underlying attention for emotions as well as automatic, spontaneous mimicry are likely to be conserved ancestral traits among the hominids. Secondly, species-specific characteristics such as their evolutionary and social environment dramatically shape how these mechanisms are expressed.

Survival and reproduction of a species are driven by adaptive mechanisms that underlie individuals' behavior and cognition (Cosmides & Tooby, 1992). Attention for emotions as well as spontaneous mimicry of behaviors may be two adaptations that are preserved in the hominid lineage. What can the results on emotion-biased attention and mimicry tell us about the most recent common ancestor of humans, bonobos, and chimpanzees? Likely, this ape-like creature was sensitive to the emotions of others, having brain mechanisms in place that guided their attention towards emotional expressions, and that elicited automatic mimicry of facial and bodily expressions. Nevertheless, findings on an attentional bias towards emotions are mixed for chimpanzees, complicating this conclusion. For instance, some studies find no evidence for an immediate bias towards emotions in chimpanzees (Kret et al., 2018; Wilson & Tomonaga, 2018), whereas another study reports that chimpanzees preferentially look at agonistic scenes (Kano & Tomonaga, 2010a). Evidence from behavioral observations, however, corroborate the idea that chimpanzees and bonobos are both sensitive to the needs of others. For instance, both species are known to console each other after stressful situations (e.g., de Waal & van Roosmalen, 1979; Goldsborough et al., 2019; Palagi & Norscia, 2013). In addition, there is evidence for contagious yawning in bonobos and chimpanzees (e.g., Campbell & de Waal, 2014; Demuru & Palagi, 2012), as well as for facial mimicry (Palagi et al., 2019b, 2020a), again suggesting that the basic mechanisms for emotion perception (De Waal & Preston, 2017) were already present in the last common ancestor of bonobos, chimpanzees, and humans.

If we look further down the phylogenetic tree to the common ancestor of humans and orangutans (Figure 2 in the introduction), we still see some evidence for sensitivity to the emotions of others. Recently, we tested orangutans' attentional bias towards emotional scenes versus neutral scenes, and our preliminary findings indicated a lack of an attentional bias towards emotions in these great apes. The only other study to date that has looked at emotion-biased attention in orangutans found that they preferentially look at the silent bared-teeth face compared to the bulging-lip face (shown during aggressive encounters), but a direct comparison between the silent bared-teeth face and a neutral face was not significant (Pritsch et al., 2017). Clearly, more research is needed to understand how and to what extent orangutans perceive the emotional expressions of others. Importantly, we find evidence for yawn and self-scratch contagion in orangutans, and one other study has found mimicry of the play face in this species as well (Davila-Ross et al., 2008). Albeit limited, there is also evidence for facial mimicry in gorillas (Palagi et al., 2019b). Whether yawn or self-scratch contagion reflect true emotion contagion is still highly debated (see e.g., Gallup, 2021; Massen & Gallup, 2017; Palagi, Celeghin, et al., 2020), but given their presence in orangutans as well as evidence for facial mimicry in gorillas, it is likely that the last common ancestor of all great apes expressed similar behaviors in response to conspecifics.

Other important findings in this dissertation relate to the influence of social and contextual factors on emotion perception. Specifically, there are crucial differences in how these factors affect human and bonobo attention for emotions, how they modulate mimicry in orangutans. Attention for emotions in humans and bonobos is affected by *familiarity*, or more specifically, by whether the emotional expressions come from group mates or unfamiliar others (Chapter 2). As for orangutans, *familiarity* with individuals does not appear to impact the occurrence of contagious yawning (Chapter 5), but social closeness (or distance) does impact the occurrence of self-scratch contagion in stressful situations (Chapter 6). These findings highlight once again that context and social factors have an interactive effect on attention and mimicry. For instance, different evolutionary environments may have contributed to shaping the sensitivity to emotions of others, such that humans are more tuned to the ingroup, and bonobos more to the outgroup (Hrdy & Burkart, 2020).

Bonobos are remarkable in their xenophilic tendencies, which likely arose due to bonobos' relatively stable feeding environment (Hare et al., 2012). With less competition over valuable resources such as food, there was also less need to fight over these resources, which over time led to selection against aggressive tendencies. Crucially, this allows bonobos to have relatively peaceful interactions with strangers and even share food with them (Tan et al., 2017; Tan & Hare, 2013). In contrast, humans (and chimpanzees) had to adapt to more arduous environments and faced more severe competition over food and resources. Aggressive tendencies would therefore be beneficial for both species to protect the group (Bowles, 2009; Hare et al., 2012). Following this line of thought, as orangutans tend to affiliate with others less often compared to for instance bonobos, their perception of emotional expressions may also be less affected by socially close others, or only be affected by seeing unfamiliar or socially distant others. While this remains an open question for future research, I can at least say that our findings support the idea that self-scratch contagion in orangutans is affected by social distance, or specifically, having a weak social bond with the observed self-scratching individual(s).

In addition to an evolutionary account, contextual factors likely exert a great influence on emotion perception. For instance, recent findings show that bonobos and chimpanzees preferentially attend to high-ranking familiar individuals compared to unfamiliar individuals (for bonobos, these high-ranking familiar individuals were females, and for chimpanzees, males) (Lewis et al., 2021). Importantly, the researchers report differences not only between the species but also between the different populations that were tested. One population of chimpanzees lived with only one resident male whereas the other population had multiple males and females. The females from the first population showed a bias towards outgroup males rather than the familiar male, likely due to the difference in social environments. In the studies on emotion-biased attention in bonobos and humans, we aimed to provide more context to the emotional expressions on our stimuli by including whole-body expressions and by embedding expressions into *scenes*. Nevertheless, we did not yet look at how contextual factors that the participants find themselves in may affect their attentional bias. Future work should aim to consider these contextual factors more closely, and steps into this direction have already been made. See for instance work by Bethell et al. (2012) on how emotional states affect social attention in macaques. Moreover, we did consider contextual factors in our studies on mimicry with orangutans, and indeed see that for instance stress can affect the occurrence of self-scratch contagion in this species. As a comparison, a next step could be to look into how stress or tension affects the occurrence of self-scratch contagion (or other forms of mimicry) in bonobos and humans.

Finally, in addition to *familiarity* and *context* as moderators of emotion perception, I wish to highlight one more example, namely *similarity*. Specifically, similarity in facial or bodily expressions of emotions. The form and potentially also meaning of emotional expressions are, to some degree, shared between primates (e.g., Darwin, 1872; Preuschoft & van Hooff, 1995). Thus, due to a common heritage, it is conceivable that humans and great apes show an attentional bias towards some of the other species' emotional expressions, or that mimicry can occur between different species. For humans, we indeed found an attentional bias towards bonobo expressions in Chapters 3 and 4, but for bonobos, we could not confirm an attentional bias towards human expressions (Chapter 2 and 4). Given the evidence at hand, only humans may be sensitive to the feelings and needs of other species, with one explanation being that humans often ascribe human-like characteristics to other animals (Williams et al., 2020). However, it is more likely that our studies did not have enough power to detect an effect, given our small bonobo sample size. The evolutionary continuity between expressions of emotions in hominids remains an active topic of research (e.g., Waller et al., 2020), and future work could tackle the current knowledge gap by for instance measuring whether different species have similar implicit associations with emotional expressions of conspecifics and heterospecifics (e.g., humans or other closely related species), for which the PIAT (Chapter 7) could be an option. I discuss this in more detail in the final paragraphs of the next part.

Methodological considerations and future directions

Studying the emotional modulation of attention and spontaneous mimicry in bonobos, orangutans, and humans has revealed intriguing commonalities and differences between the species, and applying similar methods that make inter-species comparisons possible has proved to be a worthwhile approach. Future studies should consider improving the employed methods in several ways.

Firstly, although increasingly more effort is put into studying the perception of emotions in great apes and other animals, scientists are still only scratching the surface (see Kret et al. (2020) for a review). We based our stimulus selection in Chapters 2-4 on previous work that investigated how great apes perceive emotional expressions (e.g., De Waal, 1988; Kret et al., 2016; Parr et al., 1998, 2008), but several important candidates have yet to be studied. For instance, disgust is associated with a distinct, universal facial expression in humans that may have evolved as a response to harmful foods or other substances (Curtis et al., 2011). Moreover, disgust can also be used as an intentional signal to express strong disapproval of for instance immoral behavior (Chapman et al., 2009). There is some evidence that great apes show some features of the prototypical disgust expression, i.e., nose wrinkling and tongue protrusion (Case et al., 2020), but we still know surprisingly little about disgust in great apes and other primates. Similarly, anger is a core emotion in humans (Ekman, 1999), and the bulging lip face that for instance chimpanzees and bonobos produce may be a homologue of human anger (De Waal, 1988; Parr et al., 2007). In our studies, we lacked stimuli depicting anger and aggression or disgust, as they were very hard to come by, and therefore we could not measure to what extent these emotional cues modulate attention. Thus, future studies could include a wider range of emotional categories that also include more negatively-valenced emotional states such as anger and disgust. Moreover, we did not have the sample size to zoom in on specific emotion categories. Nevertheless, in humans, there are some mixed findings indicating either an attentional bias away or towards certain emotional categories (e.g., Pool et al., 2016; van Rooijen et al., 2017; Zvielli et al., 2014). Thus, future studies could focus on investigating how valence may impact attentional biases.

Secondly, we made use of emotional scenes that contain more contextual information compared to isolated facial expressions. Previous findings have shown that providing this context facilitates the recognition of emotions (De Gelder et al., 2010; Kret et al., 2013b). Although I did not explicitly test this, it is plausible that this is also true for apes' recognition of emotion. For instance, bonobos show a bared-teeth display when scared and nervous, but also during sex (De Waal, 1988). Providing contextual information by showing a scene rather than an isolated facial expression may thus facilitate the processing of its emotional content. Nevertheless, our stimuli were static (Chapters 2-4), and only contained social information coming from the visual modality (Chapters 2-4, 6). Although human facial expressions of emotions are highly ritualized and therefore salient (Kret et al., 2020), expressions of emotions are often multi-modal, consisting of vocalizations, gestures, and facial and bodily expressions. Therefore, the perception of emotional expressions may be enhanced when emotional information is coming from multiple channels (Paulmann & Pell, 2011). Indeed, human studies have shown that emotional information across different modalities is integrated, creating holistic, enhanced emotion recognition (De Gelder et al., 1999; De Gelder & Vroomen, 2000; Schirmer & Adolphs, 2017).

Similarly, there is some work suggesting that great apes use social information coming from different modalities to categorize expressions. For instance, Parr (2004) found that when chimpanzees categorized faces, they preferentially categorized pant-hoots and play faces based on their auditory components, and scream faces based on their visual components. From an evolutionary perspective, the results suggest that the auditory modality is more informative for pant-hoots and play faces because pant-hoots are used for long-distance communication, and play faces are often concealed during rough, close-contact play. Thus, vocalizations during play may be more salient than facial expressions for indicating playful intentions (Parr, 2004). Nevertheless, despite numerous studies in primates investigating expressions in a single domain (e.g., vocalizing, gesturing, and facial expressions), multi-modal signaling is virtually unexplored (Fröhlich et al., 2019b; Liebal et al., 2014). The call for a multi-modal approach is in line with recent work stressing the effects of different natural ecologies of animals (including humans) on the evolution and development of behavior and cognition (Bräuer et al., 2020). Moving forward, comparative studies could take a multi-componential approach, and for instance investigate how dynamic emotional scenes that also include auditory cues are viewed, what behaviors these dynamic scenes elicit, and how different modalities contribute to emotion perception.

In Chapters 5 and 6 I described our studies investigating yawn and self-scratch contagion in orangutans. Yawn contagion was virtually unexplored in this species, and only a limited amount of work has previously looked into self-scratch contagion. Nevertheless, a third consideration for future work has to do with the link between yawning and emotion contagion is currently weak (Massen & Gallup, 2017). Emotion contagion requires having an emotional experience, but it is unclear what the emotional state underlying yawning might be. Yawning has been linked to boredom (see a discussion in Burn, 2017) as well as stress (Maestripieri et al., 1992; Paukner & Anderson, 2006). Moreover, some researchers argue that yawning is entirely unrelated to emotions and may simply be a form of motor mimicry (i.e., devoid of any emotional content; Yoon & Tennie, 2010). To establish whether yawn contagion is a proxy for emotion contagion, future research should aim to measure which emotional state, then, is transferred (Adriaense et al., 2020). This is of course not an easy feat as animals cannot report on their feelings, but one way to move forward is to study more closely the (social) contexts in which yawn contagion (or other examples of mimicry) occurs to determine whether it has a communicative purpose, and what that communicative purpose is.

A final methodological consideration concerns the use of the Pictorial Implicit Association Test (PIAT) for comparative research (Chapter 7). What research questions could comparative scientists answer using the PIAT, and which type of stimuli could be used? IATs are widely used in social cognitive research, for instance to study implicit associations with ethnicity or gender (e.g., Baron & Banaji, 2006; Nosek et al., 2002). Nevertheless, IATs could potentially help uncover the implicit associations underlying emotion perception in great apes.

Often, we have to make assumptions about valence and arousal of emotional signals in animals based on the contexts in which emotions are expressed and how individuals respond to them (Kret et al., 2020). However, we currently do not yet fully understand whether great apes view certain emotional expressions or scenes as positive or negative, or how they are perceived in terms of arousal. Moreover, human studies on emotion perception suffer from the same interpretive issues as animal studies, as human participants are often directly asked (e.g., through standardized questionnaires) about how they interpret emotional expressions or how they experience them. Notwithstanding the strong psychometric properties of some questionnaires, how individuals answer questions can be confounded by for instance the tendency to give desirable answers or their ability to self-reflect and articulate their emotions (Stone et al., 2000). For instance, individuals from clinical populations (e.g., autism-spectrum disorders) may find it challenging to report felt emotions or interpret them (Cook et al., 2013). Probing of implicit associations with emotions may therefore offer a less-biased way to measure how emotions are perceived, and also allows for direct comparisons between different populations and species. As such, the PIAT could potentially measure the strength of associations between emotional scenes and their valence or arousal level.

Indeed, the IAT has been successfully used to establish for instance cultural differences in implicit attitudes towards emotion regulation (Deng et al., 2019), approach and avoidance of fearful expressions (Hammer & Marsh, 2015), attitudes towards emotional expressivity (Cameron & Zeman, 2019), and stereotypical associations between certain emotional expressions (e.g., anger) and ethnicity (Bijlstra et al., 2014). Recently, one study directly investigated implicit attitudes towards emotions in adolescence with and without high-functioning autism spectrum disorder (ASD). Emotional stimuli consisted of the six basic emotion expressions (i.e., happiness, sadness, disgust, fear, anger, and surprise) and neutral expressions. The emotional expressions also varied in intensity. In this IAT, emotional stimuli were paired with words that were positive (e.g., peace, success) or negative (e.g., war, failure). Results indicated that individuals with high-functioning ASD showed larger IAT-effects (i.e., stronger positive or negative associations with the different emotional images) than individuals without ASD, indicating that it is possible to probe implicit attitudes towards emotions in humans. For a comparative study involving e.g., great apes, the words would have to be replaced by images of objects or individuals that great apes would associate with positivity or negativity, e.g., a veterinarian or a tranquillizer gun (see e.g., Allritz et al. (2015)).

Conclusion

In this dissertation, I set out to probe the emotional landscape of our closest relatives, the great apes. This type of research can help us progress our understanding of the evolution of emotional capacities in our species as well as other animals. Unfortunately, the population of all wild-living great apes is dwindling, and all great ape species now face extinction. As a consequence, the unique window into our evolutionary past is slowly but surely disappearing. Motivated by this pressing issue, I investigated the similarities and differences in emotion perception in bonobos, orangutans, and humans. Specifically, I investigated attentional and behavioral mechanisms that underlie emotion perception, which has been suggested to lay at the foundation of higher cognitive processes such as empathy (e.g., De Waal & Preston, 2017).

The results in this dissertation indicate a shared evolutionary origin for emotion-biased attention and spontaneous mimicry in *at least* the hominids. Importantly, familiarity and similarity may affect how attentional and behavioral mechanisms drive emotion perception, and these “modulators” can themselves be affected by species-specific characteristics such as sociality. The work I describe in my dissertation has raised new, important questions that need addressing in future research. At this moment, we do not fully understand which emotional expressions are the most salient or relevant to specific species (Kret et al., 2020). Furthermore, to elucidate a link between yawn and self-scratch contagion and emotion contagion, we require more work involving different animal species and more direct ways of testing the link (Massen & Gallup, 2017). Finally, establishing how great apes view emotions in terms of valence and arousal is important not only for our fundamental understanding of emotion perception but also for questions relating to animal welfare (Adriaense et al., 2020). Thus, I hope that this dissertation provides a stepping stone towards more research on emotions in our closest living relatives, but also other animals.