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

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Chapter 1

**A general introduction to
emotion perception and its
underlying mechanisms**

What are emotions? To many people, emotions are subjectively felt affective states. There is no doubt in our minds that we experience emotions, and that others do, too. Nevertheless, describing what exactly an emotion *is* has proved to be a major scientific challenge, and definitions are still highly contested (Adolphs et al., 2019; James, 1884; LeDoux, 2021; Russell & Barrett, 1999). For a long time, the lack of a clear definition for emotions stood in the way of understanding what role emotions play in not only our lives but the lives of other animals as well. Moreover, it made unraveling the evolution of emotions very difficult (Paul & Mendl, 2018). When Nikolaas Tinbergen published his seminal work on the four questions that scientists can ask to find proximate (“how”) and ultimate (“why”) explanations for animal behavior (Tinbergen, 1963), the topic of emotions in animals other than humans was still highly controversial. This was mainly due to the subjective nature of emotions, as animals cannot tell us what they feel or how they experience things. Since then, the interdisciplinary field that is concerned with emotions in humans and other animals has grown steadily and confidently and is now known by the name *comparative affective science* (Williams et al., 2020). With the rise of this new scientific field, attempts have been made to find a definition of emotion that makes it accessible to scientific inquiry. For instance, a broad definition was provided by Frans de Waal in his work *What is an animal emotion?*:

“Emotions [are] mental and bodily states that potentiate behavior appropriate to the environmental challenges” (De Waal, 2011).

These emotional states are adaptive; they are shaped through the process of natural selection to prepare individuals for the most appropriate and optimal response. Emotional states are caused by external, biologically relevant stimuli, bringing about a range of parallel changes in an organism (e.g., behavioral, psychophysiological, cognitive, and somatic). The kind of emotion that is triggered, is closely tied to the context an individual finds itself in (De Waal, 2011). Moreover, although we typically assign subjective experiences (“feelings”) to emotional states, these are arguably hard to probe in animals. However, even if we do not fully grasp the emotional experiences of animals, this understanding is not necessary to move forward (see for discussions e.g., Berridge, 2018; LeDoux, 2021; Mendl et al., 2010). Building from the premise that emotions are states that the body can be in, we can examine these states in more detail by looking at their cognitive and behavioral markers (Anderson & Adolphs, 2014; De Waal, 2011; Paul et al., 2005). These markers serve as proxies to the “inner world” of animals as well as of humans, and

understanding them will allow scientists to determine whether the behaviors that we intuitively deem indicators of emotions in animals are indeed mediated by the same or homologous mechanisms shared between humans and other animals (Panksepp, 2011). Additionally, this will also allow us to reconstruct how our human ancestors may have behaved and felt.

The focus of this dissertation lies on how emotions are *perceived* by studying three markers of emotion perception: *attention*, *spontaneous mimicry*, and *implicit associations* (Figure 1i-iii). In this dissertation, emotional modulation of attention and mimicry is compared between humans, bonobos, and orangutans, and an adaptation to an existing paradigm to study *implicit associations* is validated for potential use in comparative science in the future. As will become clear, attention, mimicry, and implicit associations are building blocks that are fundamental to social cognition. Moreover, they provide an opportunity to study what emotions mean to other animals and make direct comparisons between species possible. The goal of the dissertation is twofold, namely to better understand the evolutionary continuity of emotion perception across hominids, but also to study the uniquely derived differences in emotion perception in the three species (Figure 1a). To do this, the

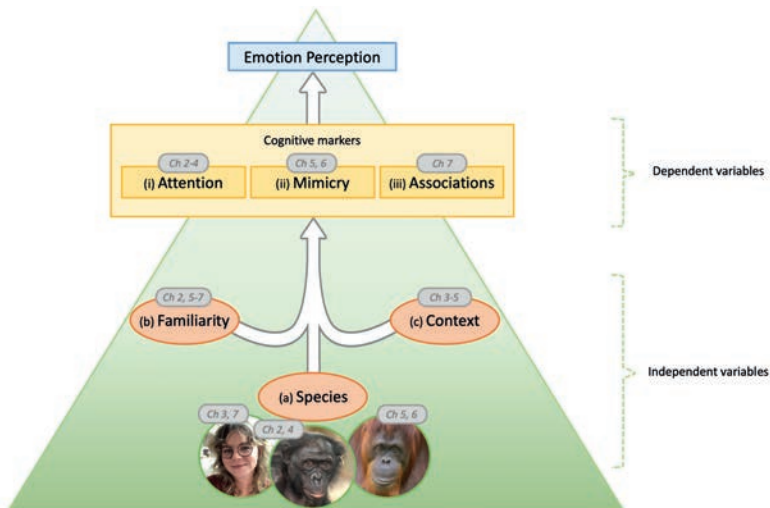


Figure 1. Schematic overview of the research topic. Emotion perception is a multifaceted phenomenon that is governed by many different cognitive mechanisms. Often, these mechanisms operate on an implicit level; automatically and unconsciously. To study emotion perception across species, I investigate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

effects of *species*, *familiarity*, and *context* (Figure 1b, 1c) on emotion perception are examined. Here, *familiarity* is defined as the familial and/or social relationship between the expressor of emotions and the observer. *Context* refers to the situation the observer and/or expressor of emotional expressions find themselves in (e.g., tense or relaxed situations).

A window into our evolutionary past

What are the evolutionary roots of emotions? In search of answers to this cardinal question, one logical step we can take is studying emotions in animals that are evolutionarily close to us: the great apes. Studying the behavior and cognition of extant (i.e., still living) great apes is extremely relevant for reconstructing the social and emotional characteristics of the last common ancestor of the *Hominidae*, as well as early *hominins* (ancestral humans) (Duda & Zrzavý, 2013). The *Hominidae* consist of the African apes: gorillas, chimpanzees, bonobos, humans, and orangutans (the only Asian great ape) (Figure 2). The last common ancestor of the African apes and orangutans likely lived about 14 million years ago (Ma) (Goodman et al., 1998), with the most recent common ancestor of chimpanzees, bonobos, and humans living at least 7 to 8 Ma (Langergraber et al., 2012). It is important to remember that evolution has continued for both the great apes as well as humans. Indeed, each of the hominids

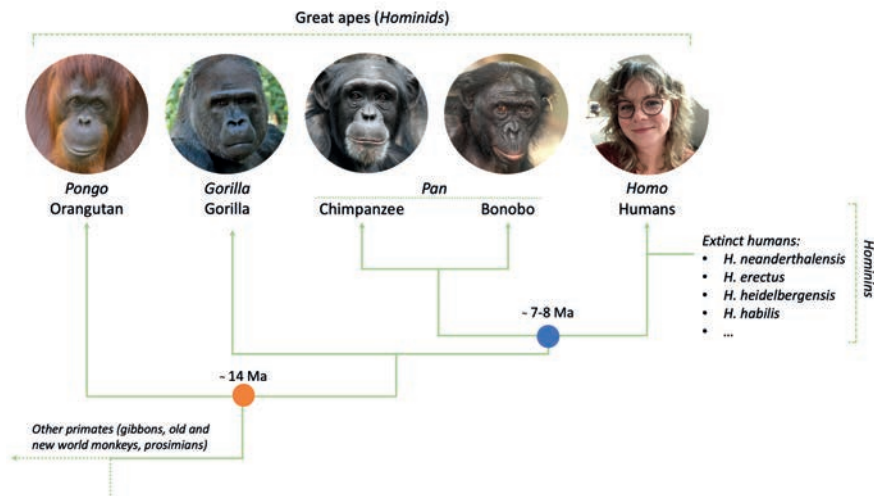


Figure 2. Great ape family tree. Bonobos and chimpanzees are humans' nearest living relatives, followed by gorillas, and then orangutans. *Pan* and *Homo* share a common ancestor roughly 7-8 million years ago (Ma). At one point in time, other human species roamed the earth together with or close in time to *Homo sapiens*. For instance, Neanderthals co-existed with *sapiens* until Neanderthals went extinct around 40,000 years ago (Higham et al., 2014).

has undergone unique changes: adaptations that made survival in their separate social and physical environments possible. Nevertheless, comparisons between species make it possible to get some sense of what our common ancestor may have lived and behaved like. If a specific characteristic is found in all the species that are compared, this may suggest a common evolutionary origin (Wilson, 2021). There are likely a lot of commonalities to be found in the behavior and cognition of great apes and humans. In this dissertation, the focus lies on two great ape species that can provide us with unique insights into the evolution of emotions, and specifically on how emotions are perceived: bonobos (*Pan paniscus*) and orangutans (*Pongo pygmaeus*).

Bonobos are known for their relatively tolerant nature, as well as their usage of sexual behaviors to reduce tension in their group, strengthen bonds with other females, and form new relationships with unfamiliar individuals (De Waal, 1988; Furuichi, 2011). Endemic to a small area in the Democratic Republic of the Congo, bonobos live in fission-fusion groups where males have life-long residency in the group and females disperse to other groups when they reach sexual maturity (Hohmann et al., 1999). Like all apes, bonobos are endangered, with a minimum estimated wild population of about 15.000-20.000, and around 225 individuals living in zoos across the world (Fruth et al., 2016). Though current research efforts into the psychology of bonobos are growing, we still understand relatively little about their social cognition. In stark contrast with their more territorial cousins, chimpanzees (*Pan troglodytes*) (Wilson et al., 2014), as well as ancestral humans (Bowles, 2009; Wrangham & Glowacki, 2012), bonobos show remarkable xenophilic tendencies. Females of different groups show high social tolerance and tend to affiliate with each other rather than fight (Furuichi & Thompson, 2007). Even within their social groups, bonobos show high levels of affiliation and cooperation, and low levels of aggression. Moreover, neuroscientific studies on the brains of bonobos have found that the brain structures involved in emotion processing and regulation are bigger in volume and have more dense connections in bonobos compared to other great apes, thus making them an important referential model for the evolution of social cognition in ancestral humans (Issa et al., 2019; Rilling et al., 2012; Stimpson et al., 2016).

Native to Borneo and Sumatra, orangutans are arboreal apes that lead a semi-solitary existence that is highly unusual among the great apes (Delgado & Van Schaik, 2000; Galdikas, 1985; Mitra Setia et al., 2009). Occasional social associations among individuals do occur, but not frequently (Singleton et al., 2009; Van Schaik, 1999). It is during these temporary formations of small groups that orangutans have the opportunity for socializing, playing, and mating. The formation of these parties, as well

as the general tendency to live on their own, likely has a close link to the availability of fruit, with fruit scarcity leading to less association, and fruit abundance to more social interactions (Roth et al., 2020). Cognitive research on orangutans has gained more traction in the last decade (Damerius et al., 2019; Hopper, 2017), but almost no work has looked at how orangutans perceive emotional expressions, and how their socio-cognitive abilities compare to the other apes and humans. Their unique semi-solitary nature may therefore provide interesting insights into the development of these capacities over evolutionary time.

Enhanced attention for emotions

One of the earliest processes involved in emotion processing is *attention* (Figure 1i). Attention is the gatekeeper that selectively filters relevant from irrelevant information coming from the environment (James, 1890). This process is crucial, as the brain cannot attend to all information at once. Remarkably, already at the very early stages of processing information from the environment, attention automatically and efficiently tunes to emotionally salient signals (Whalen, 1998). Indeed, a large body of evidence stemming from human studies has shown that emotions are so fundamental to our species, that our brains evolved sensory mechanisms that preferentially process emotional information over other, more neutral signals (Phelps & LeDoux, 2005). Especially negative emotions (for instance fear or anger) appear to strongly capture our attention. From an evolutionary perspective, this makes a lot of sense. Perceiving anger or fear in others could mean that there is imminent danger, requiring immediate action from the observer. Early studies on this so-called *implicit attentional bias* for threatening signals, showed that humans automatically attend to threatening stimuli such as snakes, spiders, or angry faces (Öhman et al., 2001a), and suggested the brain and especially its emotion center (including subcortical structures such as the amygdala) is “hard-wired” to detect such threats in the service of evolutionary goals (Öhman et al., 2007).

New research suggests that parts of the brain’s emotion centers are not just hard-wired threat detectors, but are highly sensitive to *motivationally* relevant emotional signals (Cunningham et al., 2008). Indeed, enhanced attention to negatively- or positively-valenced emotions appears to differ between individuals, across developmental trajectories and the age spectrum (Todd et al., 2012), and is affected by an individual’s current affective state (Mendl et al., 2009). This also may explain why highly anxious individuals show a particularly strong bias towards angry or fearful faces (Bar-Haim et al., 2007). Moreover, allocation of attention to emotional stimuli

could be driven by highly salient, low-level perceptual characteristics of stimuli (for instance the visibility of teeth, direct eye gaze, or simply their novelty) and therefore reflect a more bottom-up process (Öhman et al., 2001a). Attention allocation can also be driven by a top-down process that takes into account the motivations of the observers, as well as the context the observers find themselves in (Victour et al., 2020). Most likely, however, attention for emotions involves an interplay between bottom-up and top-down processes (Pessoa et al., 2006). Notwithstanding this debate, it is undisputed that expressions of emotion are automatically and swiftly attended to by humans. But is this attentional mechanism uniquely human, or can we find similar mechanisms in other animals?

Evidence for emotion-biased attention in animals is much more limited, and also mixed. Most of the work that exists is conducted with primates. One research task that can measure (implicit) selective attention towards emotions is the dot-probe task, which measures how fast individuals can touch a dot (i.e., the probe) on a screen after being presented with emotional and neutral stimuli (i.e., signals in the form of for instance a picture). Typically, individuals are faster at touching a dot when it is preceded by an emotional stimulus because emotions draw attention. Using the dot-probe task, Japanese macaque monkeys (*Macaca fuscata*) were found to have a threat-specific attentional bias (Masataka et al., 2018) that also extended to threatening facial expressions (Lacreuse et al., 2013; Parr et al., 2013). However, enhanced attention to threatening signals was not found in chimpanzees using the same paradigm (Kret et al., 2018; Wilson & Tomonaga, 2018). In contrast, bonobos showed biased attention towards more positively valenced emotional scenes. Finally, studies measuring attentional biases with eye-tracking have shown that chimpanzees and orangutans look longer at threatening stimuli such as fearful faces or aggressive interactions (Kano & Tomonaga, 2010a; Pritsch et al., 2017).

The mixed results show that more research is needed to close the knowledge gap on how expressions of emotion affect attention in other animals, especially given the importance of implicit measures of emotion processing for comparative research. The first part of this dissertation (Chapters 2 to 4) will therefore examine emotion-biased attention in humans and one great ape species, bonobos, in more detail (Figure 2a).

Spontaneous mimicry and emotion contagion

Attention allows for studying to what extent emotions can capture and hold interest, thus to a certain extent it elucidates whether emotions are meaningful to individuals. However, it does not inform us about whether emotions are meaningful for

interactions between individuals. Here, there is a role for *spontaneous mimicry*, which in the field of psychology is defined as the automatic and unconscious imitation of facial or bodily expressions of other individuals (Figure 1ii) (Chartrand & Bargh, 1999). Examples of spontaneous mimicry (henceforth: mimicry) are contagious laughter or crying, but also contagious yawning and self-scratching. Quintessentially a social phenomenon, mimicry is thought to facilitate the perception of emotions in others, as well as the transmission of emotional states between individuals (emotion contagion) (Preston & De Waal, 2002; Prochazkova & Kret, 2017).

Recently, a step-wise evolutionary development of emotion contagion was proposed, starting at multiple individuals showing a similar facial display that is automatically generated by a physiological internal state in response to external events (for instance a fearful face in response to aggressors or predators, or an expression of pain in response to bodily harm) (Palagi et al., 2020). Next, these independent facial displays may have acquired a communicative function by automatically triggering a similar response in others when observed. The function of this system may have been to synchronize activities within the group, for instance by rapidly spreading fear among group members to escape from predators. Importantly, it may have resulted in automatic emotion contagion when the displays reflected emotional states, leading individuals to feel – to a certain extent – what others are feeling. In this way, emotion contagion can help resonate with others, facilitating effective communication and social cohesion (Decety et al., 2012; Preston & De Waal, 2002). For example, spontaneous mimicry of expressions can provide a crucial fitness advantage in parental care, allowing parents to respond to the needs of their offspring (Decety et al., 2012; Roth et al., 2021).

It is important to emphasize that mimicry does not necessarily equate to uninhibited, full-blown copying of behaviors and expressions, as this would hinder individuals from appropriately responding to social situations (e.g., parents would not be able to adequately respond to their infant's needs if they would always be overwhelmed by sadness when their infant is crying (Mafessoni & Lachmann, 2019)). Rather, mimicry can be subtle, triggering the activation of a corresponding emotional state in oneself, thereby allowing the identification of what someone else is feeling and formation of an appropriate response (Preston & De Waal, 2002). As such, mimicry is considered to be a major building block for more complex socio-cognitive capacities such as empathy (De Waal & Preston, 2017; Koski & Sterck, 2010) and cooperation (e.g., to establish trust between cooperating individuals); two facets that are extensively developed in our species (Tomasello et al., 2012). Thus, through studying mimicry, we

are provided with a window into the basic capabilities of humans and other animals to process emotions.

In the last decade, interest has grown in studying contagious yawning as a form of motor mimicry (Massen et al., 2012; Miller et al., 2012b; Norscia & Palagi, 2011a). Yawning itself is a widespread behavior among vertebrates, yet it is contagious only in a limited number of social species. In addition, it has been suggested that yawn contagion is linked to emotional contagion, as contagiousness is stronger between kin and friends (Palagi et al., 2020b). At the same time, the purported link between contagious yawning and emotion contagion is heavily debated, with some researchers suggesting that the effect of social closeness on contagiousness is established not because of a fundamental emotion-sharing mechanism, but because of for instance an attentional bias to familiar individuals (Gallup, 2021; Massen & Gallup, 2017).

There are a growing number of studies showing that yawning is more contagious between strongly bonded individuals (Campbell & de Waal, 2011; Joly-Mascheroni et al., 2008; Norscia et al., 2020, 2021; Palagi et al., 2014; Romero et al., 2014), but other studies report no link with closeness (Madsen et al., 2013; Madsen & Persson, 2013; Massen et al., 2012; Neilands et al., 2020; O'Hara & Reeve, 2011), making it unclear what characteristics of social relationships (if any) modulate contagious yawning. In addition to yawning, non-facial forms of mimicry (e.g., postures, gestures) have been extensively studied in humans (see Lakin et al. (2003) for a review), but much less in animals. Self-scratch contagion – one example of non-facial mimicry – has been proposed as a candidate behavior to study the link between mimicry and emotional contagion, but work on self-scratch contagion is still limited (Feneran et al., 2013; Nakayama, 2004; Schut et al., 2015). Self-scratching can be an indicator of stress or arousal in both humans and other animals (Maestripieri et al., 1992), thus its contagiousness could potentially reveal a link with *negative* emotional contagion. Continued efforts to study the possible link between contagious yawning and self-scratching and emotion contagion remain important, especially for the advancement of our understanding of how animals process emotions. The second part of this dissertation (Chapters 5 and 6) will therefore center around contagious yawning and self-scratching.

Emotional modulation of implicit associations

Sensitivity to emotions can also be measured indirectly via *implicit associations* (Figure 1iii). To navigate the complexities of the social world, it is beneficial to form simple heuristics rather than making new social evaluations with every new situation. These

simple heuristics can come in the form of categorizing for instance other individuals into pleasant or unpleasant, and familiar or unfamiliar, and are driven by a cognitive system that automatically evaluates the environment (Greenwald & Banaji, 1995). Indeed, in the human literature, these unconscious evaluations are called *implicit associations*, and they guide our daily behavior. Emotions regulate these implicit social evaluations, making them stronger or weaker based on an individual's current state (Greenwald & Banaji, 1995).

Most of the work on implicit associations has been done in social psychology and has examined in- and outgroup implicit associations using the *Implicit Association Test (IAT)*, which measures unconscious associations between certain concepts (e.g., objects, individuals) and evaluations (e.g., "good" or "bad", "positive" or "negative") (Greenwald et al., 1998). Implicit attitudes can for instance entail an unconscious preference for one's ingroup over an outgroup, as well as having negative associations with outgroups. Notwithstanding the importance of uncovering the cognitive mechanisms underlying intergroup biases in humans, to date, relatively little research has looked at where these processes come from in the first place. The pervasiveness of negative implicit attitudes towards outgroups (paving the way for phenomena such as prejudice and discrimination) suggests an evolutionarily old origin.

Kurzban, Tooby and Cosmides (2001) hypothesized that implicit negative attitudes towards for instance individuals of another ethnicity may be a byproduct of adaptations that once evolved to help detect coalitions and alliances in our hunter-gatherer ancestors. For quick and efficient processing of the social world, the cognitive mechanism underlying this alliance-detection becomes sensitive to otherwise meaningless markers such as physical traits to create social categories. Recently, this *alliance hypothesis of race* was further strengthened by direct experimental evidence (Pietraszewski, 2021). Given that other animals show sensitivity to intergroup biases in attention and mimicry, we may find that certain animals also implicitly evaluate other individuals.

Primates have group structures that closely resemble ours, including intergroup conflicts, hierarchies, and social categories (i.e., based on biological traits such as sex, kinship, age, etc.). Yet, we do not fully grasp the emotional and cognitive processes that drive intra- and intergroup social interactions, and evidence for intergroup biases in judgments and associations is currently limited to humans. Finding ways to probe implicit associations in animals might prove useful in progressing our understanding of the link between emotions and implicit attitudes. Having a method that probes implicit attitudes in animals can not only help us study a negative bias

towards outgroups, but would also allow us to examine how animals judge emotional categories themselves.

Currently, we design experiments based on our notion of what entails an emotionally-salient cue to animals. These notions are of course grounded in the knowledge that we have gathered on emotions in animals, but it remains impossible for us to truly know the meaning of emotions to animals because they cannot use language to convey this information to us. We make a first step towards developing a way to probe all kinds of implicit associations in animals that are capable of categorizing images and working on a touchscreen in Chapter 7. Here, we validate a pictorial adaptation to the IAT in humans and adult children, with the hope that this pictorial version may one day be tested in animals. In essence, the IAT is a matching-to-sample task in which an image has to be matched to its appropriate category. Great apes have previously been shown to be capable of performing matching-to-sample tasks in which they categorized bodies in different configurations (Gao & Tomonaga, 2020), sexes (De Waal & Pokorny, 2011), genital regions (Kret & Tomonaga, 2016), familiar and unfamiliar faces (Parr et al., 2000; Pokorny & De Waal, 2009; Talbot et al., 2015; Vonk & Hamilton, 2014), facial expressions (Parr et al., 2008), and emotions (Parr, 2001). It is therefore plausible that great apes could also perform in a pictorial IAT.

Dissertation outline

This dissertation is based on six empirical research articles focusing on the unconscious and automatic cognitive and behavioral markers of emotion perception, as these markers offer a strong basis from which we can study emotions across species. Specifically, in **Chapter 2**, the role of *implicit, immediate attention* in perceiving emotions of familiar and unfamiliar conspecifics (i.e., other individuals of the same species) as well as heterospecifics (i.e., individuals of another species) is investigated in bonobos and humans (Figure 1i). Central to this chapter is i) replicating earlier findings on an emotion bias in bonobos and humans (Figure 1a), and ii) tackling how familiarity modulates attention for emotions, which to date has not yet been examined (Figure 1b).

Chapter 3 zooms in on emotion-biased attention in humans across all age categories, using emotional *scenes* as cues rather than isolated facial expressions, as they provide more contextual information to the observer (Figure 1a, c). Moreover,

how children and adults perceive the emotions of other humans and bonobos is examined to assess differences and similarities in the perception of emotional expressions across closely related species.

Chapter 4 builds on the works in Chapters 2 and 3 by examining attention for emotions in bonobos and humans in more detail using an eye-tracking paradigm. Here, the goal was to examine the similarities and differences between the two species in *focusing* attention on emotional versus neutral scenes (Figure 1a, c).

In **Chapter 5**, the dissertation moves on to study *spontaneous mimicry* (Figure 1ii). Through behavioral observations, the existence of contagious self-scratching is examined in orangutans. Moreover, the link between contagious self-scratching, context, and social closeness is studied (Figure 1a-c).

Chapter 6 follows up on this work with an experimental investigation of yawn contagion in orangutans to move towards a better understanding of the function of contagious yawning, as well as its relation with familiarity (Figure 1a, b).

Next, **Chapter 7** focuses on the validation of a touchscreen-based, pictorial adaptation to the classic *Implicit Association Test* to examine *implicit associations* (Figure 1iii, a, b). Though a validation in great apes is outside the scope of this dissertation, the chapter makes a first step towards finding ways to probe implicit associations in animals other than humans.

Finally, in **Chapter 8**, the main findings are summarized and discussed to highlight the most crucial similarities and differences in the cognitive and behavioral mechanisms that underlie emotion processing in hominids.

I would like to emphasize that all the work disseminated in this dissertation is the result of intense collaborations with colleagues. I am the first author of the works described in Chapters 2, 4, 6, and 7, and I am the second author of the works described in Chapters 3 and 5. Chapter 3 is written by Daan W. Laméris, MSc., and Chapter 5 by principal investigator Dr. Mariska E. Kret. Both of these works are important to the dissertation's overarching theme, and although most of the work can be ascribed to Drs. Daan Laméris and Dr. Mariska Kret (as evidenced by their first-authorship), I have made substantial contributions to both studies. With the permission of Daan Laméris, MSc., and Dr. Mariska Kret, Chapters 3 and 5 have therefore become a part of this dissertation.