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Citation

Berlo, E. van, Bionda, T., & Kret, M. E. (2023). Attention towards emotions is modulated by familiarity with the expressor: a comparison between bonobos and humans. *Emotion*, *7*, 1904-1917. doi:10.1037/emo0000882

Emotion

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Online First Publication, January 2, 2023. https://dx.doi.org/10.1037/emo0000882

CITATION
van Berlo, E., Bionda, T., & Kret, M. E. (2023, January 2). Attention Toward Emotions Is Modulated by Familiarity With the Expressor: A Comparison Between Bonobos and Humans. *Emotion*. Advance online publication. https://dx.doi.org/10.1037/emo0000882

AMERICAN PSYCHOLOGICAL ASSOCIATION

Emotion

ISSN: 1528-3542

https://doi.org/10.1037/emo0000882

Attention Toward Emotions Is Modulated by Familiarity With the Expressor: A Comparison Between Bonobos and Humans

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Why can humans be intolerant of, yet also be empathic toward strangers? This cardinal question can be tackled by studying emotions in our closest living relatives, bonobos. Their striking xenophilic tendencies make them an interesting model for reconstructing the socioemotional capacities of the last common ancestor of hominids. Within two dot-probe studies, we compared bonobos' and humans' attention toward scenes depicting familiar (kith and kin) or unfamiliar individuals with emotional or neutral expressions. Results show that the attention of bonobos is biased toward emotional scenes depicting unfamiliar bonobos, but not toward emotional groupmates (Study 1). In contrast, Study 2 shows that human attention is biased toward emotional rather than neutral expressions of family and friends, but not toward unfamiliar others. On the one hand, our results show that an attentional bias toward emotions is a shared phenomenon between humans and bonobos, but on the other, both species have their own unique evolutionarily informed biases. These findings support previously proposed adaptive explanations for xenophilia in bonobos that potentially biases them toward emotional expressions of unfamiliar conspecifics, and parochialism in humans, which makes them sensitive to the emotional expressions of close others.

Keywords: affect, great ape, intergroup bias, affective attention, social processing

Supplemental materials: https://doi.org/10.1037/emo0000882.supp

Emotional expressions are a major force in navigating the social world; they provide valuable insights into the emotional states of others and help to predict others' behaviors (Cosmides & Tooby, 2000). The expression of emotions is not uniquely human and is shared with other animals (Darwin, 1872; Zych & Gogolla, 2021). Yet, we still understand little about how animals perceive and understand others' emotions (Nieuwburg et al., 2021; Paul & Mendl, 2018). Here, taking a comparative perspective will be crucial in elucidating how socioemotional capacities evolved in ancestral humans as well as other animals. One way to move forward is to compare the emotional processing capacities of humans with those of closely related species.

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We thank the Kyoto University Primate Research Institute for donating an automatic feeder. We thank the animal caretakers Keetie de Koeier, Iris Schapelhouman, Grietje Grootenhuis, Jacqueline Ruijs, and Carolijn de Jong for their crucial assistance during testing. Additionally, we thank Daan Laméris for coding the videos and Berta Roura Torres for scoring the bonobo stimuli. We also thank Wendy Cieremans for facilitating research with visitors, and Iliana Samara and the numerous students who helped in collecting and validating the human data. Furthermore, we thank the following photographers for their contribution to the bonobo stimulus material: Hugh Jansman, Iris Kronenburg, Joke Kok, Frans van der Kolff, Greetje Olde Hanhof, Jan van den Berg, Petra Postma, Ans and Leo Teunissen, N. C. Bakker, Wilma Bakx, Roos Zondag, D. Paalman, Talitha Hoppe, Nick Dijkstra, Dirk van de Velde, Edwin Butter, K. Verhulst, and Tom van Deuren. Finally, we greatly appreciate the thorough feedback and insightful comments and recommendations provided by editor Dr. Tim Sweeny, as well as three anonymous reviewers.

This research is supported by the European Research Council (ERC) (Starting Grant 802979) and a grant from the Templeton World Charity Organization (TWCF0267) awarded to M. E. K. and by The Royal Netherlands Academy of Arts and Sciences Dobberke Foundation for Comparative Psychology Grant UPS/BP/4387 2014-3, to E. B.

All data and scripts are available on Dataverse via https://dataverse.nl/dataset.xhtml?persistentId=doi:10.34894/EANZC9.

Evy van Berlo served as lead for data curation, investigation, validation, visualization, writing—original draft, and writing—review and editing and served in a supporting role for conceptualization, funding acquisition, software, and supervision. Mariska E. Kret served as lead for conceptualization, funding acquisition, software, and supervision and served in a supporting role for data curation, investigation, validation, visualization, and writing—original draft. Evy van Berlo, Thomas Bionda, and Mariska E. Kret contributed equally to formal analysis, methodology, project administration, and resources. Thomas Bionda and Mariska E. Kret contributed to writing—review and editing equally.

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Within the primate order, bonobos (*Pan paniscus*) are humans' closest living relatives, together with chimpanzees (*Pan troglodytes*). Compared to chimpanzees and other apes, bonobos have strongly developed emotional pathways in the brain (Issa et al., 2019; Stimpson et al., 2016). Behaviorally, bonobos are more tolerant of others and show reduced aggression (Furuichi, 2011; Gruber & Clay, 2016; Hare et al., 2012; Tan & Hare, 2017; Tokuyama et al., 2021). Because of their xenophilic tendencies, bonobos form an interesting comparison species for gaining evolutionary insights into humans' emotional capacities (Gruber & Clay, 2016; Kret et al., 2016; Stimpson et al., 2016). We currently have limited knowledge about how bonobos perceive emotional expressions, and this is a pressing issue given that they are an endangered species (Fruth et al., 2016). Scientific progress is further hampered by bonobos being rare in zoos and sanctuaries (the worldwide zoo-managed population consists of only 225 individuals, managed by the European Association of Zoos and Aquaria [EAZA] in Europe and the Species Survival Plan in the United States; Stevens, 2020). Thus, to elucidate the socioemotional capacities of our shared common ancestor, more comparative studies are needed that include bonobos. We make a step in this direction by investigating selective visual attention for emotions in a comparative framework including bonobos and humans. Specifically, we test whether the identity of the expressor (i.e., a familiar or unfamiliar conspecific) modulates early attention for emotions.

Expressions of emotions facilitate the communication of emotions and intentions between individuals and are therefore integral to social animals (Prochazkova & Kret, 2017; Zych & Gogolla, 2021). The importance of emotional expressions is reflected in the fact that, over evolutionary time, selective pressures gave rise to brains that can quickly attend to and understand emotional expressions (LeDoux, 1998). Research in humans has demonstrated that already during the earliest stages of visual perception, attention is attuned to emotional expressions (Öhman, Lundqvist, & Esteves, 2001; Vuilleumier, 2005). Specifically, both threatening and positive signals in the environment can rapidly capture attention (Pool et al., 2016), and this attentional attunement is driven by both arousal-eliciting characteristics of the signal as well as its significance to the observer (Brosch et al., 2008; Frijda, 2017). Interestingly, a similar capacity has been observed in bonobos (Kret et al., 2016). In a study setting, bonobos showed an attentional bias toward emotional scenes depicting unfamiliar conspecifics, especially when these scenes were emotionally intense. Moreover, a recent study showed that emotional expressions interfere with attention allocation in bonobos in an emotional Stroop task (Laméris, Verspeek et al., 2022). These findings suggest that the attentional mechanisms that guide social perception have an evolutionarily old foundation and were likely already present in the last common ancestor of *Pan* and *Homo*.

Aside from being attuned to emotional expressions, the brain systems that facilitate the social bond between individuals have also evolved to prioritize the processing of familiar, socially close others. Human studies have shown that faces of friends and family are detected faster than faces of strangers (Ramon & Gobbini, 2018) and that these familiar faces recruit a broader network of brain areas involved in face, emotional, and social processing (Gobbini et al., 2004). Similarly, a recent study with chimpanzees and bonobos showed that they gaze longer at familiar faces than at unfamiliar faces of conspecifics (Lewis et al., 2021). Familiarity can also affect the expressions of emotions. For example, work on the automatic mimicry of emotional expressions shows that individuals are more likely to mimic expressions of familiar others compared to strangers (Palagi et al., 2020; Prochazkova & Kret, 2017). As attention gates that signal from the environment are preferentially processed, it is therefore plausible that evolution fine-tuned this mechanism to quickly differentiate not only between emotional and neutral cues but also between expressions of familiar, socially close group members and unfamiliar others. Interestingly, a recent study with chimpanzees and gorillas (*Gorilla gorilla*) showed that they have an attentional bias toward unfamiliar human faces showing a neutral expression (Leinwand et al., 2022), but this bias disappeared when the human models displayed an emotional (surprised) face. Currently, we do not yet know if and how familiarity and emotional expressions interact when viewing conspecifics.

Compared to the other great apes and humans, bonobos are strikingly xenophilic. Intergroup encounters in the wild proceed relatively peacefully, and neighboring groups have been observed foraging together (Fruth & Hohmann, 2018). Remarkably, two wild female bonobos have recently been observed adopting an infant from a different social group (Tokuyama et al., 2021). Furthermore, in studies settings, bonobos show a prosocial preference for unfamiliar individuals rather than group members (Tan & Hare, 2013). In contrast, humans tend to prioritize their group members over unfamiliar individuals when it comes to sharing resources (Fehr et al., 2008). Likely, the environments that both species evolved in contributed to the differences in how they interact with others. For bonobos, intergroup tolerance may have resulted from specific ecological conditions, as they live and evolved in a demarcated area in the Democratic Republic of the Congo. Here, reduced feeding competition and environmental stability led to the formation of stable social parties that decreased the occurrence of extreme territorial encounters with other groups (Hare et al., 2012; Wrangham, 1999). The picture for human evolution is different: ancestral humans migrated great distances across the globe as a result of the extraordinarily volatile climate that caused scarcities in resources for substantial periods of time. This paved the way for intergroup conflicts among our hunter-gatherer ancestors (Ember & Ember, 1992). In turn, these aggressive interactions fostered a strong focus on the in-group (e.g., family and friends) on the one hand, and xenophobia on the other (Bowles, 2009). Therefore, although humans and bonobos are both highly social animals, their different other-regarding tendencies warrant a closer look at how the two species process emotions of family, friends, and strangers. Specifically, we ask how familiarity impacts early attentional mechanisms that help distinguish between emotionally relevant signals from group members or other, unfamiliar individuals.

To make interspecies comparisons of selective attention for emotions possible, the emotional dot-probe paradigm has been proven useful (MacLeod et al., 1986; Van Rooijen et al., 2017). In the task, individuals have to press a central dot, followed by a short presentation of an emotional and a neutral stimulus. Another dot (the probe) then replaces either the emotional or neutral stimulus. Individuals are generally faster at tapping the probe that replaces the stimulus that biased their attention toward it (usually the emotional stimulus) compared to a probe replacing the other stimulus (the neutral stimulus, but see e.g., Belopolsky et al., 2011; Koster et al., 2004 for in-depth discussions on whether results in a dot-probe reflect attentional capture or disengagement). As such, the emotional dot-probe task provides a relatively easy way to tap into the underlying attentional mechanisms that guide emotion perception.

In the current study, we investigate how bonobos and humans attend to expressions of emotion of familiar and unfamiliar individuals. Here, we define familiarity as the social and familial relationship between the observer and the expressor of emotions on the one hand, and unfamiliar others on the other. Further, there is an ongoing debate on the definition of emotions and their expressions (Adolphs et al., 2019; Crivelli & Fridlund, 2018; James, 1884; LeDoux, 2021; Russell & Barrett, 1999; Waller et al., 2020). We follow the definition put forward by Anderson and Adolphs (2014) who describe emotions as adaptive brain states that produce a range of behavioral patterns (expressions). Additionally, we define *expressions* of emotions descriptively (Paul & Mendl, 2018) and broadly as visually observable facial and/or body expressions that often occur in social interactions, and that can differ in terms of valence and arousal (Russell, 1980). Here, we investigate whether bonobos have an attentional bias toward emotional expressions of unfamiliar and familiar others (Study 1). In Study 2, using a large community sample of zoo visitors, we investigate whether human attention is attuned to emotional expressions of familiar (family and friends also visiting the zoo) or unfamiliar (other zoo visitors) people.

We hypothesize that bonobos, due to their xenophilic tendencies, will show an attentional bias toward emotions expressed by unfamiliar conspecifics (Kret et al., 2016) and that a similar bias will be dampened when seeing familiar conspecifics. For humans, we hypothesize that an attentional bias toward emotions exists for expressions of unfamiliar individuals, in line with established findings (Van Rooijen et al., 2017). We also expect that this bias will be more pronounced for familiar individuals as compared to unfamiliar individuals, reflecting the more in-group-focused, parochial tendencies of humans (Bowles, 2009).

Study 1: Bonobos' Attentional Bias Toward Emotions of Conspecifics

In the first study, we investigated whether bonobos' attentional bias toward emotions differs between seeing emotional and neutral scenes of familiar group members and unfamiliar other bonobos.

Method

Participants

Four female bonobos (Besede, 11 years old; Monyama, 6 years old; Kumbuka, 17 years old; Yahimba, 7 years old and daughter of Kumbuka)[1] living in a social group of 12 individuals at Apenheul primate park in Apeldoorn, The Netherlands, took part in the study and were tested over a period of 4.5 months. All participating females were born in captivity and had prior touchscreen experience through participating in the study by Kret et al. (2016). There were 8 months of no testing between the two studies. At the time of testing, none of the individuals were pregnant or on contraceptives. All individuals were housed in large in- and outdoor enclosures (2,970 m² in total) containing several climbing structures, trees, bushes and ropes, puzzles from which they could acquire food, and small streams of water. To mimic natural fission–fusion behavior, bonobos were always housed in two separate groups that varied in composition regularly. All participants in this study were exposed to humans since birth and interacted with them daily. Their diet consisted of a variety of fruits, vegetables, branches and leaves, and pellets enriched with necessary nutrients. The bonobos were fed four to five times a day, and water was available ad libitum. Furthermore, bonobos were never deprived of water or food at any stage of the study.

Testing took place in the presence of nonparticipating group members and during winter when the park was closed for visitors. Bonobos were tested three to four times per week in one of the indoor enclosures, and one test session lasted ∼15–20 min per individual.

Tests with the bonobos were conducted adhering to the guidelines of the EAZA Ex situ Program (EEP), formulated by the EAZA. Bonobos participated voluntarily and were never separated from their group during testing. Only positive reinforcements (apple cubes) were used during training and testing, and each bonobo (including ones that were not tested) received a reward equivalent to the reward of the bonobo being tested. Nonparticipating bonobos were distracted by the animal keeper who conducted a body-part training task used for veterinary purposes.

Apparatus

The study was conducted using *Presentation* (NeuroBehavioralSystems) on an Iiyama T1931SR-B1 touchscreen (19 in., 1,280 × 1,024 pixels, ISO 5 ms) encased in a custom-made setup (Figure 1). To limit exposure to the researcher, rewards for correct responses were automatically distributed using a custom-made auto-feeder apparatus that dropped apple cubes into a funnel that ended underneath the touchscreen for the bonobo to grab. A camera was placed outside the enclosure to film the bonobos during the study.

Stimuli and Validation

Stimuli consisted of bonobo pictures collected in different zoos and from the internet. Stimuli of familiar individuals consisted of pictures of the group living in Apenheul, and unfamiliar stimuli depicted a small selection of individuals from five different zoos (Cologne Zoological Garden, ZOO Planckendael, Twycross Zoo, Cincinnati Zoo & Botanical Garden, and San Diego Zoo). We only included high-quality pictures in our sample (i.e., no pixelations and adequate lighting). In total, the study included 656 novel and unique pictures (346 pictures of familiar individuals and 310 pictures of unfamiliar individuals (Table S1 in the online supplementary materials). All pictures were resized to 330 × 400 pixels and showed either a neutral scene (i.e., individuals sitting or lying down or involved in a nonsocial activity, showing a neutral expression) or an emotional scene.

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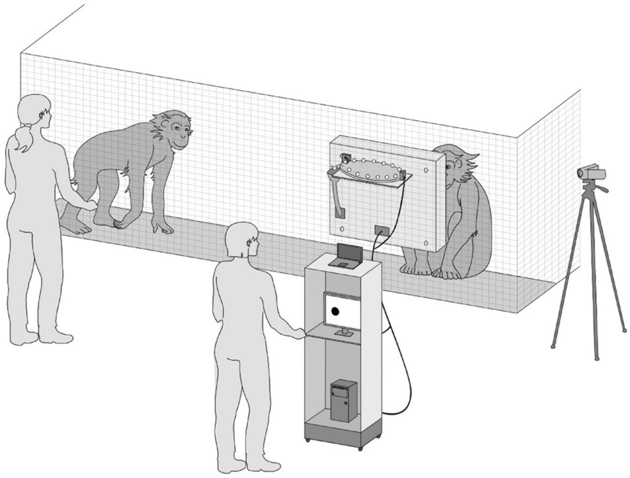
[1] We acknowledge that our sample size is limited compared to studies with humans. Nevertheless, it is in line with touchscreen-based experiments involving apes, which have an average sample size of four Egelkamp & Ross, 2019). Despite this limitation, we argue that comparative studies such as ours have scientific merit and provide crucial insights into the cognitive abilities of animals. This is especially true for bonobos, as they are a critically endangered species and rarely kept in zoos and sanctuaries (Fruth et al., 2016). Access to and testing of bonobos is very limited. To partly compensate for the low sample size, we maximized the number of trials per individual and make individuals' data available for future work.

Figure 1

Abstract Representation of the Bonobo Setup



Note. The researcher (right) controlled the study from behind the bonobo setup while a keeper (left) distracted the other bonobos. The researcher was not visible and remained silent to the bonobos most of the time, but the researcher would move to the side of the setup when an individual needed some encouragement to continue with the task. At the end of the task, the researcher and caretaker would say "good job" and "you are done" to the participating bonobo to indicate the end of the test. Bonobos were already familiar with these phrases.

While we currently do not fully understand what bonobo emotions entail, we rely on existing observational work to establish relevant socioemotional behaviors and expressions that may underlie emotional states. Here, the valence-arousal model by Russell (1980) can be used as a useful guideline. As positively valenced stimuli, we use socioemotional scenes of bonobos engaged in play, grooming, or sex. Furthermore, we included stimuli of bonobos showing signs of distress or that were self-scratching (negatively valenced, from now on: scratching) or yawning (unclear valence) as proxies of emotional states (see Table S2 in the online supplementary materials and Figure 2, for descriptions and examples). We used similar emotion categories as Kret et al. (2016) (but all novel images), with the exception that we included scratching as a new category and left out pant hoot and food-eating because these did not attract attention over neutral scenes in our previous study.

Play, grooming, and sex are important for establishing or maintaining social bonds (Moscovice et al., 2019; Palagi, 2008; Schroepfer-Walker et al., 2015) and may therefore reflect positively valenced behaviors (Furuichi, 2011). Play scenes involved playful interactions between two bonobos, or an individual playing with objects, and included the relaxed open-mouth ("play face") expression (Signe & Van Hooff, 2018). Grooming scenes involved grooming bouts between two or more individuals. Furthermore, sexual scenes displayed two or more individuals copulating or showing an erection (males) or a large genital swelling (females). Scenes showing distressed bonobos included one or more individuals displaying a fear grin that is typically produced by primates in distress (De Waal, 1988; Parr et al., 2007). Scratching scenes displayed one or two individuals scratching themselves on the head or body. Scratching is indicative of stress in both primates and humans (Troisi, 2002), and by incorporating it as an emotional stimulus, we increased the number of negatively valenced stimuli. Finally, yawning scenes showed one individual with an open mouth, with or without teeth exposure. It is unclear what emotional state may underlie yawning, for example boredom (Burn, 2017) or stress (Maestripieri et al., 1992; Paukner & Anderson, 2006), but it is a highly contagious behavior that could be a proxy for empathy (but see Massen & Gallup, 2017). Moreover, bonobos responded faster to probes replacing yawning stimuli than to probes replacing neutral stimuli in the study by Kret et al. (2016), and therefore we included it in our study.

We matched emotional and neutral scenes on the number of individuals depicted (ranging from 1 to 6), their identity, and by visually inspecting the color and luminance. All 12 bonobos in the Apenheul group were present in the familiar stimulus set, and we estimate the presence of 30 unique individuals in the unfamiliar stimuli. Furthermore, the pictures were cropped in such a way that the bonobos' faces and/or bodies covered most of the stimulus area. Backgrounds of the stimuli either showed a bit of grass or part of a tree, or, when the stimuli were of individuals in their inside enclosure, of a white-gray wall and sometimes a beam (part of the inside construction). All pictures were rated on emotional valence and intensity (arousal) by three primate experts from Apenheul and three primate researchers, who showed high intraclass correlations ($\mathrm{ICC}_{\mathrm{valence}} = 0.82$, $\mathrm{ICC}_{\mathrm{intensity}} = 0.87$ [Table S3 in the online supplementary materials]).

Procedure

The bonobos were already familiarized with the dot-probe procedure during a previous study (Kret et al., 2016), but did go through a short refamiliarization phase. We started with a 2-month training period (about seven sessions per ape, spaced across the 2 months) in which they performed a dot-probe task with pictures of black rabbits and goats. Only after all the apes were able to correctly pass 95% or more of the trials within one session, we moved on to the study. The criterion of a successful trial was to press the probe upon its appearance without hesitation, and while attending to the screen. To start a training or study session, we called forth the highest-ranking participating individual of the subgroup that was present in the enclosure. Nonparticipating bonobos (in both the refamiliarization phase and study) were distracted by the animal caretaker with a body-part training in which bonobos were instructed to present specific body parts to the animal caretaker and were rewarded with an apple cube for each correct presentation, just like the participating bonobos when they completed a trial. Importantly, bonobos were never separated from their group members, thus sometimes leading to disruptions during the study.

In the study, a trial started with the presentation of the start-dot in the middle, lower part of the screen (Figure 3). After the bonobo pressed the dot, a neutral and an emotional stimulus appeared on the left and right side of the screen for 300 ms (Kret et al., 2016, 2018; Petrova et al., 2013). Stimuli were always either of bonobos familiar to the participant or of unfamiliar individuals (thus, we never combined an emotional picture of a familiar with a neutral picture of an unfamiliar or vice versa). Stimuli were subsequently followed by another dot (the probe) replacing either the neutral or emotional stimulus. The probe remained on the screen until touched, after which an apple cube was provided through the auto-feeder system. After a delay of 2,000 ms, the next trial started.

Figure 2

Examples of Stimuli of all Emotional Categories That Were Used in Study 1

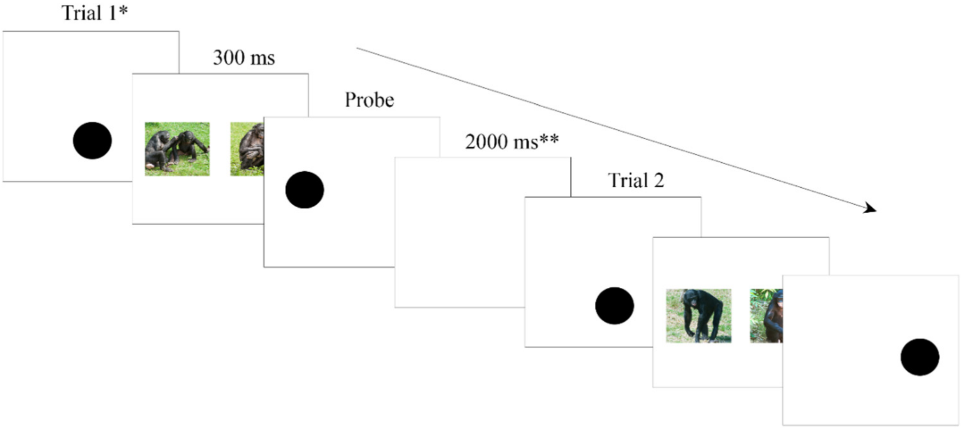
Note. An emotional picture was always paired with a neutral picture. This pair of pictures was always of either familiar or unfamiliar individuals. Thus, pictures of familiar and unfamiliar individuals were never presented together. Reprinted with permission. See the online article for the color version of this figure.

Each test session consisted of 25 trials in which the location of the stimuli on the screen (left/right) and the location of the probe (behind the emotional or neutral stimulus) were counterbalanced, and the order of stimulus presentation was randomized based on emotion category and familiarity. In each session, half of the trials consisted of emotional and neutral stimuli of familiar individuals, and half of emotional and neutral stimuli of unfamiliar individuals. If a trial was deemed unsuccessful, it was repeated at the end of the study. In total, each bonobo finished 1–2 sessions per test day (21–24 sessions in total) and on average 541 trials ($SD = 28.76$, Table S4 in the online supplementary materials).

From the recorded videos, two experts coded unsuccessful trials by looking at the following events: bonobos were distracted by other bonobos or did not attend to the screen, another individual pressed the probe, hands were switched within a trial, or bonobos performed movements that interfered with the task (scratching or nose wiping). The experts showed high agreement in coding ($\text{ICC} = 0.95$, $p < .001$).

Figure 3

Trial Outline of the Bonobo Dot-Probe Task



Note. After pressing a start-dot, an emotional and neutral stimulus pair of either a familiar or unfamiliar individual was presented for 300 ms. Next, a probe replaced one of the two stimuli. During the intertrial interval of 2 s, bonobos were rewarded for their response. See the online article for the color version of this figure.

* Trials contained either familiar or unfamiliar emotional and neutral individuals.

** In case of a correct response, a food reward was automatically provided.

Data Filtering

Based on the coding of the two experts, erroneous trials were discarded. Moreover, extreme reaction times ($RT < 250$ ms and $RT >$ 5,000 ms) were filtered out. Finally, trials with RTs higher than the median RT per subject minus 2.5 × the median absolute deviation per subject were excluded. Based on these criteria, 514 trials (23.8%) were removed from the analysis. (The majority of these invalid trials [90%] were caused by bonobos being distracted or other individuals interfering in the task. See also Table S4 in the supplementary materials.) Therefore, we had a final number of 1,650 data points (~413 per condition). We note that this is less than has recently been recommended for performing mixed model analyses (Brysbaert & Stevens, 2018), but is in line with most other dot-probe studies (Van Rooijen et al., 2017).

Statistical Analysis

We used a generalized linear mixed model (R studio [v1.4.1106], glmmTMB package, $\alpha = 0.05$; Magnusson et al., 2017; R Core Team, 2020) for the analyses, with a nested structure defined by trials nested within sessions nested within participants. We included *Congruency* (the probe replaced an emotional [congruent] or neutral [incongruent] stimulus, sum-coded) and *Familiarity* (familiar vs. unfamiliar bonobos, sum-coded), and their interaction terms as fixed factors, and used random intercepts per *ID* and *ID* × *Session*. Reaction time was used as the dependent variable. To determine which distribution family provided the closest fit to the observed data, we compared AIC statistics of models with a normal and gamma distribution (Lo & Andrews, 2015). Model assumptions were checked by visually inspecting quantile-quantile (QQ) plots and the residuals plotted against fitted values.

Results

We aimed to replicate and extend previous findings by Kret et al. (2016) and tested for a possible interaction between familiarity and emotional attention in bonobos. Using a generalized linear mixed model with a gaussian distribution (i.e., $AIC_{normal} < AIC_{gamma}$, see Table S5.1 in the online supplementary materials), we found a significant interaction effect, $\chi^2(1) = 4.14$, $p = .042$; bonobos responded faster on probes replacing emotional ($M = 521.11$, $SD = 131.50$) rather than neutral scenes ($M = 529.84$, $SD = 127.13$) in the *Unfamiliar* condition, $\beta = -10.48$, $SE = 5.13$, $t(1641) = -2.05$, $p = .041$, but not in the *Familiar* condition, $\beta = 4.59$, $SE = 5.35$, $t(1641) = 0.86$, $p = .391$ (see Figure 4 and Table S5.2–5 in the online supplementary materials for individual averages and further model results). In short, familiarity with the expressor of an emotion significantly modulated attentional bias toward emotions, with responses to emotional scenes being faster than responses to neutral scenes when they involved unfamiliar, but not familiar conspecifics.

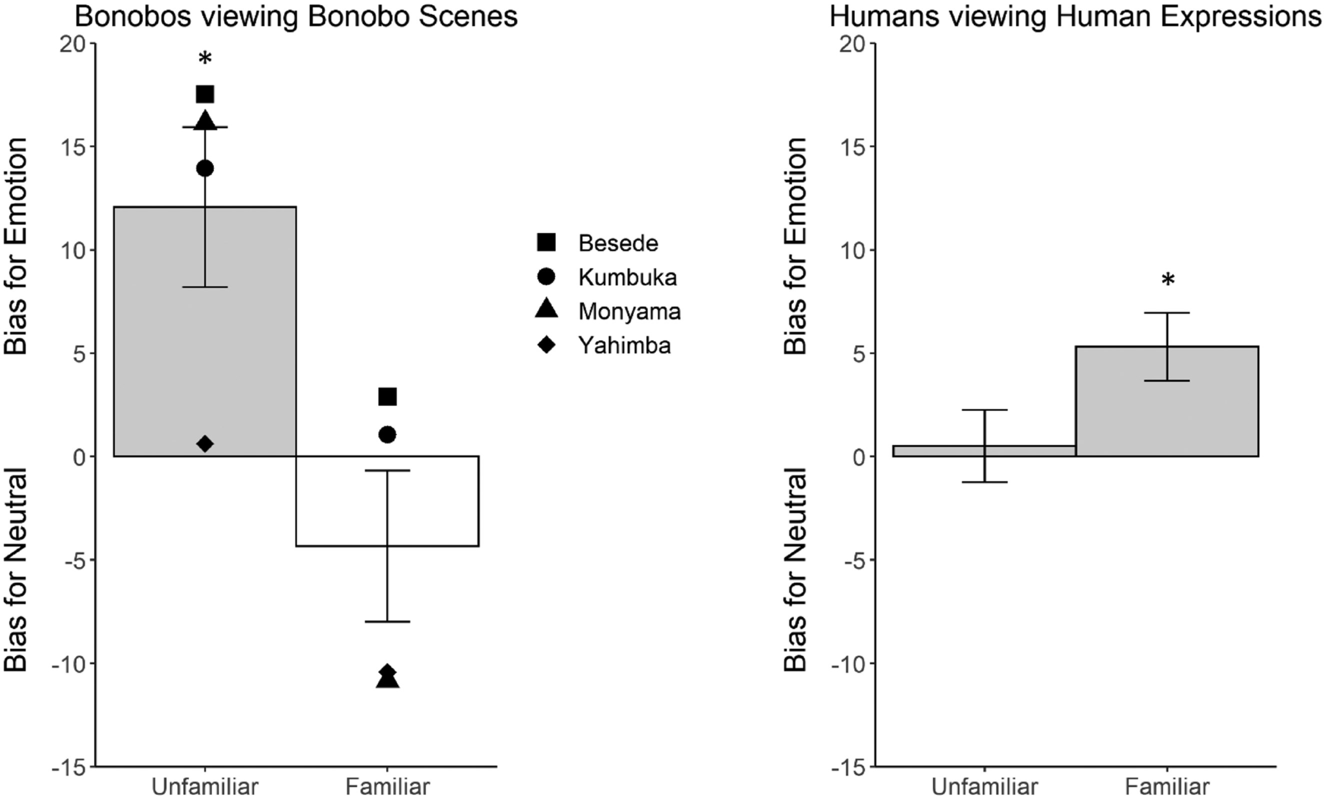
Discussion Study 1

Previous research has shown that bonobos have heightened attention to the emotional expressions of unfamiliar conspecifics, especially when these were rated as emotionally intense by their keepers (Kret et al., 2016). The current study builds on this research. Specifically, by adding photographs of group mates to the stimulus materials, Study 1 showed that familiarity with the expressor has a modulating effect on an attentional bias toward emotions; early attention appears to be modulated mostly by emotional expressions of unfamiliar individuals, but not familiar individuals. This novel finding largely confirms our a priori predictions that were based on previously conducted behavioral studies in bonobos highlighting their strong xenophilic tendencies and other-regarding preferences (Fruth & Hohmann, 2018; Tan et al., 2017; Tan & Hare, 2013; Tokuyama et al., 2021). Attention can be driven by the biological relevance of the emotional signal to the observer, for instance by the presence of dangerous animals such as snakes (Öhman, Flykt, & Esteves, 2001). It is thought that for bonobos, the benefits of bonding with new individuals outweigh the costs, thereby making socializing with unfamiliar conspecifics beneficial (Hare et al., 2012). In turn, these interactions may enhance survival by promoting cooperation among individuals (Tan et al., 2017). Although we have to be careful with generalizations given our small, female-only sample, our results appear to support this notion and suggest that the brains of (female) bonobos developed to selectively attend to emotional signals from potentially interesting unfamiliar social partners.

At the same time, it is interesting that there is no effect of emotion in the familiar condition. A recent eye-tracking study by Lewis et al. (2021) showed that bonobos attended longer to familiar group members rather than unfamiliar bonobos, indicating that seeing familiar individuals interests the bonobos. It is possible that when viewing familiar individuals, the effect of emotional expressions on attention is further affected by preexisting knowledge about those individuals. Other research indeed suggests that the social characteristics of the observer in relation to the observed individual(s) may play a role in how emotions are processed. For instance, attention can be modulated by sex (Schino et al., 2020), the social bond (Kutsukake, 2006; Whitehouse et al., 2016), rank (Lewis et al., 2021; Micheletta et al., 2015; Schino & Sciarretta, 2016), and kinship (Schino & Sciarretta, 2016). The current study sample did not allow us to disentangle the potential effects of social characteristics on an attentional bias toward emotions, but doing so in a new study would be a useful next step. Another explanation for why an attentional bias toward the emotional expressions of familiar conspecifics was not observed could be that familiar and unfamiliar conspecifics were shown within the same study (but note: not within the same trial). The emotional expressions of unfamiliar conspecifics may be of such high relevance for bonobos, that it rendered a bias toward expressions of kith and kin insignificant. Another alternative explanation for our findings is that results are driven by heightened novelty of the unfamiliar stimuli (Bradley, 2009). However, we could rule this out, because bonobos on average responded as fast to stimuli of unfamiliar (novel) as of familiar individuals. A worthwhile follow-up study is to directly compare familiar and unfamiliar individuals (emotional and neutral) within trials to disentangle the effects of emotion and familiarity (as has recently been done by Leinwand et al., 2022 using human stimuli). In addition, studying an attentional bias toward emotions of familiar and unfamiliar individuals in chimpanzees could be a fruitful next step. While chimpanzees and bonobos are very closely related to each other and equally closely related to humans, differences in social organization (with females as the dominant sex in bonobos, and males in chimpanzees), and social tolerance (chimpanzees are highly territorial) may also differentially affect where attention is allocated.

Figure 4

Overview of the Results of Study 1 and 2



Note. Study 1: Bonobos show an attentional bias toward emotions of unfamiliar, but not familiar conspecifics (left). Study 2: Humans have an attentional bias toward the emotional expressions of familiar others (right). To illustrate an attentional bias, we calculated the difference between mean reaction times (RTs) on neutral scenes minus mean RTs on emotional scenes per condition (Unfamiliar, Familiar). Bars in the positive direction indicate a bias toward emotional scenes or expressions rather than to neutral scenes or expressions. Error bars represent the SEM. $*p < .05$.

Indeed, Lewis et al. (2021) showed that bonobos preferentially attend to familiar, high-ranking females rather than unfamiliar females, whereas chimpanzees attend to familiar high-ranking males. We believe the study by Lewis et al. (2021) and ours complement each other in showing that at least for bonobos, seeing familiar conspecifics brings along a range of potentially relevant social information such as rank and emotional expressions that in turn may modulate attention differently. Furthermore, Leinwand et al. (2022) showed that chimpanzees (and gorillas) have an attentional bias toward unfamiliar humans with a neutral expression compared to familiar humans, whereas they do not have a bias toward unfamiliar or familiar humans when they show a surprised expression. Combined, the existing findings show a modulating role for familiarity and emotional expressions, but biases may be informed by species-specific characteristics and by the model species on the stimuli. Therefore, we believe an interesting next step would be to study more closely how familiarity with the expressor modulates attention for emotions across different great-ape species. Furthermore, findings by Leinwand et al. (2022) show it may be interesting to also include expressions of familiar and unfamiliar individuals of a different great-ape species, for instance to gain insight into (dis)similarities in emotional expressions across the great-ape family.

Study 2: Humans' Attentional Bias Toward Emotions of Conspecifics

In Study 2, we investigated to what extent familiarity modulates attention for emotions in a large community sample of human zoo visitors.

Method

Participants

We recruited pairs of individuals to either take part in the dot-probe task or to be on the photographs used for the *familiar* stimuli. Participants thus consisted of those partaking in the dot-probe task ($n = 449$, 196 men and 253 women), or were the to-be photographed companions ($n = 406$, 208 men and 198 women. Note that for 43 companions, data on sex and age were missing due to a technical malfunction). Participants were adults and children (Dot-probe participants: 262 adults, 187 children. Companions: 218 adults, 188 children) visiting primate park Apenheul in Apeldoorn, the Netherlands. Dot-probe participants were between 3 and 84 years old ($M = 24.9$, $SD = 16.43$), and companions were between the ages 3 and 79 ($M = 25.43$, $SD =$

17.22). Apenheul allowed us to set up a research corner close to the bonobo enclosure where we could test the visitors (Figure 5). As bonobos were only exposed to group members (kin and friends) in *familiar* trials, our human participants were also selected based on their relationship with their companions (kin and friends or colleagues. see Table S6.1 and S6.2 in the online supplementary materials for an overview of relationships). The study was approved by the ethics committee of Leiden University (adults: #2017-07-24-M.E.Kret-V1-765, children: #2017-08-29-M.E.Kret-V1-781).

Apparatus

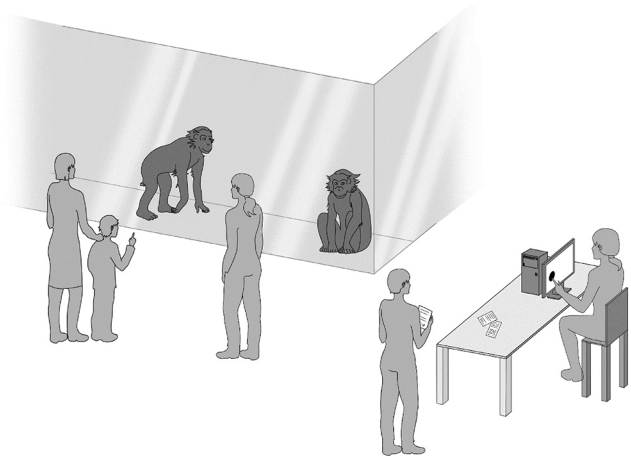
Participants performed the study on an Iiyama T1931SR-B1 touchscreen (19 in., 1,280 × 1,024 pixels, ISO 5 ms) using E-Prime 2.0. The tests were conducted in an indoor compound in which visitors could see the bonobos. The touchscreen was placed on a table and participants were seated with their backs against a wall to prevent others from distracting them (Figure 5).

Stimuli and Validation

For our human participants, rather than emotional scenes, we used isolated facial expressions as stimuli. This was done for practical reasons, as we could not ask zoo visitors to enact specific social scenes like the bonobo scenes. For humans, there is evidence for an attentional bias toward emotions using only facial expressions (Van Rooijen et al., 2017), but also for emotional scenes (Kret & van Berlo, 2021). Similarly, while a dot-probe study with bonobos found an attentional bias for emotional scenes (Kret et al., 2016), other studies found that isolated facial expressions can also modulate attention in apes (Laméris, Verspeek, et al., 2022; Pritsch et al., 2017). As such, we did not expect the discrepancy between the bonobo stimuli and human stimuli to significantly impact the outcomes of both studies.

Figure 5

Abstract Representation of the Human Setup Near the Bonobo Enclosure



Note. Participants were seated with their backs against a wall and facing a part of the bonobo enclosure.

Stimuli consisted of pictures of the face showing either an emotional (angry, fearful, happy, sad) or neutral expression presented against a neutral background. Each stimulus showed either a familiar companion (a family member, a close friend, or a colleague) or an unfamiliar individual (a companion of a previous, unfamiliar participant). We only used four out of the six basic emotions (Ekman, 1999), as the task would become undesirably long given that our participants were voluntarily taking part in our study. The pictures were sized 400 × 300 pixels.

Each participant completed 40 trials. In 20 trials, the probe appeared behind an emotional stimulus and in the other 20 trials, it appeared behind a neutral stimulus. For each of these 20 trials, 10 trials depicted a familiar individual, and 10 trials an unfamiliar individual. Since we only had eight unique photos of a familiar other as well as eight unique photos of a stranger, we repeated two stimulus pairs within each condition to reach the maximum of 40 trials. The number of stimuli per emotional category was counterbalanced across participants (including the repetitions), and stimulus combinations (emotional plus neutral) were presented in a semi-randomized order.

A total of 4,040 pictures were split into three sets and rated on intensity, emotionality (whether a stimulus depicts an emotional or neutral expression), and authenticity by 18 university graduates and PhD candidates, and on average there was good agreement ($ICC_{intensity} = 0.80$, $ICC_{emotion} = 0.80$, and $ICC_{authenticity} = 0.68$, see Table S7.1–4 in the online supplementary materials).

Procedure

Visitors passing by the bonobo enclosure with at least one other person were approached by the researchers. Visitors were told about the ongoing research with the bonobos and were asked if they wanted to take part in a similar study. If they wanted to participate, the researchers decided which participant was going to perform the dot-probe task (“dot-probe participant”) and who was going to be on the photos that subsequently served as stimulus material (“photo participant”). Individuals could only participate in the study once (and either as a dot-probe or photo participant).

After reading the information sheet and signing a consent form, photos were made of the photo participant outside of the view of the dot-probe participant. Photos were taken on the same spot near the test location, around the corner, and against a background with a brick wall. The participant was asked to express one of each of the four emotions (angry, fearful, happy, sad), based on an example from Model 1 from the NimStim database (Tottenham et al., 2009) printed on a sheet of paper. After each emotional expression, the participant was asked to show a neutral expression. This prevented the use of the same neutral photo across all trials and ensured some variation in the neutral expressions. As such, eight unique photos were taken (four emotional, four neutral). Low-quality photos were retaken on the spot.

Next, the pictures were loaded into the software (which automatically handled the resizing of stimuli), and the dot-probe participant was then seated behind the touchscreen. The researcher entered personal data (age, handedness, sex of both the dot-probe and photo participant, the nature of their relationship, and how often they typically saw each other; Tables S6.1 and S6.2 in the online supplementary materials). The instructions for the task were kept to a minimum, as the bonobos could also not receive written or verbal instructions.

The researcher told the participant that they would see a dot appear on the screen and that they would have to touch the dot as soon as it appeared by using only their dominant hand. The task started with the pictures of the four bonobos participating in Study 1, with the text "Are you faster than the bonobos? Press anywhere on the screen to continue." After three practice trials that included pictures of flowers, the participants saw a display asking them whether they understood the task and were reminded of using only one hand during the task. Participants could then move on to the study (Figure 6) by pressing the red dot on the screen. After completing all 40 trials, participants would see a screen depicting their average reaction time and how it compared to that of the bonobos. The location of the stimuli on the screen (left/right) and the location of the probe were counterbalanced, and the stimuli were presented in a randomized order. The whole procedure took about 15–20 min to complete.

Data Filtering

We filtered RTs with extreme values (i.e., RT $<$ 250 ms and RT $>$ 5,000 ms). As our dataset contained a large age range, we also filtered RTs per age category (0–5, 6–10, 11–15, …, 56–60, 61–85) and calculated the median absolute deviation for RTs per age category. Finally, we used the following filter: RT $<$ (Median RT $+$ [2.5 $\times$ Median absolute deviation]). After applying this filter, five participants had less than 5% of data points left and were thus excluded from further analysis, leading to a final *N* of 444. In total, we excluded 15.25% of the data from further analysis.

Statistical Analysis

Data were analyzed using a generalized linear mixed model in R studio (v1.4.1106, glmmTMB package, $\alpha = 0.05$; Magnusson et al., 2017; R Core Team, 2020), with trials nested within participants. We used reaction time (ms) as the dependent variable, random intercepts for all participants, and used *Congruency*, *Familiarity* (both sum-coded), and their interaction terms as fixed factors. Moreover, we used the AIC statistic to determine which distribution (gaussian vs. gamma) fit our data best (Lo & Andrews, 2015). Model assumptions were checked by visually inspecting QQ plots and the residuals plotted against fitted values.

Results

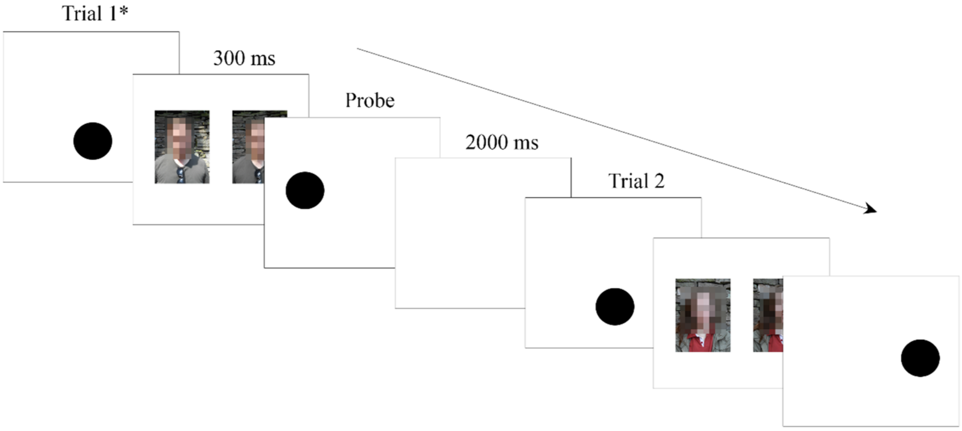
Testing whether humans have an attentional bias toward emotions of familiar and unfamiliar others, we found a significant interaction effect between *Congruency* and *Familiarity*, $\chi^2(1) = 3.47$, $p = .047$ (Figure 4 and Table S8.1–5 in the online supplementary materials). Planned comparisons showed that participants were significantly faster when a probe replaced an emotional stimulus ($M = 563.78$, $SD = 116.89$) versus a probe replacing a neutral stimulus ($M = 568.89$, $SD = 121.66$) in the *Familiar* condition, $\beta = -.01$, $SE = 0.00$, $t(16943) = -2.72$, $p = .007$, but not in the *Unfamiliar* condition ($p = .936$, see Table S8.1–5 in the online supplementary materials). See Table S9 in the online supplementary materials for an exploratory analysis of sex and familiarity effects on attentional bias toward emotions. Combined, the findings show that emotional cues from familiar individuals influence a bias for the emotions of unfamiliar individuals.

Discussion Study 2

In Study 2 using a large community sample, we show that human attention is modulated by the emotional expressions of family members and friends. Traditionally, emotional attention is studied using stimuli that depict unfamiliar individuals only. Here, we show that familiarity with the expressor in terms of their social or familial relationship differentially affects immediate attention to emotions in humans. Humans have a strong affinity with their social group and often choose to associate with others who are similar to themselves in some respect (Brewer, 1979). This tendency to focus on one's in-group is likely to be adaptive, as it bolsters cooperation between individuals within the same group, which subsequently provides protection from danger such as competitors (Bowles, 2009). As such, our results contribute to the existing literature by showing

Figure 6

Trial Outline for the Human Dot-Probe in Study 2



Note. Similar to the bonobo study, the task started with a start-dot, followed by the presentation of an emotional and neutral stimulus of a familiar or unfamiliar individual, of which one was replaced with the probe. The intertrial interval was 2 s. See the online article for the color version of this figure.
* Trials contained either familiar or unfamiliar emotional and neutral individuals.

that an intergroup bias likely already presents itself early on in social perception, and guides attention to emotions of socially close others.

Interestingly, we did not find evidence for an attention bias toward the emotions of unfamiliar individuals, even though this is commonly reported in the literature (Van Rooijen et al., 2017). The presence of familiar individuals within the same study may dampen the focus of attention on the emotional expressions of unfamiliar others (and, for bonobos in Study 1, the reverse might be true). Possibly, the social relevance of the stimuli interacts with detecting emotional expressions, prompting stronger activation of attentional and emotional brain mechanisms than when viewing emotions of less-relevant others. Indeed, the social relevance of the individuals on the stimuli in relation to the observer likely impacts attentional mechanisms (Wirth & Wentura, 2019). One example of this is that an attentional bias toward threatening stimuli such as angry faces is more pronounced in people with high anxiety compared to individuals with low anxiety, and sometimes not even observed in non-anxious people (Bar-Haim et al., 2007). As the relevance of stimuli can be determined by a range of factors including personal goals, values, and needs (Brosch et al., 2008; Pool et al., 2016), it could be interesting to explore these factors and how they affect attention in more detail in a comparative framework in the future.

General Discussion

Emotional expressions are pivotal to understanding the internal state of others and predicting their future behavior, and as such, receive privileged access to attention (Adolphs, 2008; LeDoux, 1998; Öhman, Lundqvist, & Esteves, 2001). Crucially, emotions can arise in social situations involving close others, yet are rarely studied in this context. In this study, we investigated the potential link between emotional attention and familiarity with the expressor in two closely related species: humans and bonobos. In Study 1, the attention of bonobos appeared to be attuned to emotional scenes depicting unfamiliar others, but not to emotional scenes depicting familiar others. For our human zoo-visitor sample in Study 2, we found that emotional expressions of familiar companions (family, friends, or colleagues), but not unfamiliar others, modulate attention. Below we discuss these results within a comparative framework and consider the limitations of the two studies.

Humans and bonobos seem to share an immediate bias for emotional scenes and expressions (Kret et al., 2016; Kret & van Berlo, 2021) and we here show that this bias is modulated by familiarity. Interestingly, studies with chimpanzees (Kret et al., 2018; Wilson & Tomonaga, 2018) and our study with orangutans (*Pongo pygmaeus*) (Laméris, van Berlo, et al., 2022) did not find a bias for emotions using the dot-probe paradigm. No data exist on gorillas. It is possible that, compared to other apes, bonobos are more sensitive to emotions, evidenced by their strongly connected brain pathways involved in emotion processing (Issa et al., 2019; Stimpson et al., 2016). However, three dot-probe studies with more distantly related primates (rhesus macaques, *Macaca mulatta*) did find an attentional bias toward threatening faces of conspecifics (King et al., 2012; Lacreuse et al., 2013; Parr et al., 2013). Moreover, looking-time paradigms have shown that chimpanzees, orangutans, and rhesus macaques looked longer at (negative) emotional expressions than to neutral expressions (Bethell et al., 2012; Howarth et al., 2021; Kano & Tomonaga, 2010; Pritsch et al., 2017). Overall, these findings suggest that an attentional bias toward emotional signals is shared at least within the primate order (and potentially also in other animals, although results are mixed; Kremer et al., 2021; Lee et al., 2018; Luo et al., 2019).

The brain is proficient at distinguishing between faces of familiar, socially close others and strangers, evidenced by the prioritized and highly optimized processing of familiar faces (Ramon & Gobbini, 2018). Here, we have shown that familiarity further interacts with the processing of emotional expressions at a very early stage of visual attention. Moreover, our findings also suggest that *how* familiarity interacts with the processing of emotional expressions can depend on species-specific characteristics, such as other-regarding tendencies. While humans and bonobos are both social species, humans tend to prefer the social in-group over the out-group (Fehr et al., 2008), whereas bonobos are known to preferentially share food with out-group members (Hare & Kwetuenda, 2010) and peacefully interact with them (Furuichi, 2011). How familiarity with and emotions of conspecifics modulate attention has not yet been studied in other species, but chimpanzees would be an interesting comparison species as they typically empathize with group members but not with unfamiliar chimpanzees (Campbell & De Waal, 2014; Wilson & Wrangham, 2003) and gaze longer at familiar rather than unfamiliar males (Lewis et al., 2021). As such, one hypothesis could be that chimpanzees have a stronger attentional bias toward emotional expressions of familiar conspecifics than of unfamiliar individuals.

Studies on emotion perception and attention in the other great apes—gorillas and orangutans—are, to the best of our knowledge, rare, but are very important to improve our understanding of how evolution shaped emotion processing in the great-ape family. Gorillas and orangutans have unique social systems, with gorillas living in harem-like societies with one adult male and multiple females and their offspring (Robbins et al., 2004) and orangutans living a semisolitary life (Singleton et al., 2009). While we did not find an emotion bias in orangutans in another study (Laméris, van Berlo, et al., 2022), previous work shows that they look longer at negative facial expressions (Pritsch et al., 2017) and automatically mimic facial expressions (Davila-Ross et al., 2008), but that mimicry is not necessarily affected by familiarity (van Berlo et al., 2020). Furthermore, gorillas are known to affiliate less frequently with conspecifics than for instance chimpanzees (Cordoni et al., 2018), but they do appear to mimic facial expressions, specifically the play face that occurs during playful interactions (Bresciani et al., 2021). We currently do not have clear predictions on how familiarity might modulate emotional attention in these species, but given the existing evidence, an immediate bias toward emotional expressions may only be present in species that have high affiliative tendencies (like bonobos, chimpanzees [but see Kano & Tomonaga (2010) and Kret et al. (2018)], humans, and some monkey species), given that they continuously need to monitor behaviors of others in the group. Again, more research is needed to pin down differences between different species' attention allocation to emotional expressions, and how these interact with social factors such as familiarity.

The results of our studies should be viewed in light of their limitations. The most pertinent one is the disparity between our bonobo and human sample size. Unfortunately, comparative studies often suffer from low sample sizes due to the limited access to individuals and the major efforts and resources that are necessary to conduct noninvasive studies with animals. Indeed, a recent overview of touchscreen-based studies with great apes in zoos shows an average sample size of four (Egelkamp & Ross, 2019). Nevertheless, the findings are still valuable for improving our understanding of our evolutionary roots and great apes' sociocognitive competencies (similar to how findings in one or two patients with unique brain lesions have been crucial for understanding the neuroscientific foundations of emotion recognition [e.g., Adolphs et al., 1994]). In our study, we partly replicate earlier findings by Kret et al. (2016), showing that using the dot-probe task can lead to reliable results. We also report individual means (see the online supplemental materials) in the hopes that these data can eventually lead to combined datasets for future examinations of great-ape (social) cognition.

A second limitation is that we were only able to test female bonobos. For ethical reasons, we did not separate individuals from the group while testing. The females were eager to participate and did not allow the males behind the screen, thus the three potential male subjects could not be tested. Nevertheless, this makes it difficult to generalize our findings. For instance, there may be sex differences in attentional biases for emotions, and in humans, there is some evidence for this idea (for a review, see Kret & De Gelder, 2012). Nevertheless, we did not find any effect of sex of the participant performing the dot-probe and sex of the individual on the stimuli in Study 2 (Table S11 in the online supplemental materials). We recently also conducted a dot-probe study involving human emotional scenes (rather than faces), and found no sex differences in attentional bias toward emotional scenes (Kret & van Berlo, 2021). Yet, two primate studies did show that sex can impact attention allocation (Lewis et al., 2021; Schino et al., 2020). It, therefore, remains possible there are sex differences in bonobos' attention to emotions that we could not capture in our study.

Other limitations in our studies involve the differences between the configuration of the stimuli used for bonobos (emotional and neutral scenes) and humans (emotional and neutral faces), the emotional categories (socioemotional categories in bonobos, emotional facial expressions in humans), and the number of unique individuals in the stimulus set (human participants saw only one familiar and one unfamiliar individual, whereas bonobos saw multiple unique individuals). These discrepancies are important to consider but the studies do allow for a qualitative comparison of the results. To the best of our knowledge, this study is the first to look at the modulating effects of familiarity (i.e., kin and friends) on attention for emotions of conspecifics. Thus, we opted to base our study designs on existing literature on attentional biases for emotional facial expressions in humans (see Van Rooijen et al., 2018, for a review) and emotional scenes in bonobos and chimpanzees (Kret et al., 2016, 2018).

Finally, while our results extend previous findings by Kret et al. (2016), the average difference between emotional and neutral trials in the unfamiliar condition is numerically smaller than the difference reported by Kret and colleagues (i.e., about 9 ms in our study vs. 34 ms in the original study). This is likely due to crucial methodological differences. First, the trials in the original study by Kret et al., (2016) paired emotional or neutral bonobos with control animals (sheep or rabbits). To directly test how emotional and neutral scenes compete for attention, in the current study, we chose to present emotional and neutral stimuli within the same trial. Second, Kret et al. (2016) used slightly different categories, that is, eating and panthoot, but these categories did not elicit an attentional bias and thus were replaced by scratching in our study. Third, our design also included stimuli of familiar individuals, which likely attenuated the effect we found for unfamiliar individuals.

To conclude, our study contributes to the understanding of how evolution may have shaped other-regarding preferences of bonobos and humans by showing that they are deeply ingrained in early social perception and, crucially, are shared between the species. The results also demonstrate that *how* familiarity modulates emotional attention can differ between species. Importantly, differences in the environments of bonobos and humans may have helped shape the striking differences in how bonobos and humans attend to the emotions of familiar and unfamiliar others. It could therefore be interesting for future work to examine the link between emotional attention and familiarity in a wider range of species, progressing our understanding of the origins of the social mind.

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Received May 20, 2020
Revision received November 3, 2022
Accepted November 7, 2022 ■