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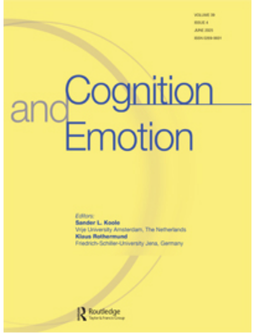

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Priming using human and chimpanzee expressions of emotion biases attention toward positive emotions

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ABSTRACT
Perceiving and correctly interpreting emotional expressions is one of the most important abilities for social animals' communication. It determines the majority of social interactions, group dynamics, and cooperation – being highly relevant for an individual's survival. Core mechanisms of this ability have been hypothesised to be shared across closely related species with phylogenetic similarities. This study explored homologies in human processing of species-specific facial expressions using eye-tracking. Introducing a prime-target paradigm, we tested the influences on human attention elicited by priming with differently valenced emotional stimuli depicting human and chimpanzee faces. We demonstrated an attention shift towards the conspecific (human) target picture that was congruent with the valence depicted in the primer picture. We did not find this effect with heterospecific (chimpanzee) primers and ruled out that this was due to participants interpreting them incorrectly. Implications about the involvement of related emotion-processing mechanisms for human and chimpanzee facial expressions are discussed. Systematic cross-species-investigations of emotional expressions are needed to unravel how emotion representation mechanisms can extend to process other species' faces. Through such studies, we can better understand the implications of humans' and apes' shared evolutionary ancestry and better understand "*Where our emotions come from*".

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Emotional priming; chimpanzee; eye-tracking; cognition; attention

Introduction

The ability to perceive and interpret emotional expressions is a cornerstone of social communication among animals, playing a critical role in determining inter-individual interactions, group dynamics, and cooperation – all of which have a direct impact on survival (Bourjade, 2017). While the importance of emotions in regulating and navigating the lives of social species is well established (Hooff, 1972), much research has focused on how humans process facial expressions within their own species, and relatively little is known about how humans interpret emotional cues from other species. In this study, we aimed to investigate how humans discern emotional expressions in one of their closest evolutionary relatives, the chimpanzee (*Pan troglodytes*), and how these expressions influence attentional biases compared to human facial expressions.

The universality of emotions and their expression across species has been debated since Darwin's seminal work on emotional evolution (Darwin, 1972). Darwin proposed that humans and other animals exhibit emotional states through remarkably similar facial and bodily actions, which may reflect shared evolutionary roots. Further supporting this notion, the facial musculature of chimpanzees is

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nearly identical to that of humans, enabling them to activate complex combinations of facial muscles, known as action units (AUs), that closely resemble human facial expressions musculature (Parr & Waller, 2006; Vick et al., 2007). Notably, chimpanzees show minimal individual variation in facial muscles involved in producing basic emotional expressions (Waller et al., 2008), which underscores the evolutionary continuity in the mechanisms of emotion expression.

Despite these similarities, it remains unclear to what extent humans can translate their internal representation of emotions to interpret expressions in heterospecifics. Based on the theory of emotion universality and facial expressions having an innate basis leading to a stereotypical appearance, evolutionary closely related species should be able to process each other's facial expressions. If faces of different species that roughly share the spatial arrangement of face elements (eyes, nose, mouth, etc.) are associated with one and the same face prototype, the formation of emotion representations and the correct interpretation of these may be facilitated (Pollick & de Waal, 2007). Hence, a particular expression in two different species would, in this case, be classified as homologous and assigned to the same category, presumably eliciting similar reactions in the observer. Using the first objective and standardized instrument (ChimpFACS) salient expressions communicating agonistic and affiliative affective states have been validated with a fair degree of certainty in the chimpanzee (Vick et al., 2007). However, comparative studies on how humans perceive and respond to emotional expressions from other species yield mixed results. While some studies suggest that affective stimuli from heterospecifics can elicit similar attentional and physiological responses as conspecific stimuli (Dufour et al., 2006; Parr et al., 1998), others show a clear advantage in the processing and understanding of conspecific facial expressions (Hattori et al., 2010).

From an evolutionary perspective, the human brain is tuned to prioritise attention to socially relevant stimuli, particularly those that signal threat or affiliation (Vuilleumier, 2005; Wilson et al., 2022). For example, threatening faces are detected more quickly in visual search tasks, suggesting that attentional mechanisms are biased toward cues of evolutionary importance. However, in environments where positive events outweigh negative consequences, attention may shift toward positive stimuli, as described by Fredrickson's broaden-and-build model, which posits that positive emotions temporarily broaden an individual's thought-action repertoire (Fredrickson, 1998; Wadlinger & Isaacowitz, 2006). These shifts in attention are often studied using semantic prime-target paradigms, where a primer stimulus influences the perception and reaction to a subsequent target (Carroll & Young, 2005; Higgins et al., 1985). In this study, we build on this framework to explore the bidirectional priming effects of emotional expressions across species. Previous studies have demonstrated that facial expressions can act as direct elicitors of affect, regardless of whether the representations are verbal or nonverbal (Carroll & Young, 2005).

Building on the parallels between chimpanzee and human facial structures, we propose that emotional primers depicting chimpanzee expressions have the potential to modulate attentional shifts in humans. Nonetheless, due to the evolutionary advantages associated with conspecific processing, we anticipate that priming effects will be more pronounced for human emotional expressions.

This study seeks to elucidate how emotional primers, varying in valence and species origin, influence attentional biases toward emotional target stimuli. Specifically, we hypothesise:

H_1: Priming with emotionally valenced faces (positive and negative), compared to neutral faces of both species (i.e. humans and chimpanzees) introduces an attentional bias towards the emotion representations on the target screen.

H_2: The direction of the attention shift depends on the congruency with the primer valence. Attention is shifted towards the stimulus on the target screen that is congruent with the valence previously presented in the primer picture.

H_3: The elicited attentional bias is larger upon seeing pictures of conspecifics compared to seeing heterospecifics.

By examining these effects, we aim to deepen our understanding of the mechanisms underlying cross-species emotion recognition and their influence on attentional processes.

Methods

Participants

A total of 50 participants recruited at Leiden University took part in the eye-tracking experiment after filling in the informed consent. The required number of participants was determined by a power analysis (see Supplementary Material I). The participants were reimbursed with course credit. The sample consisted of 30 women and 20 men with an average age of 26.5 years old (*SD* = 6.59). All participants had normal or corrected-to-normal vision and no history of clinically diagnosed psychiatric or neurological conditions. Participants' pet ownership or familiarity with animals was not assessed, as the primary objective was to study responses to species with limited direct exposure (chimpanzees). Data were collected in June 2022. The procedure and methods were approved by the Leiden University Ethics Committee (CEP: 2022-02-20-M.E. Kret-V1-3988).

Stimulus material

The human face stimuli were taken from the validated Chicago Face Database (CFD), while the chimpanzee face stimuli were collected from different resources such as researcher's archives, animal photographers' work, and the iNaturalist webpage for uploading high-quality pictures of different species, suitable for research purposes. Chimpanzee stimuli were selected and validated based on classification ratings by both experts and non-experts to ensure consistent association with valence categories (positive or negative). For the purposes of this study, these stimuli were categorised based on their perceived valence rather than specific emotional nuances. The stimuli set that was used for the primer pictures contained 18 unique primer pictures for each of the six conditions, resulting in 108 primer pictures in total. No primer pictures were re-used as target stimuli.

Since each trial required an affiliative and an agonistic picture of a human for the target screen, our stimulus set for the targets consisted of (108 trials * 2 valences) 216 target pictures in total. We could have had 216 unique target pictures depicting human emotional expressions, however, due to the limited resources of emotional stimuli of chimpanzees, we were not able to entirely avoid repetition of the emotionally valenced target pictures in this group. The additional material was also taken from the Chicago Face Database. Thus, we added 27 extra pictures of positively and 27 extra pictures of negatively valenced human emotional expressions to our stimulus set which were repeated 4 times during the trials (27 pictures * 2 valences * 4 repetitions = 216). To account for this limitation, we made sure that 1) there is no overlap between the primer and one of the target pictures within the same trial 2) the target does not contain any picture from the previous and the next trial, and 3) the position of the target (left/right) regarding the emotional valence depicted, is pseudo-randomized and counterbalanced across trials and sessions. The coloured pictures had a dimension of 420 × 320 pixels on a 1280 × 1024 computer display.

We selected stimuli of emotional expressions in humans and chimpanzees that appear to be well represented across these species. For the affiliative (positive) pictures of humans, we selected images that were labelled as "happy" in the CFD and for the agonistic (negative) pictures, we selected images that were labelled as "angry". These emotional categories are found in other primates and equivalent facial expressions communicating these internal states have been observed in chimpanzees. Expressing an angry face for humans includes the activation of AU4, AU7, AU10, AU16, AU25, AU5, AU20, AU9 and AU26, whereas expressing a happy face includes the activation of AU12, AU7, AU26, AU6, AU10, AU1 and AU25 (Kohler et al., 2004). Nevertheless, relying purely on the AU activation for deducing similarities in expressions between species can be misleading. Entangling the activation of facial muscles in chimpanzees for expression production has shown that some identical AUs (i.e. AU10, AU16) were indeed active for chimpanzee agonistic faces as for human angry and fearful (agonistic) faces. However, finding homologous expressions in the prototypical chimpanzee facial expression repertoire is more challenging, because a related expression can communicate different affective signals. For instance, the AUs active in a human smile are overlapping with AUs in fear-grin and bared-teeth displays in chimpanzees (i.e. AU12, AU25) which occur predominantly in stressful situations (Parr & Waller, 2006). This makes two facial expressions communicating contrasting signals in humans and chimpanzees, related to each other. While there was no significant difference in valence ratings between experts and non-experts ($F(1, 49) = 0.96$, $p = 0.33$), neither for the indicated arousal levels ($F(1, 48) = 0.44$, $p = 0.51$), we acknowledge that some expressions might convey varying affective signals, including fear or submission, rather than anger or aggression (see Supplementary Material II).

For the equivalent of a "happy" face in chimpanzees we chose to base our affiliative stimuli selection following the proposed parallels between human laughter and a non-human "play-face" (Hooff and Bourjade, 1972). All AUs present in a chimpanzee play-face (AU12, AU25, AU26) are within the subset of a human happy-face (Parr & Waller, 2006). For the selection of agonistic stimuli, we matched the "angry" face in humans with the bared-teeth and screaming displays in chimpanzees. Knowing that this could potentially be a source for interpretation mistakes in our participants and consequently lead to wrong priming effects, we compared their classification ratings (in valence and arousal of the seen stimuli) with the ratings of seven non-human primate experts and found no significant difference between the non-experts and experts (see Supplementary Material II., Supplementary Figure 2). In addition, we confirmed that valence and arousal ratings of human and chimpanzee stimuli were generally in line with our expectations (Supplementary Figure 1).

Calibration

Participants were calibrated using the 5-point automated calibration procedure in Tobii Pro Lab. Calibrations were accepted when the error displayed after finishing the calibration was minimal (less than one degree) and the data loss was less than 1%.

Design and procedure

Participants were actively recruited by the experimenter in the facilities of Leiden University. After reading the information letter for the study and signing the consent form, participants were individually tested in an eye-tracking laboratory at Leiden University. By signing the consent form they allowed to use their data for further analyses and publications.

We developed a within-subject design with three predictor conditions (affiliative, agonistic, neutral) of the priming factor and two valence levels (affiliative, agonistic) shown on the target screen. Unlike traditional priming studies, participants in this experiment were asked to freely view the images to measure spontaneous attentional biases rather than task-driven responses. This approach ensures the measurement of automatic processes underlying attentional shifts. In the prime-target paradigm, positively and negatively valenced picture targets of emotional expressions were presented adjacently (4 s), preceded by a positive, negative, or neutral facial expression prime of either a human or chimpanzee face (2 s). Importantly, the target screen always depicted affiliative and agonistic human facial expressions. The order of the trials and the position of the positive and negative target images (left/right) were pseudo-randomized and counterbalanced across trials and sessions. Two trial sequences of different primer species conditions can be found in Supplementary Figure 3.

The experiment was run via Tobi Pro Lab (version 1.181.37603) on a Windows computer. After the 5-point calibration procedure, the programme proceeded to the eye-tracking trials. During the eye-tracking procedure, the participants had no active task to perform, but were asked to freely view the images on the computer screen. Their eye movements were measured via a Tobii Pro-Fusion eye-tracker attached to the monitor. A session started with a fixation cross that was shown for 1 s. This was followed by a primer depicting the facial expression of a human or a chimpanzee (classified as either affiliative, agonistic, or neutral) that flashed up for 2 s in the middle of the screen, then directly followed by a 4 s target screen showing two emotionally valenced pictures depicting humans. The primer picture was spatially not overlapping with the position of the target pictures to prevent inaccuracies in the gaze fixation assessment. A trial ended with a blank screen that was shown for 3 s. After the 9th session, a short break was programmed into the experiment, so that the participants could rest their eyes and look away for a couple of seconds. Once the second part was finished (108 trials in total), a Qualtrics questionnaire was opened remotely on the participant's screen that first assessed the participants' demographic information and then proceeded to the rating task. Participants were asked to rate all the primer pictures (108 in total) on two separate sliders, both on valence (negative to positive) and arousal (low to high). Since the primer pictures were only shown once, keeping the familiarisation effects at its minimum compared to the target pictures, we decided to limit the rating to the sub-set of the primer pictures. The answers were coded on a 100-point scale with 50 indicating the neutral "zero-point" of the slider. Numbers smaller than 50 represented the rating in the negative/low spectrum and numbers larger than 50 represented the rating in the positive/high spectrum. Participants were given a debrief form explaining the background information and the goal of the study after they had finished the task, as well as the opportunity to ask remaining questions. The experiment took about 30–40 minutes to finish.

Data preparation

Before the analyses, we plotted the gaze data with the locations of the stimuli on the screen to check whether the raw fixation data matched with the areas of the stimuli on the screen. We drew a 430 × 320 ROI (region of interest) square around each of the primer pictures and around each of the two simultaneously presented target pictures. A fixation was classified as a "look" if it occurred within a predefined ROI around the face stimuli. Through Tobii Pro Lab's *Metrics* option, we extracted the data on *Total Fixation Duration* per ROI using the Tobii Pro Lab Fixation Filter.

Statistical analyses

To answer our research questions and test whether emotional primers elicit attentional bias, we performed a multi-level analysis using Bayesian mixed modelling to analyse the total fixation duration. Our key question was whether fixations on the emotionally valenced targets were influenced by the previously seen primer emotion and species. Since the target screen depicted two facial expressions simultaneously, the looking durations toward the targets were highly correlated. Thus, we calculated our dependent variable from the proportional looking duration towards the positive target picture (based on Tobi Pro Lab's *Total Fixation Duration* (TFD), from here on: bias score) using the following formula:

$$\frac{\textit{TFD positive target}}{\textit{TFD positive target} + \textit{TFD negative target}}$$

Since the bias score reflects the probability of looking at the positive picture, the "remaining" probability is the attentional bias towards the negative picture. Thus, there is no need of computing an extra negative bias score. The measure of the bias score higher than 0.5 indicates a longer fixation duration towards the positive emotional expression in the target screen. Hence, a bias score lower than 0.5 indicates a longer fixation duration towards the negative emotional expression.

To analyze the eye-tracking data, we used a zero-one inflated Bayesian beta regression model, which is suitable to analyze continuous proportions containing zeros and ones. For examining positivity bias across trials, we ran a multilevel model analyzing the main effects, as well as the interaction between variables *primer species (2)* and *primer emotion valence (3)*. Details on the models and their notation can be found in Supplementary Material II.

We report the medial estimate coefficients, the logit transformed regression coefficients, and the odds ratio coefficients together with the 95% credible interval (CI). In addition, we also report the probability of direction (pd), which indicates the certainty that an effect goes in a specific direction. All analyses were conducted using RStudio (v. 4.1.2) and the packages *brms, emmeans,* and *ez.*

Results

The results in Table 1 show that firstly, the positivity bias on the emotional target pictures is higher than 0.5. This effect was robust for primers depicting humans (*Mdn* = .510, 95% *CI* [0.501 - 0.518], *pd* = 99%), as well as primers depicting chimpanzees (*Mdn* = .515, 95% *CI* [0.506 - 0.523], *pd* = 98%), meaning that all priming effects combined (positive, negative, neutral) led to human participants reliably looking longer at the affiliative compared to agonistic target pictures (see Table 1, Model 1).

We then separately investigated the specific emotion categories (*primer valence*), as well as their

Table 1. Overview of results per factor level of interest for the three models. Robust effects are in bold.

Model	Primer Species	Primer Valence	*Median*	*CI 95%*	*pd*
1 (Primer Species)	Chimpanzee	**All**	**0.515**	**[0.506 - 0.523]**	**0.99**
	Human	**All**	**0.510**	**[0.501 - 0.518]**	**0.98**
2 (Valence)	All	Agonistic	0.491	[0.481 - 0.502]	0.95
	All	**Affiliative**	**0.545**	**[0.535 - 0.555]**	**1.00**
	All	Neutral	0.501	[0.490 - 0.511]	0.54
3 (Primer Species*Primer Valence)	Chimpanzee	**Agonistic**	**0.515**	**[0.501- 0.529]**	**0.98**
		Affiliative	**0.529**	**[0.516- 0.543]**	**1.00**
		Neutral	0.499	[0.486- 0.513]	0.54
	Human	**Agonistic**	**0.467**	**[0.452- 0.481]**	**1.00**
		Affiliative	**0.560**	**[0.547 - 0.574]**	**1.00**
		Neutral	0.502	[0.488- 0.516]	0.60

interaction effect with the *primer species*. In the model where we included *primer valence* as a factor (H_1), we found robust evidence for increased positivity bias and hence, a decreased negativity bias when the participants were primed with an affiliative primer (*Mdn* = .545, 95% *CI* [0.535 - 0.555], *pd* = 100%) compared to when the primer was either neutral or negative. Summarised across both species, there was no robust effect from seeing agonistic or neutral primers. Hence, we could confirm that averaged over species, only affiliative emotional primers introduce an attentional bias compared to neutral and agonistic primers (H_1) (see Table 1, Model 2).

Examining the interaction between *primer valence* and *primer species* ($H_{2,}$ H_3), we observed that attention shift towards the affiliative stimulus on the target screen was linked to presenting chimpanzee primers of affiliative nature (*Mdn* = .471, 95% *CI* [0.457-0.484], *pd* = 1.00), as well as presenting human primers of affiliative nature (*Mdn* = .485, 95% *CI* [0.426 - 0.453], *pd* = 1.00. Furthermore, we found robust evidence for human participants looking longer at the agonistic stimulus in the target screen compared to the affiliative stimuli, given an agonistic human face primer (*Mdn* = .533, 95% *CI* [0.519- 0.548], *pd* = 1.00). The opposite effect was found for primers depicting agonistic chimpanzee faces (*Mdn* = .485, 95% *CI* [0.471- 0.499], *pd* = 0.98) (H_3). This disparity also drives the main effect of agonistic valenced primers to being not robust. Neutral primers of both species did not introduce any reliable effect, thus, seeing a neutral primer did not cause a shift in the attention toward a positively or negatively valenced target picture. Entangling this interaction effect confirms that priming with emotionally valenced faces (positive and negative), compared to neutral faces of both species (i.e. humans and chimpanzees) introduces an attentional bias toward the emotion representations in the target screen (H_1). Inspecting the main effect of valence, this result is not present due to agonistic primers of both species presumably having contrary effects and cancelling each other out.

Zooming in on the interaction effect, we compared the amount of positivity bias introduced by differently valenced emotional primers showing different species (see Supplementary Table 2). In addition, we specified the model to estimate the precision of the beta distribution, the zero – one inflation probability, and the conditional one-inflation probability as a function of the positivity bias. We found the main effect of *primer species* to be significant, with seeing human primers leading to a decreased positivity bias compared to seeing chimpanzee primers ($\beta_{\text{species\_human}} = -.20$, *CI* [−0.12 – (−0.28), *OR* = 1.22). For the chimpanzee primers (reference category), there was no significant difference found in positivity bias regardless

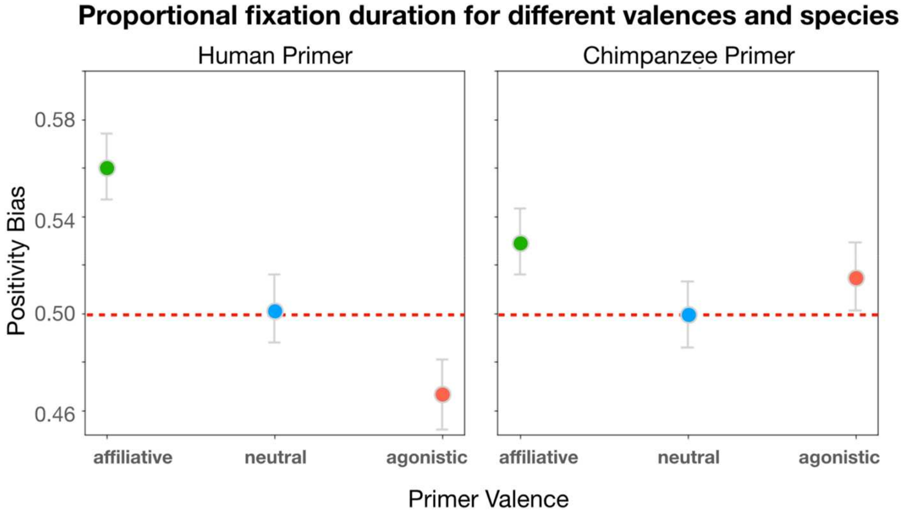

Figure 1. Proportional fixation duration for different valences and species.

Note: Graphs displaying the proportional fixation duration (predicted model data) to emotional stimuli (positivity bias) of conspecifics and heterospecifics by human participants. Error bars reflect the 95% credible interval, dots represent the median. The measure of the positivity bias score higher than 0.5 indicates a longer fixation duration towards the positive emotional expression in the target screen. Hence, a positivity bias score lower than 0.5 indicates a longer fixation duration towards the negative emotional expression.

of the primer valence. This is confirmed by the overlapping credible intervals for the interaction effect between chimpanzee primer and the three valence levels (see Table 1, model 3 and Figure 1).

Details on the interaction effects (e.g. to what extent the strength of the positivity bias introduced by the valence effect differs for seeing primers of different species) are summarised in Supplementary Table 2.

Discussion

Understanding the emotions of others is a crucially valuable skill for social animals to successfully master group interactions and to navigate in their environment (De Waal, 2011). Introducing a prime-target paradigm, we compared how our participants' attentional bias is influenced by emotional expressions of their own, as well as by other species, investigating to what extent emotion processing mechanisms in humans are transferable to accurately perceive and interpret the emotional expressions of our closest living relative, the chimpanzee. As hypothesised, the attentional shifts occurred towards the targets that were congruent with the previously seen primer. Importantly, this effect was robust for humans viewing human emotional expressions, but partly contradictory and weaker for viewing chimpanzee emotional expressions. In our study, we confirmed that priming with emotional facial expressions introduces attentional biases toward emotional stimuli of conspecifics. Participants looked reliably longer at an emotional target stimulus that was congruent with the valence of the conspecific primer they saw before. Hence, a priorly presented affective stimulus depicting a human changed the amount of attention that participants allocated to afterward presented positive and negative visual information. Eventually, most likely due to their less pronounced relevance, neutral primers did not introduce this effect. The demonstrated priming effect elicited by positively and negatively connotated emotional displays confirms previous findings about the moderating role of valenced primers (Smith et al., 2006).

Contrary to our predictions, we did not find heterospecific (chimpanzee) primers to influence participants' attention in a comparable way to conspecific (human) primers. This result is somewhat surprising, as previous research has demonstrated humans to be equally sensitive toward social cues from both species (Hattori et al., 2010). However, testing functional implications, in the present study we did not find the attentional bias of chimpanzees to have a robust priming effect. In regard to the negatively and neutrally valenced chimpanzee primers, the tendency of attentional bias shifts was somewhat comparable to the shifts upon viewing primers depicting humans. Positively valenced primers increased positivity bias, whereas neutral primers barely changed the fixation duration towards the two emotional targets. Negatively valenced primers did not have a robust impact on attention.

To verify that the participants' correctly encoded chimpanzees' facial expressions, we analyzed their valence and arousal ratings for the priming stimuli of both species. We found that negative emotional expressions were rated accordingly with more negative valence scores, as well as positive emotional expressions were rated accordingly with more positive valence scores. Ratings in valence mirrored the depicted emotional expressions' categories, irrespective of the species. Similarly, we found emotional stimuli (positive and negative) to induce higher arousal in the participants, compared to neutral stimuli. These findings are in line with previous studies on the emotional perception of different species (Kret et al., 2018) and confirm participants' understanding and correct classification of chimpanzee emotional expressions. Furthermore, comparisons with ratings that were assigned to human primers show that the perceived valence and arousal of the emotional stimuli depicting different species are fairly similar. These data support a developed sensitivity for the perception and successful discrimination of emotional expressions in our close living relatives and possibly other related animals. This sensitivity might be contingent upon the extent of shared characteristics (Parr et al., 1998). We were able to validate the rating results of the participants with the rating results by experienced primate social cognition experts.

Given the participants' validated understanding of chimpanzees' emotional expressions, the induction of comparable effects on i.e. attention bias should conceivably be feasible. However, our results yielded a tendency of a positivity bias increase (negativity bias decrease) upon viewing a negatively valenced chimpanzee primer. Zooming in on potential explanations for this contradictory observation, the selected chimpanzee stimuli need to be closely examined. For the stimulus sub-set communicating negative affective states in chimpanzees, we chose one of the most frequently observed facial expressions across nonhuman primates: the bared-teeth display. Although in chimpanzees the expression predominantly occurs in agonistic interactions (Waller & Dunbar, 2005), it can signal different affective states in other species. Importantly, in addition to chimpanzees, bonobos are humans' other closest living relatives, but they use the bared-teeth display somewhat differently. While chimpanzees, who exhibit a more despotic social structure, often use this expression in dominance-related contexts, bonobos primarily display it as a signal of appeasement, particularly during periods of social tension. Moreover, in bonobos, the bared-teeth display does not appear to be linked to social status, highlighting a key difference in communication between the two species (Vlaeyen et al., 2022). Important in this context is that the activation of AUs that highly overlap with AUs forming a bared-teeth display, can resemble a smiling face in humans (Hooff, 1972). Hence, some participants of the present study might have misinterpreted the negative affective state in chimpanzees for a smile and evaluated it as a positive expression, which might have averaged out the expected effect. An identical leakage effect from one emotional category to another was found in children who perceived pictures of distressed bonobos rather positively than negatively (Kret & Van Berlo, 2021). The study argued that children, as opposed to adults, have not yet learned to take contextual information into account and incorporate this for their interpretation of an emotional expression. In our eye-tracking study, this misclassification of the bared-teeth display occurred in the prime-target paradigm where the stimulus was presented on the screen for 2 s, but not in the post-hoc rating questionnaire where participants had no time restriction for indicating the perceived valence and arousal of the viewed primers. From this mismatch in the participant's emotion classification abilities, we can conclude that the exposure time to an affective stimulus might play a consequential role. Supporting this relation, perceptual awareness of faces has been shown to increase gradually with longer presentation durations (Lohse & Overgaard, 2019). The primes were displayed for a fixed duration of 2 s, providing consistent exposure across participants; however, this fixed timeframe may not have been sufficient to fully capture the complexity of certain emotional expressions, particularly for heterospecific stimuli, and occasional lapses in attention could not be entirely ruled out. Thus, future studies investigating humans' understanding of other animals' emotions should take the time exposure aspect into account and eventually increase the presentation duration of heterospecific primer pictures.

One limitation of the current study that should be focused on in future work is the categorisation of different emotional expressions. Establishing salient categories and classifying human expressions has been a great challenge, with disagreement in the field. Since expressions in non-human primates have been studied far less, the disagreement in their categorisation is even more pronounced, introducing increased variability in experimental designs. Quantifying the neural, physiological, and phenomenological organisation of human emotions has produced a categorical structure of various emotions across different sources for arousal and brain activity. Similar methods could be applied using chimpanzee emotional stimuli to incorporate the different domains of arousal for (proposed) distinct emotion categories in non-human primates. Comparing these activations for heterospecific and conspecific stimuli would potentially reveal homologies in emotion expression, perception, and processing in different species. In the present study, we chose two opposing valences to test the effects of priming on attention, however, even with ecologically validated stimuli, we presumably encountered partial leaking from one category to another. This variability highlights the inherent challenge in cross-species research on emotional expressions, where certain expressions may not directly map onto human emotional categories. Studying a larger variety of emotional expressions in non-human primates can help to distinguish salient cues and benefit the more precise identification of facial expressions. Future research should aim to disentangle these nuances by incorporating dynamic stimuli or employing AI algorithms to create more ecologically valid representations of specific emotional states. In the current study, we used static pictures of facial expressions in humans and chimpanzees which might have limited the participants' ability to recognise an affective state correctly.

In addition, our study faces another constraint regarding the match between chimpanzee and human primers. While all chimpanzee photographs were taken opportunistically in a naturalistic setting, the human photographs as a subset of the Chicago Face Database were depicting acted, overly clear emotional expressions in a highly standardised environment. This introduces a disbalance to the comparison of the presented stimuli and limits the experimental control, which might have influenced the perception of emotions.

Based on the parallels between humans and non-human primates that since Darwin's pioneering work have only unfolded further, it can be assumed that there is an evolutionary continuity in the emotional behaviours and their processing in humans and non-human primates. Aiming to find homologies in human processing of facial expressions in their own species, and in an evolutionary closely related species, we tested the influences on attention introduced by priming with differently valenced emotional stimuli depicting humans and chimpanzees. Attention was shifted toward the emotional target picture that was congruent with the valence of the conspecific emotional expression shown in the primer picture. Contrary to our expectations, we did not find this effect to occur with chimpanzee primers. Additional cross-species systematic investigations with slight adjustments are needed to fully address the gap of a shared evolutionary ancestry, and ultimately rule out the idea of emotions being unique to humans.

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