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Emotion Processing Across and Within Species: A Comparison Between Humans (*Homo sapiens*) and Chimpanzees (*Pan troglodytes*)

Mariska E. Kret
Leiden University and Leiden Institute for Brain and Cognition
(LIBC), the Netherlands

Akiho Muramatsu and Tetsuro Matsuzawa
Kyoto University

For social species, recognizing and adequately yet quickly responding to the emotions of others is crucial for their survival. The current study investigates attentional biases toward emotions in two closely related species, humans and chimpanzees. Prior research has demonstrated that humans typically show an attentional bias toward emotions. We here build on that literature by studying the underlying unconscious mechanisms within and across humans and chimpanzees and aim to gain insight into the evolutionary continuity of expressions. Experiment 1 tested whether chimpanzees show an attentional bias toward the expressions of conspecifics and whether this putative bias is modulated by the stimulus presentation duration, being 33 ms or 300 ms. The stimuli were followed by a visual mask in the form of a neutral body image. This backward-masking procedure eliminated the visibility of the stimuli that were presented for 33 ms, rendering their presentation subliminal. In contrast to our prediction, no attentional bias toward emotions was observed in chimpanzees. The goal of Experiment 2 was to verify this finding and to investigate chimpanzees' reaction to human stimuli. Replicating Experiment 1, no evidence of an attentional bias toward emotions was observed in chimpanzees. In Experiment 3 we used the same chimpanzee and human expressions in 711 museum visitors and confirmed that humans do have an attentional bias toward emotions. Interestingly, this bias was independent of the stimulus presentation duration and most strikingly, independent of the species that was observed. Implications for theorizing about species differences in attentional mechanisms in processing emotions are discussed, as well as directions for future research, to investigate our preliminary findings and this potential species difference further.

Keywords: emotion, affect, body language, great apes, implicit task

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For social species, recognizing emotions from conspecifics has great survival value. Research in humans and chimpanzees (*Pan troglodytes*) shows that both species (a) recognize conspecifics' emotional expressions (for research in humans, Ekman, & Friesen, 1982; Ekman, Friesen, & Ellsworth, 2013; for studies with chimpanzees, see Buttelmann, Call, & Tomasello, 2009; Parr, 2001), (b) have better memory for pictures showing emotional as compared to neutral expressions (humans, Reisberg, & Heuer, 1992; chimpanzees, Kano, Tanaka, & Tomonaga, 2008), and (c) show prolonged attention to emotional versus nonemotional images (for

a review in humans, see Palermo & Rhodes, 2007; for a study in chimpanzees, see Kano, & Tomonaga, 2010). The majority of emotion research in humans has focused on the perception of facial expressions (Adolphs, 2002; Haxby, Hoffman, & Gobbini, 2000). In everyday life, however, affective states are expressed by the whole body, revealing it, in turn, to the observer (Atkinson, Dittrich, Gemmell, & Young, 2004; Atkinson, Heberlein, & Adolphs, 2007; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Kret, & de Gelder, 2010, 2013; Kret, Pichon, Grèzes, & de Gelder, 2011a, 2011b; Mondloch, Nelson, & Horner, 2013; Sinke, Kret, & de Gelder, 2011; for a review, see de Gelder, van Honk, & Tamietto, 2011). Thus far, it is not known whether humans and chimpanzees can recognize each other's bodily expressions of emotion. In the current study, we take a comparative approach and investigate the similarities and differences between humans and chimpanzees in their reactions to conspecifics' or other species' whole body expressions of emotion.

Seeing a conspecific being emotional and expressing that via facial expressions or through body language immediately attracts attention and automatically triggers action tendencies in observers (Frijda, 2016, 1987; Prochazkova & Kret, 2017). Emotions' potential for action supports an evolutionary account, which assumes that emotions evolved to benefit the organism by responding more adequately to threats in the environment (de Waal, 2011; Nesse, 1990). Indeed, we use another's emotion signals to guide our actions, for example, to initiate an approach reaction toward a person who is happily smiling at you or to avoid someone with an angry expression. Even more basic responses, such as fight or flight reactions, can be triggered by observing emotional expressions in others (LeDoux, 1996; Öhman & Soares, 1993). The field of emotion research is dominated by investigations of facial expressions and studies including bodily expressions are still scarce. However, two of the most illustrious theoreticians of emotion, Darwin and James, discussed whole-body expressions at great length. Darwin famously included postural descriptions in *The Expression of the Emotions in Man and Animals*, revealing similarities across species and their ancient functions (Darwin, 1872), and James (1890) investigated the recognition of emotion with photographs of whole-body postures. Faces and bodies are equally salient and familiar in daily life and often convey some of the same information (de Gelder, Van den Stock, Meeren, Kret, & Tamietto, 2009). Interestingly, when they do not, it is oftentimes the body that reveals the expresser's genuine feelings (Aviezer, Trope, & Todorov, 2012).

In recent decades, researchers have taken up the issue of bodily expression recognition, and results from a number of behavioral experiments using independent stimulus sets now allow us to conclude that recognition performance for bodily expressions is very similar to face stimuli. For instance, in line with numerous studies that have demonstrated attentional biases to facial expressions of emotion, a study by Kret and de Gelder (2013) showed that when two body postures were presented simultaneously on a computer screen, angry postures attracted the most attention and more so than happy ones. Another more recent study measured action tendencies toward fearful, angry, and neutral facial and bodily expressions. Specifically, participants stood in front of a computer touch-screen and were instructed to tap as fast as they could on emotional expressions that appeared on either side of the screen. Results showed an attentional bias towards expressions of

anger and fear, with faster responses following these, as compared with neutral expressions, independent of whether the emotions were expressed by the face or the body (de Valk, Wijnen, & Kret, 2015).

Since as early as Darwin (1872), researchers have noted similarities between the expressions of emotion in human and nonhuman primates. These species have a broad repertoire of stereotyped facial behaviors and body postures that are seen as expressions of emotions (Andrew, 1963; Chevalier-Skolnikoff, 1973; Hinde & Rowell, 1962; Maestripieri, 1997; Redican, 1975; Steiner, Glaser, Hawilo, & Berridge, 2001; van Hooff, 1967). Behavioral observations have demonstrated that nonhuman primate emotional expressions and human emotional expressions can play similar functional roles (Kret & Straffon, 2018). For example, human infants tend to use a pout face to solicit their mother's attention, and a similar facial expression can be found in infant chimpanzees for the same bonding functions (Blurton Jones, 1971; van Lawick-Goodall, 1968). Furthermore, chimpanzees exhibit silent bared-teeth displays and play faces that assist in social bonding and the maintenance of social groups. In humans, the same bonding function is served by smiling, which looks similar to those chimpanzee displays (Burrows, Waller, Parr, & Bonar, 2006; Chevalier-Skolnikoff, 1973, 1982; Kret & Straffon, 2018; Preuschoft & van Hooff, 1995; van Hooff, 1967, 1972; see Gaspar, 2006, for a review).

Nonhuman primates are able to not only merely express emotions but also successfully distinguish emotional expressions in others. Chimpanzees are capable of discriminating an emotional facial expression made by two different individuals from that of a neutral expression of a third individual. Successful discrimination of different emotional expressions was dependent on the amount of shared features between the two expressions, as is also known to be the case in humans (Parr, Hopkins, & de Waal, 1998). In another study comparing chimpanzees and rhesus macaques, it was shown that both species are able to use facial expressions to discriminate unfamiliar conspecifics, although the macaques required more trials to learn the task (Parr, Winslow, Hopkins, & de Waal, 2000). Rhesus monkeys are also capable of discriminating emotional expressions from neutral expressions, yet they showed more difficulties with discriminating two distinct emotional expressions (Parr & Heintz, 2009). Moreover, other research has demonstrated that macaque cardiac physiology is sensitive to the valence of passively viewed sensory stimuli (Bliss-Moreau, Machado, Bauman, & Amaral, 2013). One key mechanism that is at play when processing conspecifics' expressions of emotion, is increased attention toward these expressions.

Attention toward the expressions of conspecifics is a topic that has been addressed in a number of previous experimental studies. In a recent eye-tracking study for instance, it was shown that macaque monkeys attend more quickly and also attend longer to monkeys showing aggressive or submissive compared with neutral behaviors. This effect was driven by heightened attention to the body (Bliss-Moreau, Moadab, & Machado, 2017), a finding replicating earlier findings in humans (Kret, Stekelenburg, Roelofs, & de Gelder, 2013). In that latter study, it was also found that humans' level of arousal was higher when they observed images of people of whom both the face and the body showed anger or fear compared with happiness (see also Kret, Roelofs, Stekelenburg, & de Gelder, 2013). Thus, prior research has shown that emotions are

expressed by the face and the body and that expressions, especially threat displays, are readily picked up by observers and facilitate fast actions.

The underlying neural mechanism that makes us attend to emotions is still not understood completely. The literature shows that subcortical, evolutionary old brain structures play key roles in emotion processing across and beyond different primate species (Bliss-Moreau, Bauman, & Amaral, 2011, for a review, see Pessoa & Adolphs, 2010) One possible way to tap into this mechanism is by visually masking experimental stimuli. Visual masking results in the reduction or elimination of the visibility of one brief stimulus by the presentation of a second brief stimulus, called the "mask." If a stimulus is followed by a blank screen, the perceptual presentation duration of the stimulus is somewhat prolonged due to the after image. When instead of a blank screen a carefully selected visual mask is presented, there is no such after image, and the stimulus presentation duration is better secured. Masking stimuli would yield similar or even larger effects on emotional attention than unmasked stimuli (Bar-Haim, Lamy, Pergamin, Bakermans-Kranenburg, & van IJzendoorn, 2007; Hedger, Gray, Garner, & Adams, 2016). We here aim to examine this possibility by investigating attentional biases toward subliminally (below thresholds) and supraliminally (can be processed consciously) presented emotional expressions in human and chimpanzee observers, by using the dot-probe task (MacLeod, Mathews, & Tata, 1986). In the dot-probe task, two pictures are briefly being presented next to each other on a computer screen. Next, one of the two is replaced by a dot, the location of which participants need to indicate as fast as possible by using the arrows "left" and "right" on a keyboard, or by touching the dot directly on a touch screen. Typically, as attention is attracted to biologically relevant stimuli, touching the dot is faster when it replaces an emotion compared with neutral image. This task is often used in psychology and has a lot of potential for testing emotional attention across primate species primarily because this test is implicit and because evidence, although still scarce, is accumulating that it does not require verbal instruction. Moreover, subjects need no or minimal training to perform the test successfully (King, Kurdziel, Meyer, & Lacreuse, 2012; Kret, Jaasma, Bionda, & Wijnen, 2016; Parr, Modi, Siebert, & Young, 2013; Tomonaga & Imura, 2009; see van Rooijen, Ploeger, & Kret, 2017 for a review). The majority of dot-probe studies have used a stimulus presentation duration of 500 ms. A limitation of this presentation duration is that attention may already have shifted between the two stimuli. Thus, responses given after a stimulus presentation of 500 ms do not necessarily provide information about participants' initial orientation (Bradley, Mogg, & Millar, 2000). To avoid this, other dot-probe studies used a shorter or even subliminal stimulus presentation. A meta-analysis showed that the effect size of subliminal presentation was twice as large as that of supraliminal presentation in anxious individuals (Bar-Haim et al., 2007). A more recent meta-analysis of 28 masked dot-probe experiments found a small effect of a threat bias, comparable with the effect of the supraliminal presentation in the review of Bar-Haim et al. (2007) (Hedger et al., 2016).

If this evolutionary ancient route that facilitates the processing of emotions is indeed involved, then it is likely that chimpanzees will process emotions similarly as humans. Thus, they will show similar attentional biases, especially toward the masked stimuli. We aim to investigate this possibility in the current study. More-

over, we will address the question of whether humans are perceiving chimpanzee expressions similarly as humans, and vice versa. Darwin (1872) claimed that some emotional expressions have evolutionary ancient roots and are innate: "the young and the old of widely different races, both with man and animals, express the same state of mind by the same movements" (p. 348; see also Scherer, Clark-Polner, & Mortillaro, 2011). Following this rationale, one could argue that if so, species might be able to recognize the emotional expressions of other species. Research on the perception of emotion in other species is still scarce, but some studies suggest that this might indeed be the case. In a recent article, Fillipi et al. (2017) showed that fundamental aspects of vocal emotional expressions are shared across all extant species that trace their ancestry to early terrestrial tetrapods. More specifically, in their study, they identified acoustic universals that conveyed the same emotional information across a broad range of vocalizing species and showed that humans can use these universals to correctly infer the emotional state of other species. Cross-species emotion perception has also been investigated in a study with dogs. The study combined visual and auditory cues in a cross-modal preferential looking paradigm. Dogs were presented human or dog faces with different emotional valences (happy/playful vs. angry/aggressive), paired with a single vocalization from the same individual with either a positive or negative valence or Brownian noise. The results showed that dogs looked significantly longer at the face whose expression was congruent rather than incongruent to the valence of the vocalization, for both conspecifics and heterospecifics. This result demonstrates that dogs can extract and integrate bimodal sensory emotional information and discriminate between positive and negative emotions from both humans and dogs (Albuquerque et al., 2016). In the case of domestic dogs, it can be argued that it might be particularly advantageous to recognize the emotions of humans as these are their daily companions. Also, human–dog coevolution might have facilitated this process. However, primate observation studies came to similar conclusions. For instance, Diana monkeys understand the meaning and underlying cause of other primate species' alarm calls, guinea fowl alarm calls, and different kinds of chimpanzee screams (Zuberbühler, 2000). Another study in humans listening to human, macaque, or cat vocalizations also suggests there are shared emotional systems across species (Belin et al., 2008). However, none of these studies directly compared the processing of emotion signals from their own to other species in a cross-species experimental setting. Therefore, comparing human and chimpanzees' attentional biases toward emotional expressions from their own compared with the other species will show similarities and differences and indirectly inform us about the evolution of processing emotional expressions. Research on emotion perception across these two closely related species may provide crucial insights in the adaptive value of emotional expressions and their perception.

In three experiments, we took a comparative approach to get more insight into emotional attention within and across two closely related species. Using the emotional dot-probe paradigm, Experiment 1 tested whether chimpanzees, like humans, show an attentional bias toward the expressions of conspecifics and whether this putative bias is modulated by the stimulus presentation duration, being 33 ms or 300 ms, both visually masked (i.e., the stimulus is immediately followed by a visual mask in the form of a neutral body image, after which the probe appears). The goal of Experi-

ment 2 was to replicate and extend findings from Experiment 1 by using the same paradigm, but with additional stimuli showing human expressions. In a previous study conducted in humans, these same stimuli have reliably yielded an attentional bias toward the ones showing emotional compared to neutral content (de Valk et al., 2015). Other research has investigated the role of expertise and conceptual knowledge on how other species emotions are categorized (Fugate, Gouzoules, & Barrett, 2010; Pongrácz, Molnár, & Miklósi, 2006). However, whether expertise has any influence on implicit attentional biases is hitherto not known. By using the exact same paradigm as Experiment 2, Experiment 3 tested attentional biases toward emotions in 711 visitors of a science museum in The Netherlands.

Hypotheses

We predicted that chimpanzees (Experiment 1 and 2) and humans (Experiment 3) would show an attentional bias toward the emotional expressions of conspecifics. Whereas some research suggests that species experience the emotions of other species similarly to those expressed by their conspecifics, other research contradicts that (Fugate et al., 2010; Madsen, Persson, Sayehli, Lenninger, & Sonesson, 2013; Martin-Malivel, & Okada, 2007). From an evolutionary perspective (Darwin, 1872), we expect that species would process expressions from conspecifics and other species similarly. Based on our previous study with a similar paradigm (de Valk, Wijnen, & Kret, 2015), we do not predict differences between fear and anger in this task. Both emotions are salient, biologically relevant stimuli that are likely to drive attention. Following the same reasoning, we do not expect to see differences between chimpanzees' expressions of dominance (display) or submission. Finally, based on a previous meta-analysis, we predict that the putative attentional bias toward emotions is stronger when stimuli are presented subliminally versus supraliminally (Bar-Haim et al., 2007).

Experiment 1: Emotional Dot-Probe Task in Chimpanzee Observers With Chimpanzee Expressions

Method

Participants. Eight chimpanzees (two female juvenile and one male juvenile, and four female and one male adult) participated in this study. They were 24 years old on average ($SD = 12$). At the time of testing, the chimpanzees lived within a social group of 14 individuals in an enriched environment with a 700-m² outdoor compound and an attached indoor residence that was illuminated during day time at the Kyoto University Research Unit in Inuyama, Japan. The outdoor compound was equipped with climbing frames, ropes, small streams, and various species of trees. Access to the outdoor compound was available to them every other day during the day. Daily meals included a wide variety of fresh fruits and vegetables fed throughout the day supplemented with nutritionally balanced biscuits (fed twice daily) and water available ad libitum. The chimpanzees have been familiar with humans since birth and interact with them on a daily basis (especially during feeding and prior to and after the experiments). They have taken part in various cognitive experiments since youth. For the daily experiments, the chimpanzees left the social group volun-

tarily on the request of experimenters, moved into the experimental booth with the guidance of experimenters, and moved back to the social group after the completion of experiments (approximately 1 hr). The care and use of the chimpanzees adhered to the third edition of the *Guide for the Care and Use of Laboratory Primates* issued by Primate Research Institute, Kyoto University (KUPRI) in 2010, which is compatible with the guidelines issued by the National Institute of Health in the United States of America. The research design was approved by the Animal Welfare and Animal Care Committee of Primate Research Institute, Kyoto University and by the Animal Research Committee of Kyoto University (#2011–078). All procedures adhered to the Japanese Act on Welfare and Management of Animals.

Stimulus material. A total of 161 pictures of male chimpanzees' whole body postures showing submission (fear grimace), display (lip press and erased hair), and neutral expressions were selected from a large database containing pictures of chimpanzees from the Chimpanzee Sanctuary Uto, Kumamoto Sanctuary, and Higashiyama zoo in Nagoya. The pictures were cropped to minimize the visibility of the background and contained 640×1024 pixels. Interfering objects that were visible in the background were removed using Adobe Photoshop (Adobe Systems, San Jose, CA). Based on the emotion-recognition and intensity scores of three independent raters who work with chimpanzees on a daily basis, we selected 12 clear images per emotion category. The chimpanzee pictures were turned to grayscale, and the overall luminance of each picture was adjusted to achieve the mean luminance of all the selected pictures. The reason for turning the images to grayscale is threefold. First, colored images do not allow accurate measurements of luminance. This is important as brighter images could have popped out from the gray background more than darker images and could have subsequently biased attention. So the average luminance level of each image was scaled to the mean luminance. A second reason for doing so is to be consistent with the literature on visual masking that generally uses grayscaled images (also to better deal with potentially confounding effects of low-level differences between stimuli from different conditions). Third, prior studies in chimpanzees showed they, like humans, can recognize emotional expressions from desaturated (e.g., grayscale) images (Kano & Tomonaga, 2010; Parr, Dove, & Hopkins, 1998). See Figure 1.

To level out the possible effect of low-level differences between the stimuli on reaction times (RTs) in the emotional dot-probe task, we scrambled all stimuli with a mosaic pattern of 12×20 squares by using MATLAB. These scrambled images contained luminance identical to the originals and were only used to verify whether significant effects were not related to possible low-level differences between the stimuli. In addition to the scrambled images, the stimulus material consisted of two types of visual masks that were carefully pilot-tested (See methods in the online supplemental material). We choose to include two types of masks to reduce effects of specific properties of the mask.

Each trial showed two images simultaneously, and the dot subsequently appeared on the position of one of these images. The stimuli were presented supraliminally (for 300 ms) or subliminally (for 33 ms) and then immediately masked with a neutral body image. Although we could not verify whether chimpanzees perceived these stimuli consciously or not, we first verified in humans that they were not consciously aware of the stimuli presented at 33
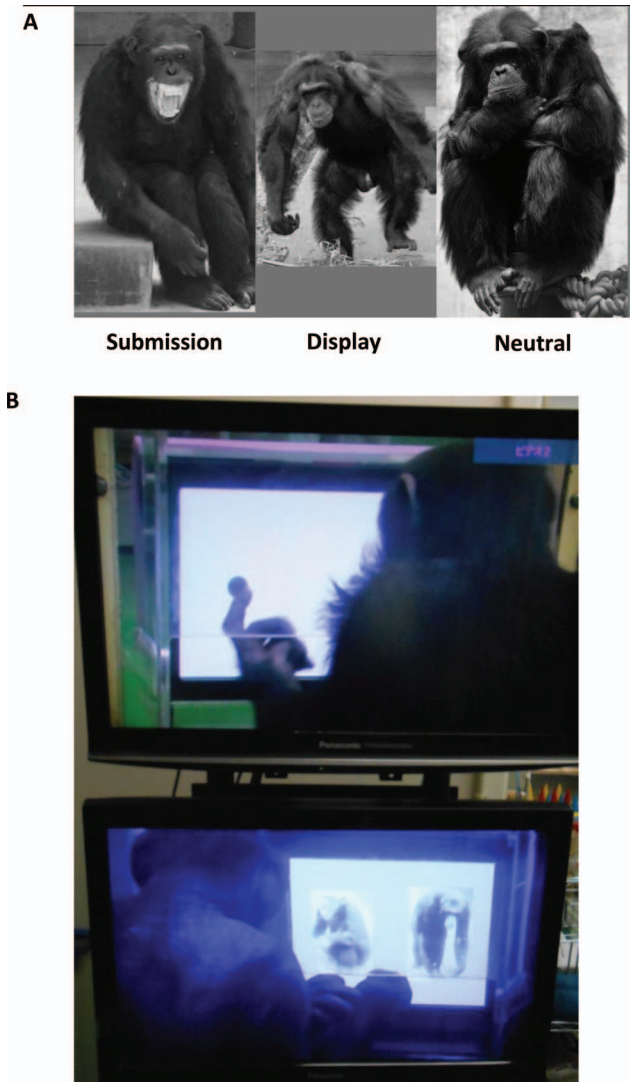
Figure 1. (A) Stimulus examples of chimpanzee expressions. (B) Mother and son (Ai and Ayumu), separated by a glass panel, performing the task simultaneously. See the online article for the color version of this figure.

ms. A detailed description of this procedure and the piloting of different types of visual masks can be found in the Methods in the online supplemental material.

Procedure. Subjects sat in an experimental booth (2.5 m wide × 2.5 m deep × 2.1 m high), with the experimenter and the subjects separated by transparent acrylic panels. The subjects viewed a 17-in. LCD display (1280 × 1024 pixels). Distance to the computer screen was 60 cm. Stimuli were presented on a computer screen with a 60-Hz refresh rate and with a distance of 218 pixels between the two stimuli. A food reward was provided after the chimpanzee tapped on the target. Each chimpanzee completed 1,120 trials on 10 days in total, spread out over a 2-week period. There were one or two testing sessions per day, at most times, one in the morning and one in the afternoon. The trials were randomized. We equally divided the number of trials over the condition, Presentation Duration (2), Target-Distracting Expression (6)

Scramble/Nonscramble (2), and Dot Location (2), and also counterbalanced the trials by mask type (2, as we had two different versions of masks). A trial started with a dot presented at the middle, lower part of the computer screen. After touching the dot, two pictures (always both scrambled or both normal) were presented for 33 ms (300 ms), followed by a masking image presented for 300 ms (33 ms), followed by a dot on the position of one of the pictures. Subjects touched the dot, followed by a blank gray screen that was presented for 1,000 ms. The dots were presented until subjects touched the dot.

Experimental design and data analysis. Within a trial, there were always two different emotions presented (fear–anger, fear–neutral, and neutral–anger). Thus, target emotion and distracting emotion were not independent because the same emotions were never presented next to each other in one trial. Data were analyzed in a two-level generalized mixed model implemented in SPSS Version 20, IBM Statistics where trials were nested within sessions and within participants. Reaction times larger than 2,500 ms were excluded (1.97%). As the data were skewed, a gamma probability distribution was selected with a log link function (which is similar to a log transformation). The statistical model had the following fixed factors included: Target Emotion (anger, fear, or neutral), Presentation Duration (33/300 ms), Target Emotion × Presentation Duration, Distracting Emotion (anger, fear, or neutral), Distracting Emotion × Presentation Duration, and Age of Subject. Because the value of the intercept may differ over participants, a random intercept was included. Traditionally, the dot-probe task is analyzed with bias scores. However, it has recently been recommended to refrain from that method if the sample is very small. A better procedure for the application of the dot-probe task in samples with a small N is to not average any data points and nest all trials within each subject via a multilevel statistical procedure. That way, RTs can be analyzed as a function of the picture that appeared previously on the location of the probe and as a function of the picture that earlier appeared on the other location, the location opposite of the probe (van Rooijen et al., 2017). This procedure was also followed in our previous study with bonobos (Kret et al., 2016).

Results

An analysis of the RTs showed that overall, chimpanzees did not show the classical attentional bias typically observed in the dot-probe task, as has been described often in the human and nonhuman primate literature (faster RTs toward emotions [for a review see van Rooijen et al., 2017]; $p = .906$). Instead, there was an interaction between Presentation Duration and Distracting Emotion, $F(2, 4.565) = 3.033$, $p = .048$. Simple contrasts show that Presentation Duration only matters when the distracting image shows a neutral stimulus. Reaction times are longer in the trials where stimuli were shown for 300 ms rather than for 33 ms and where the distracting image showed an individual in a neutral state, $t(4.565) = 2.634$, $p = .008$. Age did not significantly predict RTs, although a trend towards significance was observed $F(2, 4.565) = 3.619$, $p = .057$. See Table 1.

Conclusion

The effect that has been observed many times in humans, as well as in bonobos (Kret et al., 2016) and macaques (Parr et al., 2013),

Table 1
Study 1 Results

| Target Context | Presentation duration | | | |
| | 33 ms | | 300 ms | |
	M	SE	M	SE
Display Fear	672.535	12.360	682.329	13.290
Display Neutral	650.276	10.921	680.867	14.523
Fear Display	671.628	13.139	662.960	11.237
Fear Neutral	662.545	11.561	696.749	15.821
Neutral Display	670.704	12.283	664.416	10.201
Neutral Fear	681.447	13.320	668.370	11.674

was not replicated in chimpanzees. A previous study has shown that chimpanzees' attention is grabbed by neutral faces more than by different objects (Tomonaga & Imura, 2009), and we therefore had not expected this finding. There can be many reasons for why this null-finding was obtained, one of them being chance. An unanticipated effect that we did obtain, however, was an interaction between Presentation Duration and Distracting Emotion. To confirm this effect and to confirm the null finding with regard to Target Emotion, we ran the experiment one more time for confirmation and in addition added human expressions, which in the past have yielded reliable attentional biases in humans (de Valk et al., 2015).

Experiment 2: Emotional Dot-Probe Task in Chimpanzee Observers Observing Chimpanzee and Human Expressions

Method

Participants. Seven chimpanzees of the previous study again participated two years later. Due to circumstances, one adult female could not be tested.

Stimulus material. In addition to the stimuli used in Experiment 1 (12 clear images of chimpanzees per emotion category),

we selected 36 (3 × 12) images showing human expressions. The heads in the human stimuli are taken from the NimStim stimulus set (Tottenham, Borscheid, Ellertsen, Marcus, & Nelson, 2002). Pictures of human bodily expressions of emotion were taken from the stimulus database Bodily Expressive Action Stimulus Test (BEAST), containing 254 digital pictures (de Gelder & van den Stock, 2011). The pictures were shot in a professional photo studio under constant lighting conditions. Nonprofessional actors were individually instructed in a standardized procedure to display different expressions with the whole body. The instructions provided a few specific and representative daily events typically associated with each emotion (for more details, see de Gelder et al., 2009). For the current study, we selected the best male actors, with recognition scores above 80% correct for the emotions anger, fear, and neutral. Pictures were presented in grayscale, against a gray background. Using Adobe Photoshop, the luminance of each stimulus was modified to the average luminance. A final check was made with a light meter on the test computer screen. See Figure 2.

Procedure. The experimental setup and procedure was similar to Experiment 1 except that we had in addition to chimpanzee images, an equal number of human images included. The chimpanzees completed 96 trials per session. The completed one or two sessions per day (one in the morning and one in the afternoon) spread out over 6 days that all fell within a few couple of weeks. In total, each chimpanzee completed 576 trials. There were 24 trials in total per condition (Species [2], Emotion [3], Presentation Duration [2], Scramble-Normal [2]). The order of presentation was randomized.

Experimental design and data analysis. The statistical design was similar to Experiment 1, with Species Stimulus and interactions with the other factors in addition. Again, trials with RTs larger than 2,500 ms were excluded (1.05%). The data were analyzed in the same way as in Experiment 1.

Results

Again, chimpanzees did not show the classical dot-probe effect as humans (e.g., faster RTs toward emotions; $p = .603$). None of the other main or interaction effects were significant ($ps \geq 0.080$).

A. Stimulus examples

B. Visual Mask (neutral body)

Figure 2. A) Stimulus examples showing a fearful and an angry body posture. B) Two examples of neutral body masks.

Conclusion

Confirming Experiment 1, chimpanzees did not show an attentional bias toward the emotions of either conspecifics or humans. The previous finding of an interaction between Presentation Duration and Distracting Emotion was not replicated. Because this effect was not anticipated in the first place and was only small, we have to conclude that this was probably a false positive. In the next experiment, we investigate how human observers perceive chimpanzee compared with human expressions. See Table 2.

Experiment 3: Emotional Dot-Probe Task in Human Observers Observing Chimpanzee and Human Expressions

Method

Participants. A total of 711 (342 female) visitors of the science museum NEMO in Amsterdam, The Netherlands, participated. Participants were 25 years old on average, and their age ranged from 4 to 103 years old. The sample included 241 children (<18 years old). Participants were approached by the test leaders, attracted via posters that hang in the museum, or were informed via a call on the museums' "Science Live" website. All participants filled out an informed consent before taking part in the experiment. The study was performed in accordance with the Declaration of Helsinki and approved by the local medical ethical committee.

Stimulus material. The same stimulus material was used as in Experiment 2. Hence, people saw chimpanzee and human images.

Experimental procedure. The testing room was located in a separate and quiet section of the science museum NEMO in Amsterdam. Two museum visitors were tested at a time and were supervised by two experimenters. Upon their arrival to the testing room, participants, often families, were seated at a table and given an information brochure to read. There were two versions, one for adults and one for children. After reading, the test leader provided a verbal summary. If the procedures were understood correctly, the test leader handed them the informed consent to sign. Parents were signing for their children.

Participants were seated behind the computer screen and completed two tasks: first an emotional dot-probe task and then an emotional-intensity rating task. For the emotional-intensity rating task, participants were presented with angry, fearful, and neutral human and chimpanzee images and instructed to rate "how anx-

ious" and "how angry" the presented individuals were on a 7-point scale, ranging from *not at all* to ". Although we are aware that "display" is not a synonym for "anger," and "submission" is not exactly the same as "fear," we choose to stick to these labels because most people, children included, would know these terms. It was stressed that there were no correct or incorrect answers and that they had to follow their intuition. After the dot-probe task, each participant rated a randomly drawn subset of 24 images (12 chimpanzees and 12 humans) from our total stimulus set. These were presented in a random order.

The instruction for the emotional dot-probe task to the museum visitors was held short and simple:

> In this experiment, you will see different pictures of humans and chimpanzees. You will also see a dot on the screen. Your task is to tap on that dot as fast as you can. Chimpanzees have conducted the exact same task. Do you think you can be faster than the chimpanzees?

At the end of the experiment, participants saw a bar graph with their mean RT next to a bar representing the chimpanzee data (see Experiment 2). All participants were given a debriefing brochure at the end of the experiment in which they could read more background information of the study and its hypotheses.

Participants were presented with pictures of angry, fearful, and neutral chimpanzees and humans. Each participant completed 48 trials (half with scrambled images). A trial started with a dot presented at the middle, lower part of the computer screen. After touching the dot, two pictures (always both scrambled or both normal) were presented for 33 ms (300 ms), followed by a masking image presented for 300 ms (33 ms), followed by a dot in the position of one of the pictures. Participants touched the dot, followed by a blank gray screen that was presented for 1,000 ms. In the literature, mixed findings have been observed in the emotional dot-probe task that might be related to differences in the task setup. Most prior studies have used button boxes to record responses, but studies with animals have used touch screens (King et al., 2012; Lacreuse, Schatz, Strazzullo, King, & Ready, 2013). To solve that issue, half of the participants in the museum conducted the task with a button box and half of them with the touch screen. Because there was no difference observed between these two samples and their RTs following the different images, we further ignored that factor in the statistical analyses.

After the experiment, participants were thanked and given a written debriefing with more background information of the ex-

Table 2
Study 2 Results

Target-Context	Chimpanzee stimulus				Human stimulus			
	Presentation duration				Presentation duration			
	33 ms		300 ms		33 ms		300 ms	
	M	SE	M	SE	M	SE	M	SE
Display Fear	437.145	20.900	488.310	29.238	454.687	24.975	445.179	20.066
Display Neutral	486.627	33.034	438.940	20.178	462.904	22.006	451.560	20.649
Fear Display	516.585	37.960	421.716	14.074	461.310	29.185	476.313	32.489
Fear Neutral	432.964	23.633	477.060	25.363	500.190	41.268	439.451	19.725
Neutral Display	476.667	26.307	488.337	31.041	444.060	27.024	439.169	21.391
Neutral Fear	483.096	29.517	473.634	28.294	534.602	38.339	432.446	23.047

periment, and they could leave their e-mail address if they wished to remain informed on the outcomes of the study.

Experimental design and data analysis. Anger and fear intensity scores were analyzed in a two-level generalized mixed model, implemented in SPSS Version 20. The 24 different trials were nested within participants. RTs larger than 2,500 ms were excluded (0.25%). Because the data were skewed, a gamma probability distribution was selected with a log link function (Kret et al., 2016). Fixed factors included the following: Species Stimulus (human or chimpanzee), Emotion Stimulus (anger, fear, or neutral), Rating Type (fear or anger intensity), and their interactions. Because the value of the intercept may differ over participants, a random intercept was included.

The dot-probe task had the same design as Experiment 2. Within a trial, there were always two different emotions presented (fear–anger, fear–neutral, and neutral–anger). Data were analyzed in a two-level generalized mixed model, where the trials were nested within participants. Due to the large age variability in the sample and the known effects of age on RTs, age was added as an additional variable.

Results

Intensity rating. There were main effects of emotion, $F(2, 33.366) = 3.358,792, p < .001$, species stimulus, $F(1, 33.366) = 420,559, p < .001$, and rating type, $F(1, 33.366) = 864,006, p < .001$, indicating that people gave higher ratings to angry and fearful versus neutral expressions ($ps < 0.001$), higher ratings for humans than for chimpanzees ($p < .001$), and higher anger ratings than fear ratings ($p < .001$). An interaction between Emotion and Species, $F(2, 33.366) = 1.073,772, p < .001$, showed that the intensity ratings for angry stimuli were higher for human as compared with those for chimpanzee stimuli ($p < .001$). A much smaller, but also significant, opposite effect was found for fearful stimuli, which were rated as more intense in case stimuli showed a chimpanzee versus human ($p < .001$). There was also an interaction between emotion and rating type, $F(2, 33.366) = 3.053,534, p < .001$, simply showing that angry pictures gained higher anger

scores than fear scores, and it was the other way around for fearful stimuli ($ps < 0.001$). A Species–Rating Type interaction, $F(1, 33.366) = 226,329, p < .001$, showed that chimpanzee stimuli on average received lower fear ratings then anger ratings ($p < .001$). The same effect, although much smaller, was also found for human stimuli ($p < .001$). Finally, there was a three-way interaction between emotion, species stimulus and rating type, $F(2, 33.366) = 5.104,191, p < .001$. Most strikingly, this showed that fearful chimpanzees were recognized as being angry rather than fearful ($p < .001$). See Figure 3.

Dot-probe task. As we predicted, we observed a main effect for target emotion with faster responses following angry and fearful as compared with neutral expressions, $F(2, 16.966) = 5.115, p = .006$. Interestingly, this effect was not further qualified by interactions with species stimulus, distracting emotion or stimulus presentation, which adds to the robustness for this effect in humans. Another anticipated effect was an effect of age where the older participants had slower RTs than the younger ones, $F(2, 16.966) = 10.967, p < .001$. Age did not interact with any of the other predictors.

Unanticipated other main effects were observed for other predictors, which for brevity are shown in Table 3. These main effects were further qualified by higher order interactions. There was a three-way interaction between species stimulus, distracting emotion and stimulus presentation duration, $F(2, 16.966) = 9.082, p < .001$, supported by a two-way interaction between species stimulus and stimulus presentation duration, $F(1, 16.966) = 13.823, p < .001$. Follow-up simple contrasts showed several significant effects, which are listed in Table 4. Visual inspection of the means showed that in the case of fearful and angry expressions, the effect of presentation duration flipped for chimpanzee as compared with human expressions (Figure 4). This demonstrates that fear and anger were not processed in the same way when expressed by a human versus when expressed by a chimpanzee. But please note that this result is specific for the distracting emotion and does not apply to the target emotion. Another interesting observation is that presentation duration had little effect on
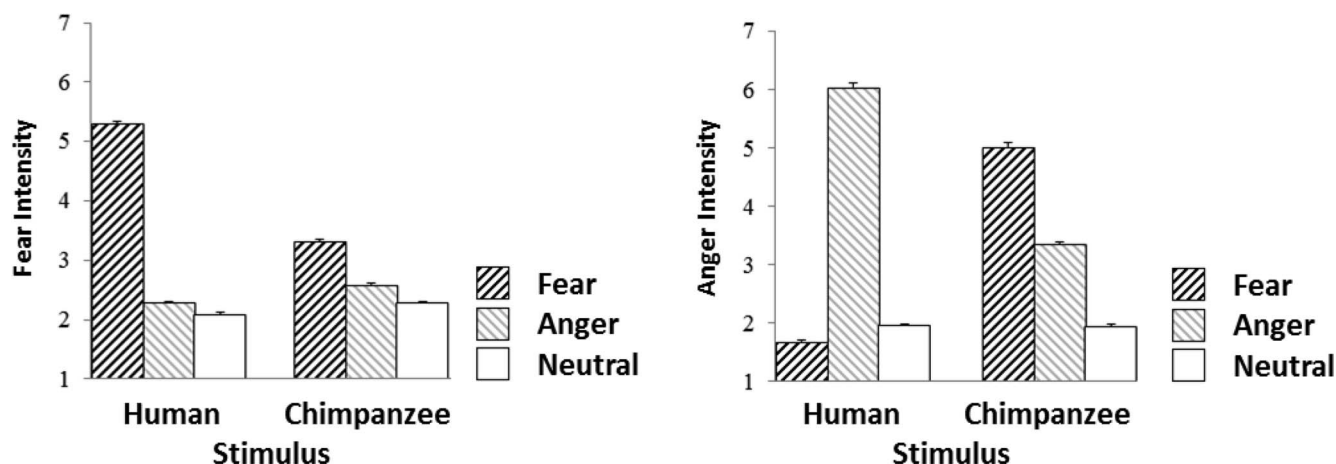

Figure 3. Emotional intensity scores from human observers. People gave relatively high fear-intensity scores to fearful humans and also high anger-intensity scores to angry humans. In contrast, they rated fearful chimpanzees as being more angry than fearful. Error bars represent the standard error of the means.

Table 3
Experiment 3: Emotional Dot-Probe Task in Human Observers

Fixed factor	F	$df\,1$	$df\,2$	Significance
Corrected Model	4.972	18	16,966	.000
Stimulus Presentation Duration	7.741	1	16,966	.005
Distracting Emotion	3.994	2	16,966	.018
Target Emotion	5.115	2	16,966	.006
Species Stimulus	4.702	1	16,966	.030
Age of Subject	10.967		16,966	.001
Distracting Emotion × Stimulus Presentation Duration	8.304	2	16,966	.000
Target Emotion × Stimulus Presentation Duration	2.716	2	16,966	.066
Species Stimulus × Stimulus Presentation Duration	13.823	1	16,966	.000
Species Stimulus × Distracting Emotion	0.532	2	16,966	.588
Species Stimulus × Target Emotion	2.116	2	16,966	.120
Species Stimulus × Distracting Emotion × Stimulus	9.082	2	16,966	.000

					95% CI	
Random factor	Estimate	SE	Z	Sig.	Lower	Upper
Variance	.094	.001	90.152	.000	.092	.096
Variance (Intercept)	.076	.004	17.856	.000	.068	.085

the processing of fearful distractors, whether human or chimpanzee. However, presentation duration did modulate the effect of angry and neutral distractors on RTs. This last finding, for example, the slower RTs during trials where the distracting image showed a neutral individual and that was presented for 33 ms rather than 300 ms, is opposite to what was found in Study 1 with the chimpanzee subjects.

Conclusion

Humans gave high fear ratings to stimuli depicting fearful humans and high anger ratings to pictures showing angry humans. Their emotion-intensity ratings were much less distinctive for fearful and angry chimpanzee stimuli. They recognized that chimpanzee expressions of fear (~submission) and anger (~display) were not neutral but often intermingled the specific emotion labels.

In line with the literature on the emotional dot-probe task, we observed faster responses toward emotional expressions as compared with neutral expressions, independent of stimulus presentation duration and the depicted species. In addition, there was a

three-way interaction between species stimulus, distracting emotion, and stimulus presentation duration. The interpretation of this result remains admittedly speculative, but it is possible that fearful chimpanzees, who were actually recognized as angry, highly negative, and aroused, were processed as a direct threat, for example, as showing anger, and triggered corresponding action tendencies similar to those evoked by stimuli showing angry humans. It is interesting that the pattern for the two emotional expressions reverses when expressed by chimpanzees.

Discussion

To successfully navigate the social environment, it is of crucial importance for primates to understand the actions and emotions of others (de Waal, 2011). In primates, humans included, nonverbal expressions such as facial expressions and body language are used to guide social decisions, such as to stay away from an aggressive individual or to greet someone who smiles at you. Emotions can be expressed unconsciously but can also be meant as communicative signals, like the smile in humans. Either way, expressions of

Table 4
Results of Simple Contrast Tests

Species Stimulus	Stimulus Presentation Duration (ms)	Distracting Emotion	Contrast estimate	Sig.
Chimpanzee	33	Fear vs. Anger	−20.772	.002[a]
Chimpanzee	33	Neutral vs. Fear	26.065	.001[a]
Chimpanzee	33 vs.300	Neutral	31.44	.000[a]
Chimpanzee	33 vs.300	Anger	22.155	.000[a]
Human	33	Neutral vs. Anger	23.629	.000[a]
Human	33	Neutral vs. Fear	18.567	.005
Human	300	Fear vs. Anger	−16.051	.014
Human	33 vs.300	Neutral	13.357	.031
Human	33 vs.300	Anger	−20.443	.001[a]
Anger	33	Chimpanzee vs. Human	28.715	.000[a]
Anger	300	Chimpanzee vs. Human	−13.883	.024

[a] With 24 simple contrasts, these comparison survive a Bonferroni correction for multiple comparisons.
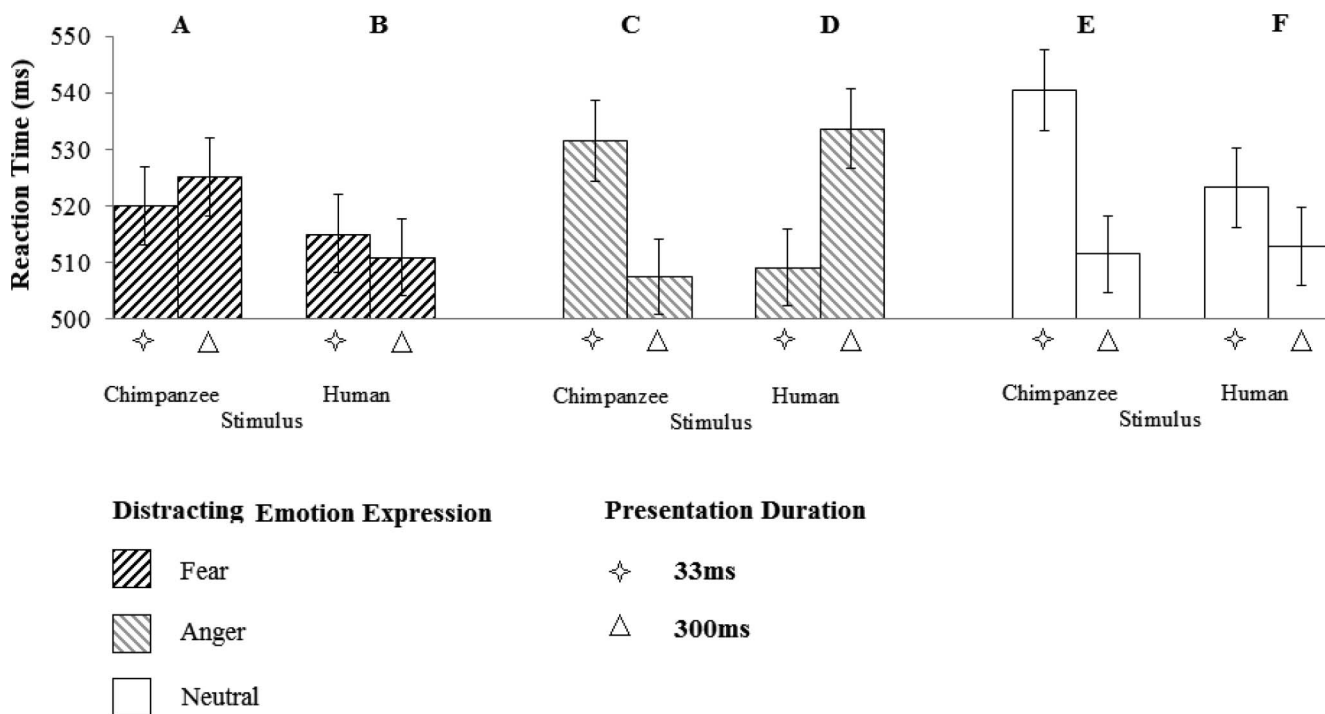
Figure 4. Emotional dot-probe task in human observers. Visualization of three-way interaction between species stimulus, context emotion, and stimulus presentation duration. Error bars represent the standard error of the means.

emotion provide relevant information for observers and influence their subsequent actions, often to the benefit of expresser and observer (Öhman, & Soares, 1993; LeDoux, 1996). By taking a comparative approach, the current study aimed to provide insight into emotion processing within humans and their closest living relatives, the chimpanzee.

Efficiently responding to others' emotions has great survival value, especially for social species such as primates who establish close, long-term bonds with group members (Darwin, 1872; Spoor & Kelly, 2004). Prior research in humans has shown that one component of this strong sensitivity to others' emotions is heightened attention to their affective states (Phelps, Ling, & Carrasco, 2006; Schupp, Junghöfer, Weike, & Hamm, 2003; Vuilleumier, 2005; van Rooijen et al., 2017). Together with the chimpanzee, the bonobo is the closest living relative of humans. Studying components of their emotional behavior, such as emotional attention, not only helps us to understand these species better but also provides insight into (human) emotions and their evolutionary past (Anderson & Adolphs, 2014; de Waal, 2014; Panksepp, 1998). We recently demonstrated that bonobos, like humans, show increased immediate attention to scenes depicting conspecifics showing emotions compared with scenes with conspecifics in a neutral state (Kret et al., 2016). In contrast to our prediction, investigating a putatively similar attentional bias toward emotions in chimpanzees in Experiments 1 and 2 failed to show any such effect with isolated whole body expressions, although we did find such a bias in humans, by testing a large sample of participants.

The question of why we could not find evidence for an attentional bias toward emotions in chimpanzees has several potential

answers. One explanation is that chimpanzees do not care about the emotions of conspecifics, and therefore their attention is not driven toward them. This interpretation, however, is unlikely, as many previous studies, observational studies and experimental ones alike, have shown that they do care (Buttelmann et al., 2009; de Waal, 2011; Izumi, & Kojima, 2004; Kano et al., 2008; Kano & Tomonaga, 2010; Parr, 2003; Parr, Waller, & Heintz, 2008) and even mimic subtle expressions (Kret, Tomonaga, & Matsuzawa, 2014). Moreover, this would also go in against evolutionary arguments stating that emotional expressions evolved as adaptations and are likely to be continuous (Darwin, 1872; Scherer et al., 2011; van Rooijen et al., 2017). Another possibility is that our stimulus material was not ecologically valid enough to yield effects in this particular task in chimpanzees. In our previous study with bonobos, more complex, naturalistic social-emotional scenes in color were used (Kret et al., 2016). In that study, the emotional pictures included scenes where bonobos (one or more individuals) showed clear signs of distress (fights, fear grimace, and threat displays) or were playing and also scenes that can be associated with stress, such as when there is food at play, or more positive scenes, such as images of bonobos having sex, which can be used as a means of (re)establishing social bonds, as is grooming. Furthermore, we included pictures where bonobos were calling each other (pant hoot) or were yawning. The stimulus set not only showed more ecologically valid scenes, but was with the large total number of unique stimuli and the various emotion categories, much richer than the stimulus set in the current study. The current stimulus set was better controlled, but possibly at the cost of naturalness. From the RT data and observations of the behavior, it became very clear

that the emotional scenes evoked emotions in bonobo observers. From the seven different emotion categories, significant biases were observed following the pictures showing sex, grooming sessions, and images of yawns. A trend toward significance was observed for pictures showing distress. Perhaps, had we used naturalistic scenes in color, or positive emotional scenes, attentional biases toward emotions in the chimpanzees would have emerged as well. That said, it is unlikely that chimpanzees did not recognize the emotional content in our images. Previous research has consistently shown that chimpanzees can explicitly recognize conspecifics' emotions, even from grayscaled images (Izumi, & Kojima, 2004; Parr, 2003, 2004; Parr et al., 2008). Kano and Tomonaga (2010) investigated sustained attention by measuring looking times with eye-tracking equipment. They found that chimpanzees attended longer to desaturated video clips showing agonistic scenes than to neutral scenes but found no differences with scenes showing play or excitement. Still, in another study that investigated the holistic processing of faces and behinds in humans and in the same chimpanzees as in our current study, desaturating the images had no effect on the "face inversion effect" (demonstrating expertise in recognizing identities through this modality) in humans but rendered the "behind inversion effect" that was specifically observed in chimpanzees when observing images in color, nonsignificant (Kret & Tomonaga, 2016).

The question that then still remains is whether our stimulus material was sufficiently strong, carried enough emotionally intense information, to evoke biases in immediate attention or not. In our study with bonobos, we observed that the more emotionally intense a picture was rated by their keepers, the faster the bonobos' responses were when the dot replaced these pictures (Kret et al., 2016). It must however be noted that the exact same stimuli that in chimpanzees did not drive attention reliably captured attention in humans, as was shown in Experiment 3. A possibility is that this is because humans are more used to derive meaning from symbolic, schematic, or otherwise more artificial images than chimpanzees. However, research has shown that also in humans, the more emotional information that is available in a stimulus, whether from a facial expression, body posture, or social scene, the greater their level of arousal (as measured by pupil size). In that particular study, the pupillary response was the greatest following angry body postures that were placed in violent scenes (Kret et al., 2013). One idea to follow this up in chimpanzees is to measure arousal, for example, with thermal imaging or pupillometry, and to directly compare the effects of photos showing isolated body postures with those of photos showing naturalistic scenes showing multiple emotional components from different individuals.

Experiment 3 investigated to what extent humans can recognize human and chimpanzee expressions of fear and anger as compared with neutral expressions. We observed that humans are better at recognizing expressions of fear and anger when shown by a human as compared with a chimpanzee. Chimpanzee expressions of fear were often rated as angry, possibly due to the display of the sharp canines, which might have been interpreted as purely threatening. Whereas subsequent fear- and anger-intensity ratings were positively correlated when they concerned chimpanzee stimuli, they were negatively correlated in response to human stimuli. This means that humans rated the chimpanzee stimuli more on arousal and the human stimuli on fearfulness and anger specifically (see also Results in the online supplemental material where humans did

not recognize the angry chimpanzee stimuli as being negative and arousing stimuli, whereas the fearful chimpanzees were rated as very negatively and very arousing). It is without doubt useful to be able to differentiate between different expressions of emotion from conspecifics. For example, not being able to distinguish between anger and fear will likely result in inappropriate responses with negative or even dangerous consequences. From the evolutionary perspective, it is also relevant for humans to recognize emotions in other animals to some extent, but perhaps it is oftentimes sufficient to know whether an animal is stressed and agitated as compared with when it is relaxed and at ease.

The humans that we tested had no experience with chimpanzees whatsoever, and it is possible that accurate cross-species emotion recognition comes with experience and learning (Martin-Malivel, & Okada, 2007). That said, there were no differences in attentional bias toward fearful as compared with angry stimuli. Both expressions attracted attention more than neutral ones (for similar results, see de Valk et al., 2015). Most interestingly, this was also true for the chimpanzee expressions: Humans attended to those more readily than to images of chimpanzees in a relaxed, neutral state. It is possible that had we added sound and dynamics to the stimulus material, naïve humans would have also explicitly recognized the specific emotion in chimpanzees. The similar attentional bias for human and chimpanzee expressions fits with the findings of a previous study that also tested Darwin's emotional continuity hypothesis (Belin et al., 2008). In their study, authors compared humans' perception of human and animal vocalizations on the explicit, behavioral level and on the neurophysiological level. The results showed that although humans failed to accurately discriminate rhesus macaques' and cats' affective vocalizations and whether these were positive or negative, the functional MRI results revealed successful discrimination, with the patterns of neural activation mirroring those obtained for human affective vocalizations. Possibly, this auditory activation pattern reflected low-level acoustical differences between the vocalizations. Similarly in our study, structural differences related to arousal or valence that are similar across humans and chimpanzees might have accounted for the attentional bias toward emotional expressions. Overall, this suggests an important degree of evolutionary continuity with respect to the underlying mechanisms.

There is a large literature showing that emotional expressions of others may be processed without awareness (Tamietto et al., 2009; Tamietto, & De Gelder, 2010). A predication that we therefore had and that was further based on a meta-analysis (Bar-Haim et al., 2007) was that the predicted attentional bias toward emotions would be stronger when stimuli were presented subliminally compared with those when stimuli were presented supraliminally (e.g., when processed unconsciously compared to consciously). This is not what we found. Presentation duration did not modulate the relationship between the emotional content presented on the target image and RTs on touching the probe. Instead, presentation duration did have an effect on RTs depending on the emotion of the distracting image and differentially so for human as compared with chimpanzee expressions. The precise pattern is complex, but it is potentially interesting to note that it is exactly reversed for chimpanzee compared with the human expressions, whereas no such reversal occurs for the neutral expressions. What this means exactly needs to be determined in future research.

Our study has several limitations. A limitation of this study is that the chimpanzees were captive animals having interacted with humans throughout their lives. Although they might not have seen human expressions of anger or fear that often, it is still possible that their reactions to human emotion expressions are not generalizable to wild animals, who might have shown different responses to stimuli of humans whom they have rarely encountered. Another limitation is that our study did not have sufficient power to specifically compare biases toward anger as compared with fear. Our study did not include a neutral–neutral condition. Future studies might benefit from such an experimental condition, as this allows for the investigation of attentional biases versus difficulties with disengaging from certain stimuli. Specifically, one can then compare RTs on threat-neutral trials with neutral–neutral trials (Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2004). Previous research has shown that certain factors might modulate the effects obtained on the emotional dot-probe task, one of them being threat intensity (Koster, Crombez, Van Damme, Verschuere, & De Houwer, 2005; Koster, Crombez, Verschuere, & De Houwer, 2004, 2006; Mogg, Bradley, Miles, & Dixon, 2004). For example, Wilson and MacLeod (2003) found that both high and low trait anxious individuals exhibited attentional biases toward highly threatening stimuli in the dot-probe task, though only high trait anxious individuals exhibited attentional biases toward mildly threatening stimuli. Future studies should therefore aim to take these factors into account (for a critical review on this task and further recommendations, see Cisler, Bacon, & Williams, 2009).

To conclude, applying well-established psychological paradigms to our closest relatives represents a promising approach to providing insight into similarities and differences between humans and apes. Over 500 articles have been published on the dot-probe task, showing that humans have an attentional bias toward emotional expressions, especially to those representing threats (for a review, see van Rooijen et al., 2017). For social species such as primates, efficiently responding to others' emotions has great survival value. The present study applies a popular psychological test to the chimpanzee and compares findings with humans. Even though the lack of effects in the chimpanzee subjects requires further investigation, we demonstrate that humans have heightened attention to emotional as compared with neutral individuals, independent of whether these individuals are humans or chimpanzees, thus partly supporting evolutionary continuity claims.

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