1 **Emotion processing across and within species.**

2 **A comparison between humans and chimpanzees (*Pan Troglodytes*).**

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Abstract

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 towards emotions in two closely related species, humans and chimpanzees. Previous research has demonstrated that humans typically show an attentional bias towards 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 towards the expressions of conspecifics and whether this putative bias is modulated by the stimulus presentation duration, being 33ms or 300ms. 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 33ms, rendering their presentation subliminal. In contrast to our prediction, no attentional bias towards 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 towards 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 towards 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

Introduction

For social species, recognizing emotions from conspecifics has great survival value. Research in humans and chimpanzees *(Pan troglodytes)* shows that both species *i)* recognize conspecifics' emotional expressions (for research in humans, e.g.e.g., Ekman, & Friesen, 1982; Ekman, Friesen, & Ellsworth, 2013); for studies with chimpanzees, see Parr, 2001; Buttelmann, Call, & Tomasello, 2009), *ii)* have better memory for pictures showing emotional as compared to neutral expressions (humans, e.g.e.g., Reisberg, & Heuer, 1992; chimpanzees, e.g.e.g., Kano, Tanaka, & Tomonaga, 2008) and *iii)* show prolonged attention to emotional versus non-emotional images (for a review in humans, see Palermo & Rhodes, 2007; for a study in chimpanzees, see Kano, Tanaka & Tomonaga, 2010). The majority of emotion research in humans has focused on the perception of facial expressions (Haxby et al., 2000; Adolphs, 2002). 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, Herberlein, & Adolphs, 2007; Sinke, Kret & de Gelder, 2013; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Kret, & de Gelder, 2010, 2013; Mondloch, Nelson, & Horner, 2013; for a review, see de Gelder et al., 2010). 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, 1987; Prochazkova & Kret, 2017). Emotions' potential for action supports an evolutionary account, which assumes that emotions evolved to benefit the organism by

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responding more adequately to threats in the environment (Nesse, 1990; de Waal, 2011). Indeed, we use another's emotion signals to guide our actions, for example, to initiate an approach reaction towards 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 (Öhman & Soares, 1993; LeDoux, 1996). 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 et al., 2009). Interestingly, when they do not, it is oftentimes the body that reveals expressors' genuine feelings (e.g., Aviezer, Trope, & Todorov, 2012).

In recent decades, researchers have taken up the issue of bodily expression recognition, and results from a number of behavioural 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 (2012) also showed that when two body postures were presented simultaneously on a computer screen, angry postures attracted most attention and more so than happy ones. Another more recent study measured action tendencies towards 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

99   expressions that appeared on either side of the screen. Results showed an attentional bias towards

100   expressions of anger and fear, with faster responses following these, as compared to neutral

101   expressions, independent of whether the emotions were expressed by the face or the body (de

102   Valk, Wijnen & Kret, 2015).

103   From as early as Darwin (1872), researchers have noted similarities between the expressions of

104   emotion in human and nonhuman primates. These species have a broad repertoire of stereotyped

105   facial behaviors and body postures that are seen as expressions of emotions (Andrew, 1963;

106   Chevalier-Skolnikoff, 1973; Hinde & Rowell, 1962; Maestripieri, 1997; Redican, 1975; van

107   Hooff, 1967; Steiner et al., 2001). Behavioural observations have demonstrated that non-human

108   primate emotional expressions and human emotional expressions can play similar functional

109   roles (Kret & Straffon, 2018). For example, human infants tend to use a pout face to solicit their

110   mother's attention, and a similar facial expression can be found in infant chimpanzees for the

111   same bonding functions (Blurton Jones, 1971; van Lawick-Goodall, 1968). Furthermore,

112   chimpanzees exhibit silent bared teeth displays and play faces that assist in social bonding and

113   the maintenance of social groups. In humans, the same bonding function is served by smiling,

114   which looks similar to those chimpanzee displays (van Hooff, 1967, 1972; Chevalier-Skolnikoff,

115   1973, 1982; Preuschoft & van Hooff, 1995; Burrows, Waller, Parr & Bonar, 2006; Kret &

116   Straffon, 2018; see Gaspar, 2006, for a review).

117   Nonhuman primates are not merely able to express emotions, but they also successfully

118   distinguish emotional expressions in others. Chimpanzees are capable of discriminating an

119   emotional facial expression made by two different individuals from that of a neutral expression

120   of a third individual. Successful discrimination of different emotional expressions was dependent

121   on the amount of shared features between the two expressions, as is also known to be the case in

122   humans (Parr, Hopkins, & de Waal, 1998). In another study comparing chimpanzees and rhesus

123   macaques, it was shown that both species are able to use facial expressions to discriminate

124   unfamiliar conspecifics although the macaques required more trials to learn the task (Parr,

125   Winslow, Hopkins & de Waal, 2000). Rhesus monkeys are also capable of discriminating

126   emotional expressions from neutral expressions, yet they showed more difficulties with

127   discriminating two distinct emotional expressions (Parr & Heintz, 2009). Moreover, other

128   research has demonstrated that macaque cardiac physiology is sensitive to the valence of

129   passively viewed sensory stimuli (Bliss-Moreau, Machado, & Amaral, 2013). One key

130   mechanisms that is at play when processing conspecifics' expressions of emotion, is increased

131   attention towards these expressions.

132   Attention towards the expressions of conspecifics is a topic that has been addressed in a number

133   of previous experimental studies. In a recent eye tracking study for instance, it was shown that

134   macaque monkeys attend more quickly and also attend longer to monkeys showing aggressive or

135   submissive compared to neutral behaviors. This effect was driven by heightened attention to the

136   body (Bliss-Moreau, Moadab & Machado, 2017), a finding replicating earlier findings in humans

137   (Kret, Stekelenburg, Roelofs & de Gelder, 2013). In that latter study it was also found that

138   humans' level of arousal was higher when they observed images of people of whom both the

139   face and the body showed anger or fear compared to happiness (see also Kret, Roelofs,

140   Stekelenbrug & de Gelder, 2013). Thus, previous research has shown that emotions are

141   expressed by the face and the body and that expressions, especially threat displays, are readily

142   picked up by observers and facilitate fast actions.

143   The underlying neural mechanism that makes us attend to emotions is still not understood

144   completely. The literature shows that subcortical, evolutionary old brain structures play key roles

145 in emotion processing across and beyond different primate species (e.g. Bliss-Moreau, Moadab,

146 Bauman & Amaral, 2011; 2013). One possible way to tap into this mechanism is by visually

147 masking experimental stimuli. Visual masking results in the reduction or elimination of the

148 visibility of one brief stimulus by the presentation of a second brief stimulus, called the "mask".

149 If a stimulus is followed by a blank screen, the perceptual presentation duration of the stimulus is

150 somewhat prolongued due to the after image. When instead of a blank screen a carefully selected

151 visual mask is presented, there is no such after image and the stimulus presentation duration is

152 better secured. Masking stimuli would yield similar or even larger effects on emotional attention

153 than unmasked stimuli (Bar-Haim et al., 2007; Hedger, Gray, Garner, & Adams, 2016). We here

154 aim to examine this possibility by investigating attentional biases towards subliminally (below

155 conscious thresholds) and supraliminally (can be processed consciously) presented emotional

156 expressions in human and chimpanzee observers, by using the dot-probe task (MacLeod,

157 Mathews, & Tata, 1986). In the dot-probe task, two pictures are briefly being presented next to

158 each other on a computer screen. Next, one of the two is replaced by a dot, the location of which

159 participants need to indicate as fast as possible by using the arrows 'left' and 'right' on a

160 keyboard, or by touching the dot directly on a touch-screen. Typically, as attention is attracted to

161 biologically relevant stimuli, touching the dot is faster when it replaces an emotion compared to

162 neutral image. This task is often used in psychology and has a lot of potential for testing

163 emotional attention across primate species, primarily because this test is implicit and because

164 evidence, although still scarce, is accumulating that it does not require verbal instruction.

165 Moreover, subjects need no or minimal training to perform the test successfully (King, Kurdziel,

166 Meyer, & Lacreuse, 2012; Kret, Jaasma, Bionda, & Wijnen, 2016; Parr, Modi, Siebert, & Young,

167 2013; Tomonaga & Imura, 2009, see van Rooijen, Ploeger & Kret, 2017 for a review). The

168   majority of dot-probe studies have used a stimulus presentation duration of 500 ms. A limitation

169   of this presentation duration is that attention may already have shifted between the two stimuli.

170   Thus, responses given after a stimulus presentation of 500 ms do not necessarily provide

171   information about participants' initial orientation (Bradley, Mogg, & Millar, 2000). To avoid

172   this, other dot-probe studies used a shorter or even subliminal stimulus presentation. A meta-

173   analysis showed that the effect size of subliminal presentation was twice as large as that of

174   supraliminal presentation in anxious individuals (Bar-Haim et al., 2007). A more recent meta-

175   analysis of 28 masked dot probe experiments found a small effect of a threat bias, comparable to

176   the effect of the supraliminal presentation in the review of Bar-Haim et al. (2007) (Hedger et al.,

177   2016).

178   If this evolutionary ancient route that facilitates the unconscious processing of emotions, is

179   indeed involved, then it is likely that chimpanzees will process emotions similarly as humans.

180   Thus, they will show similar attentional biases, especially towards the masked stimuli. We aim to

181   investigate this possibility in the current study. Moreover, we will address the question of

182   whether humans are perceiving chimpanzee expressions similarly as humans, and vise-versa.

183   Darwin (1872) claimed that some emotional expressions have evolutionary ancient roots and are

184   innate: 'the young and the old of widely different races, both with man and animals, express the

185   same state of mind by the same movements' (p. 348, see also Scherer, Clark-Polner &

186   Mortillaro, 2011). Following this rationale, one could argue that if so, species might be able to

187   recognize the emotional expressions of other species. Research on the perception of emotion in

188   other species is still scarce, but some studies suggest that this might indeed be the case. In a

189   recent article, Filippi et al (2017) showed that fundamental aspects of vocal emotional

190   expressions are shared across all extant species that trace their ancestry to early terrestrial

191 tetrapods. More specifically, in their study, they identified acoustic universals that conveyed the

192 same emotional information across a broad range of vocalizing species and showed that humans

193 can use these universals to correctly infer the emotional state of other species. Cross-species

194 emotion perception has also been investigated in a study with dogs. The study combined visual

195 and auditory cues in a cross-modal preferential looking paradigm. Dogs were presented human

196 or dog faces with different emotional valences (happy/playful versus angry/aggressive), paired

197 with a single vocalization from the same individual with either a positive or negative valence or

198 Brownian noise. The results showed that dogs looked significantly longer at the face whose

199 expression was congruent rather than incongruent to the valence of the vocalization, for both

200 conspecifics and heterospecifics. This result demonstrates that dogs can extract and integrate

201 bimodal sensory emotional information, and discriminate between positive and negative

202 emotions from both humans and dogs (Albuquerque et al., 2016). In the case of domestic dogs, it

203 can be argued that it might be particularly advantageous to recognize the emotions of humans as

204 these are their daily companions. Also, human-dog co-evolution might have facilitated this

205 process. However, primate observation studies came to similar conclusions. For instance, Diana

206 monkeys understand the meaning and underlying cause of other primate species' alarm calls,

207 guinea fowl alarm calls, and different kinds of chimpanzee screams (Zuberbühler, 2000).

208 Another study in humans listening to human, macaque or cat vocalisations also suggest there are

209 shared emotional systems across species (Belin et al., 2008). However, none of these studies

210 directly compared the processing of emotion signals from their own as compared to other species

211 in a cross-species experimental setting. Therefore, comparing human and chimpanzees'

212 attentional biases towards emotional expressions from their own compared to the other species,

213 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 towards the expressions of conspecifics and whether this putative bias is modulated by the stimulus presentation duration, being 33ms or 300ms, 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 Experiment 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 in humans, these stimuli have reliably yielded an attentional bias towards the emotional compared to neutral ones (de Valk et al., 2015). Other research has investigated the role of expertise and conceptual knowledge on how other species emotions are categorized (e.g. Fugate, Gouzoules, & Nygaard, 2008; 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 towards 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 towards the emotional expressions of conspecifics. Whereas some research suggests that species experience the emotions of other species similarly as those expressed by their conspecifics, other research contradicts that (e.g. Madsen, Persson, Sayehli, Lenninger, & Sonesson, 2013; Martin-Malivel, & Okada, 2007; Fugate et al., 2010). From an evolutionary perspective (Darwin, 1872), we expect that species would process expressions from

237   conspecifics and other species similarly. Based on our previous study with a similar paradigm

238   (de Valk, Wijnen & Kret, 2015), we do not predict differences between fear and anger in this

239   task. Both emotions are salient, biologically relevant stimuli that are likely to drive attention.

240   Following the same reasoning we do not expect to see differences between chimpanzees'

241   expressions of dominance (display) or submission. Finally, based on a previous meta-analysis,

242   we predict that the putative attentional bias towards emotions is stronger when stimuli are

243   presented subliminally versus supraliminally (Bar-Haim et al., 2007).

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246   **Experiment 1 Emotional dot probe task in chimpanzee observers with chimpanzee**

247   **expressions**

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249   **Method Experiment 1**

250   *Participants.* Eight chimpanzees (two female juvenile and one male juvenile, four female and

251   one male adult) participated in this study. They were 24 years old on average (SD = 12). At the

252   time of testing, the chimpanzees lived within a social group of fourteen individuals in an

253   enriched environment with a 700 m2 outdoor compound and an attached indoor residence that

254   was illuminated during day-time at the Kyoto University Research Unit in Inuyama, Japan. The

255   outdoor compound was equipped with climbing frames, ropes, small streams, and various

256   species of trees. Access to the outdoor compound was available to them every other day during

257   the day. Daily meals included a wide variety of fresh fruits and vegetables fed throughout the

258   day supplemented with nutritionally balanced biscuits (fed twice daily) and water available ad

259   libitum. The chimpanzees have been familiar with humans since birth and interact with them on

260   a daily basis (especially during feeding and prior to and after the experiments). They have taken

261   part in various cognitive experiments since youth. For the daily experiments, the chimpanzees

262   left the social group voluntarily on the request of experimenters, moved into the experimental

263   booth with the guidance of experimenters, and moved back to the social group after the

264   completion of experiments (approx. 1 hour). The care and use of the chimpanzees adhered to the

265   3rd edition of the Guide for the Care and Use of Laboratory Primates issued by Primate Research

266   Institute, Kyoto University (KUPRI) in 2010, which is compatible with the guidelines issued by

267   the National Institute of Health in the United States of America. The research design was

268   approved by the Animal Welfare and Animal Care Committee of KUPRI and by the Animal

269   Research Committee of Kyoto University (#2011-078). All procedures adhered to the Japanese

270   Act on Welfare and Management of Animals.

271   *Stimulus Material.* A total of 161 pictures of male chimpanzees' whole body postures showing

272   submission (fear grimace), display (lip press and erased hair) and neutral expressions were

273   selected from a large database containing pictures of chimpanzees from the Chimpanzee

274   Sanctuary Uto (CSU), Kumamoto Sanctionary and Higashiyama zoo in Nagoya. The pictures

275   were cropped to minimize the visibility of the background and contained 640 by 1024 pixels.

276   Interfering objects which were visible in the background were removed in Photoshop. Based on

277   the emotion recognition and intensity scores of three independent raters who work with

278   chimpanzees on a daily basis, we selected 12 clear images per emotion category. The

279   chimpanzee-pictures were turned to grayscale and the overall luminance of each picture was

280   adjusted to achieve the mean luminance of all the selected pictures. The reason for turning the

281   images to grayscale is threefold. First, colored images do not allow accurate measurements of

282   luminance. This is important as brighter images could have popped out from the grey

283   background more than darker images and subsequently bias attention. So each image average

284   luminance was scaled to the mean luminance. A second reason for doing so is to be consistent

285   with the literature on visual masking that generally use greyscaled images (also to better deal

286   with potentially confounding effects of low-level differences between stimuli from different

287   conditions). Third, previous studies in chimpanzees showed they, like humans, can recognize

288   emotional expressions from desaturated (e.g., grayscale) images (Parr et al, 1998; Kano et al,

289   2010). See Figure 1.

290   In order to level out the possible effect of low level differences between the stimuli on reaction

291   times in the emotional dot probe task, we scrambled all stimuli with a mosaic pattern of 12 x 20

292   squares by using MATLAB. These scrambled images contained identical luminance as the

293   originals and were only used to verify whether significant effects were not related to possible

294   low-level differences between the stimuli. In addition to the scrambled images, the stimulus

295   material consisted of two types of visual masks that were carefully pilot-tested (see supplemental

296   methods). We choose to include two types of masks to reduce effects of specific properties of the

297   mask.

298   Each trial showed two images simultaneously and the dot subsequently appeared on the position

299   of one of these images. The stimuli were presented supraliminally (for 300ms) or subliminally

300   (for 33ms) and then immediately masked with a neutral body image. Although we could not

301   verify whether chimpanzees perceived these stimuli consciously or not, we first verified in

302   humans that they were not consciously aware of the stimuli presented at 33ms. A detailed

303   description of this procedure and the piloting of different types of visual masks can be found in

304   the Supplementing Methods.

305

Insert Figure 1. here

Procedure. Subjects sat in an experimental booth (2.5 m wide x 2.5 m deep x 2.1 m high), with the experimenter and the subjects separated by transparent acrylic panels. The subjects viewed a 17-inch LCD display (1280 x 1024 pixels). Distance to the computer screen was 60 cm. Stimuli were presented on a PC screen with a 60 Hz refresh rate and with an distance of 218 pixels between the two stimuli. A food reward was provided after the chimpanzee tapped on the target. Each chimpanzee completed 1120 trials on ten days in total, spread out over a two-week period. There were one or two testing sessions per day, 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/Non Scramble (2), 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 33ms (300ms), followed by a masking image presented for 300ms (33ms), followed by a dot on the position of one of the pictures. Subjects touched the dot, followed by a blank grey screen that was presented for 1000ms. The dots were presented untill subjects touched the dot.

Experimental Design and Data-analysis. Within a trial there were always two different emotions presented (fear-anger; fear-neutral; neutral-anger). Thus, Target Emotion and Distracting Emotion were not independent since the same emotions were never presented next to each other in one trial. Data were analyzed in a two-level Generalized Mixed Model

327   implemented in SPSS version 20, where trials were nested within sessions and within

328   participants. Reaction times larger than 2500ms were excluded (1.97%). As the data were

329   skewed, a gamma probability distribution was selected with a Log link function (which is similar

330   to a log-transformation). The statistical model had the following fixed factors included: Target

331   Emotion (anger, fear or neutral), Presentation Duration (33/300ms), Target Emotion *

332   Presentation Duration, and Distracting Emotion (anger, fear or neutral), Distracting Emotion *

333   Presentation Duration and Age of Subject. As the value of the intercept may differ over

334   participants, a random intercept was included. Traditionally, the dot-prob task is analyzed with

335   bias scores. However, it has recently been recommended to refrain from that method if the

336   sample is very small. A better procedure for the application of the dot-probe task in samples with

337   a small N is to not average any data points and nest all trials within each subject via a multilevel

338   statistical procedure. That way, reaction times can be analyzed as a function of the picture that

339   appeared previously on the location of the probe, and as a function of the picture that earlier

340   appeared on the other location, the location opposite of the probe (van Rooijen et al., 2017). This

341   procedure was also followed in our previous study with bonobos (Kret et al., 2016)

342

343   **Results Experiment 1**

344   An analysis of the reaction times showed that overall, chimpanzees did not show the classical dot

345   probe effect as has been described often in the human and non-human primate literature (e.g.

346   faster reaction times towards emotions (for a review see van Rooijen et al., 2017)) ($p = 0.906$).

347   Instead, there was an interaction between Presentation Duration * Distracting Emotion $F_{(2, 4.565)} = 3.033$,

348   $4.565) = 3.033$, $p = 0.048$. Simple contrasts show that Presentation Duration only matters when

349   the distracting image shows a neutral stimulus. Reaction times are longer in the trials where

350 stimuli were shown for 300ms rather than 33ms and where the distracting image showed an

351 individual in a neutral state $t(4.565) = 2.634$, $p = 0.008$. In addition, there was a trend towards a

352 significant main effect of age $F(2, 4.565) = 3.619$, $p = 0.057$. See Table 1.

353

354

355 "Insert Table 1 here"

356

357 **Conclusion Experiment 1**

358 The effect that has been observed many times in humans, as well as in bonobos (Kret et al.,

359 2016) and macaques (Parr et al., 2013), was not replicated in chimpanzees. A previous study has

360 shown that chimpanzees attention is grabbed by neutral faces more than by different objects

361 (Tomonaga & Imura, 2009) and we therefore had not expected this finding. There can be many

362 reasons for why this null-finding was obtained, one of them being chance. An unanticipated

363 effect that we did obtain however, was an interaction between Presentation Duration and

364 Distracting Emotion. In order to confirm this effect and to confirm the null-finding with regard to

365 Target Emotion, we ran the experiment one more time for confirmation, and in addition added

366 human expressions, which in the past have yielded reliable attentional biases in humans (de Valk

367 et al., 2015).

368 **Experiment 2 Emotional dot probe task in chimpanzee observers observing chimpanzee**

369 **and human expressions**

370

Method Experiment 2

Participants. Seven chimpanzees of the previous study again participated two years later (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 x 12) images showing human expressions. The heads in the human stimuli are taken from the NimStim stimulus set (Tottenham et al., 2002). Pictures of human bodily expressions of emotion were taken from the stimulus database BEAST, containing 254 digital pictures (de Gelder & van den Stock, 2011). The pictures were shot in a professional photo studio under constant lighting conditions. Non-professional 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, 2008). 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 grey 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.

"insert Figure 2 here"

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

392   chimpanzees completed 96 trials per session. The completed one or two sessions per day (one in

393   the morning, one in the afternoon) spread out over six days that all fell within a few couple of

394   weeks. In total, each chimpanzee completed 576 trials. There were 24 trials in total per condition

395   (species (2), emotion (3), presentation duration (2), scramble-normal (2)). The order of

396   presentation was randomized.

397   ***Experimental Design and Data-analysis.*** The statistical design was similar to Experiment 1 with

398   Species Stimulus and interactions with the other factors in addition. Again, trials with reaction

399   times larger than 2500ms were excluded (1.05%). The data were analyzed in the same way as

400   Experiment 1.

401   **Results Experiment 2**

402   Again, chimpanzees did not show the classical dot probe effect as humans (e.g. faster reaction

403   times towards emotions) ($p = 0.603$). None of the other main or interaction effects were

404   significant ($ps \geq 0.080$).

405

406   **Conclusion Experiment 2**

407   Confirming Experiment 1, chimpanzees did not show an attentional bias towards the emotions of

408   either conspecifics or humans. The previous finding of an interaction between Presentation

409   Duration and Distracting Emotion was not replicated. As this effect was not anticipated in the

410   first place and was only small, we have to conclude that this was probably a false positive. In the

411   next experiment we investigate how human observers perceive chimpanzee compared to human

412   expressions. See Table 2.

413

414   "insert Table 2 here"

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Experiment 3 Emotional dot probe task in human observers observing chimpanzee and human expressions

419

Method Experiment 3

Participants. 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.

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.

436 Participants were seated behind the computer-screen and completed two tasks, first an emotional

437 dot-probe task and then an emotional intensity rating task. For the emotional intensity rating task,

438 participants were presented with angry, fearful and neutral human and chimpanzee images and

439 instructed to rate "how anxious" and "how angry" the presented individuals were on a 7-point

440 scale ranging from "not at all" to "very much". Although we are aware that 'display' is not a

441 synonym for 'anger' and 'submission' not exactly the same as 'fear', we choose to stick to these

442 labels as most people, children included, would know these terms. It was stressed that there were

443 no correct or incorrect answers and that they had to follow their intuition. After the dot-probe

444 task, each participant rated a randomly drawn subset of 24 images (12 chimpanzees and 12

445 humans) from our total stimulus set. These were presented in a random order.

446 The instruction for the emotional dot probe task to the museum visitors was held short and

447 simple: *"In this experiment, you will see different pictures of humans and chimpanzees. You will*

448 *also see a dot on the screen. Your task is to tap on that dot as fast as you can. Chimpanzees have*

449 *conducted the exact same task. Do you think you can be faster than the chimpanzees?"* At the

450 end of the experiment, participants saw a bar-graph with their mean reaction time next to a bar

451 representing the chimpanzee data (see Experiment 2). All participants were given a debriefing

452 brochure at the end of the experiment in which they could read more background information of

453 the study and its hypotheses.

454 Participants were presented with pictures of angry, fearful and neutral chimpanzees and humans.

455 Each participant completed 48 trials (half with scrambled images). A trial started with a dot

456 presented at the middle, lower part of the computer screen. After touching the dot, two pictures

457 (always both scrambled or both normal) were presented for 33ms (300ms), followed by a

458 masking image presented for 300ms (33ms), followed by a dot in the position of one of the

459   pictures. Participants touched the dot, followed by a blank grey screen that was presented for

460   1000ms. In the literature, mixed findings have been observed in the emotional dot probe task that

461   might be related to differences in the task-setup. Most previous studies have used button boxes to

462   record responses but studies with animals have used touch-screens (King et al., 2012; Lacreuse et

463   al., 2013). To solve that issue, half of the participants in the museum conducted the task with a

464   button-box, and half of them with the touch-screen. As there was no difference observed between

465   these two samples and their reaction times following the different images, we further ignored

466   that factor in the statistical analyses.

467   After the experiment, participants were thanked and given a written debriefing with more

468   background information of the experiment and they could leave their email address if they

469   wished to remain informed on the outcomes of the study.

470   ***Experimental Design and Data-analysis.*** Anger and fear-intensity scores were analysed in a

471   two-level Generalized Mixed Model, implemented in SPSS version 20. The 24 different trials

472   were nested within participants. Reaction times larger than 2500ms were excluded (0.25%). As

473   the data was skewed, a gamma probability distribution was selected with a Log link function

474   (Kret et al., 2016). Fixed factors included: Species Stimulus (human or chimpanzee), Emotion

475   Stimulus (anger, fear or neutral), Rating Type (fear or anger intensity) and their interactions. As

476   the value of the intercept may differ over participants a random intercept was included.

477   The dot-probe task had the same design as Experiment 2. Within a trial there were always two

478   different emotions presented (fear-anger; fear-neutral; neutral;-anger). Data were analysed in a

479   two-level Generalized Mixed Model where the trials were nested within participants. Due to the

480   large age variability in the sample and the known effects of age on reaction times, age was added

481   as an additional variable.

482

Results Experiment 3

484   *Intensity rating.* There were main effects of emotion $F(2, 33.366) = 3.358,792$, $p < 0.001$,

485   species stimulus $F(1, 33.366) = 420,559$, $p < 0.001$ and rating type $F(1, 33.366) = 864,006$, $p <$

486   0.001, indicating that people gave higher ratings to angry and fearful versus neutral expressions

487   (ps < 0.001), higher ratings for humans than for chimpanzees ($p < .001$), and higher anger-ratings

488   than fear-ratings ($p < 0.001$). An interaction between emotion and species $F(2, 33.366) =$

489   1.073,772, $p < 0.001$ showed that the intensity ratings for angry stimuli were higher for human as

490   compared to chimpanzee stimuli ($p < 0.001$). A much smaller, but also significant opposite effect

491   was found for fearful stimuli, which were rated as more intense in case stimuli showed a

492   chimpanzee versus human ($p < 0.001$). There was also an interaction between emotion by rating

493   type $F(2, 33.366) = 3.053,534$, $p < 0.001$, simply showing that angry pictures gained higher

494   anger-scores than fear-scores, and the other way around for fearful stimuli (ps < 0.001). A

495   species by rating type interaction $F(1, 33.366) = 226,329$, $p < 0.001$ showed that chimpanzee

496   stimuli on average received lower fear-ratings then anger ratings ($p < 0.001$). The same effect,

497   although much smaller, was also found for human stimuli ($p < 0.001$). Finally, there was a three-

498   way interaction between emotion, species stimulus and rating type $F(2, 33.366) = 5.104,191$, $p <$

499   0.001. Most strikingly, this showed that fearful chimpanzees were recognized as being angry

500   rather than fearful ($p < 0.001$). See Figure 3.

501

22

502   "Insert Figure 3 here"

503

504   ***Dot probe task.*** As we predicted, we observed a main effect for target emotion with faster

505   responses following angry and fearful as compared to neutral expressions $F(2, 16.966) = 5.115$, p

506     $= 0.006$. Interestingly, this effect was not further qualified by interactions with species stimulus,

507   distracting emotion or stimulus presentation, which adds to the robustness for this effect in

508   humans. Another anticipated effect was an effect of age where the older participants had slower

509   reaction times than the younger ones $F(2, 16.966) = 10.967$, $p < 0.001$. Age did not interact with

510   any of the other predictors.

511   Unanticipated other main effects were observed for other predictors which for brevity are shown

512   in Table 3. These main effects were further qualified by higher order interactions. There was a

513   three-way interaction between species stimulus * distracting emotion * stimulus presentation

514   duration $F(2, 16.966) = 9.082$, $p < 0.001$, supported by a two-way interaction between species

515   stimulus * stimulus presentation duration $F(1, 16.966) = 13.823$, $p < 0.001$. Follow-up simple

516   contrasts showed several significant effects which are listed in Table 4. Visual inspection of the

517   means showed that in the case of fearful and angry expressions, the effect of presentation

518   duration flipped for chimpanzee as compared to human expressions (Figure 4). This

519   demonstrates that fear and anger were not processed in the same way when expressed by a

520   human versus chimpanzee. But please note that this result is specific for the distracting emotion

521   and does not apply to the target emotion. Another interesting observation is that presentation

522   duration had very little effect on the processing of fearful distractors, whether human or

523   chimpanzee, but did modulate the effect of angry and neutral distractors. This last finding, e.g.,

524   slower reaction times in trials where the disctracting image showed a neutral individual and that

525   were presented for 33ms rather than 300ms is opposite to what was found in Study 1 with the

526   chimpanzee subjects.

527

528   "Insert Table 3 here"

529

530   "Insert Table 4 here"

531

532   **Conclusion Experiment 3**

533   Humans gave high fear ratings to stimuli depicting fearful humans and high anger ratings to

534   pictures showing angry humans. Their emotion intensity ratings were much less distinctive for

535   fearful and angry chimpanzee stimuli. They recognized that chimpanzee expressions of fear

536   (~submission) and anger (~display) were not neutral, but often intermingled the emotion labels.

537   In line with the literature on the emotional dot probe task, we observe faster responses towards

538   emotional expressions as compared to neutral expressions, independent of stimulus presentation

539   duration and the depicted species.

540   In addition, there was a three-way interaction between species stimulus * distracting emotion *

541   stimulus presentation duration. The interpretation of this result remains admittedly speculative

542   but it is possible that fearful chimpanzees, who were actually recognized as angry, highly

543   negative and aroused, were processed as a direct threat, e.g., as showing anger, and triggered

544   corresponding action tendencies similar to those evoked by stimuli showing angry humans. It is

545   interesting that the pattern for the two emotional expressions reverses when expressed by

546   chimpanzees.

547

548

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 emotion provide relevant information for observers and influence their subsequent actions, often to the benefit of expressor 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). Previous 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, Junghofer, 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, may help us not only to understand these species better, but also provides insight into (human) emotions and their evolutionary past (Panksepp, 1998; Anderson & Adolphs, 2014; de Waal, 2014). We recently demonstrated that bonobos, like humans, show increased immediate attention to scenes depicting conspecifics showing emotions compared to scenes with conspecifics in a neutral state (Kret et al., 2016). In contrast to our prediction, investigating a putatively similar attentional bias towards emotions in chimpanzees in Experiments 1 and 2, failed to show any such effect with isolated

573   whole body expressions, although we did find such a bias in humans, by testing a large sample of

574   participants.

575   The question of why we could not find evidence for an attentional bias towards emotions in

576   chimpanzees has several potential answers. One explanation is that chimpanzees do not care

577   about the emotions of conspecifics and therefore their attention is not driven towards them. This

578   interpretation however, is unlikely, as many previous studies, observational studies and

579   experimental ones alike, have shown that they do care (e.g. Parr, 2003; Parr et al., 2008; Kano et

580   al., 2008; Kano et al., 2010; Buttelmann, Call & Tomasello, 2009; de Waal, 2011; Izumi, A., &

581   Kojima, 2004) and even mimic subtle expressions (Kret et al., 2014). Moreover, this would also

582   go in against evolutionary arguments stating the emotional expressions evolved as adaptations

583   and are likely to be continuous (Darwin, 1872; Scherer et al, 2011; van Rooijen et al., 2017).

584   Another possibility is that our stimulus material was not ecologically valid enough to yield

585   effects in this particular task. In our previous study with bonobos, more complex, naturalistic

586   social emotional scenes in color were used (Kret et al., 2016). In that study, the emotional

587   pictures included scenes where bonobos (one or more individuals) showed clear signs of distress

588   (fights, fear grimace, threat displays) or were playing, but also scenes that can be associated with

589   stress, such as when there is food at play, or more positive scenes, such as images of bonobos

590   having sex, which can be used as a means of (re)establishing social bonds, as is grooming.

591   Furthermore, we included pictures where bonobos were calling each other (pant hoot) or were

592   yawning. From the reaction time data and observations of the behavior, it became very clear that

593   the emotional scenes evoked emotions in bonobo observers. From the seven different emotion

594   categories, significant biases were observed following the pictures showing sex, grooming

595   sessions, and images of yawns. A trend towards significance was observed for pictures showing

596   distress. Perhaps, had we used naturalistic scenes in color, or postive emotional scenes,

597   attentional biases towards emotions in the chimpanzees would have emerged as well. That said,

598   it is unlikely that chimpanzees did not recognize the emotional content in our images. Previous

599   research has consistently shown that chimpanzees can explicitly recognize conspecifics'

600   emotions, even from greyscaled images (Parr, 2003, 2004; Parr et al., 2008; Izumi, & Kojima,

601   2004). Kano et al. (2010) investigated sustained attention by measuring looking times with eye

602   tracking equipment. They found that chimpanzees attended longer to desaturated video clips

603   showing agonistic scenes than to neutral scenes, but found no differences with scenes showing

604   play or excitement. Still, in another study that investigated the holistic processing of faces and

605   behinds in humans and in the same chimpanzees as in our current study, desaturating the images

606   had no effect on the 'face inversion effect' (demonstrating expertise in recognizing identities

607   through this modality) in humans, but rendered the 'behind inversion effect' that was specifically

608   observed in chimpanzees, non-significant (Kret & Tomonaga, 2016).

609

610   The question that then still remains is whether our stimulus material was sufficiently strong,

611   carried enough emotionally intense information, to evoke biases in immediate attention, or not.

612   In our study with bonobos, we observed that the more emotionally intense a picture was rated by

613   their keepers, the faster bonobos' responses were when the dot replaced these pictures (Kret et

614   al., 2016). It must however be noted that the exact same stimuli that in chimpanzees did not drive

615   attention, in humans reliably captured attention, as was shown in Experiment 3. A possibility is

616   that this is because humans are more used to derive meaning from symbolic, schematic or

617   otherwise more artificial images than chimpanzees. However, research has shown that also in

618   humans, the more emotional information that is available in a stimulus, whether from a facial

619 expression, body posture or social scene, the greater their level of arousal (as measured by pupil

620 size). In that particular study, the pupillary response was greatest following angry body postures

621 that were placed in violent scenes (Kret, Roelofs, Stekelenburg & de Gelder, 2013). One idea to

622 follow this up in chimpanzees is to measure arousal, for example with thermal imaging or

623 pupillometry, and to directly compare the effects of photos showing isolated body postures with

624 photos showing naturalistic scenes showing multiple emotional components from different

625 individuals.

626

627 Experiment 3 investigated to what extent humans can recognize human and chimpanzee

628 expressions of fear and anger as compared to neutral expressions. We observed that humans are

629 better at recognizing expressions of fear and anger when shown by a human as compared to a

630 chimpanzee. Chimpanzee expressions of fear were often rated as angry, possibly due to the

631 display of the sharp canines, which might have been interpreted as purely threatening. Whereas

632 subsequent fear- and anger-intensity ratings were positively correlated when they concerned

633 chimpanzee stimuli, they were negatively correlated in response to human stimuli. This means

634 that humans rated the chimpanzee stimuli more on arousal and the human stimuli on fearfulness

635 and anger specifically (see also supplementing results where humans did not recognize the angry

636 chimpanzee stimuli as being negative and arousing stimuli, whereas the fearful chimpanzees

637 were rated as very negatively and very arousing). It is without doubt useful to be able to

638 differentiate between different expressions of emotion from conspecifics. For example, not being

639 able to distinguish between anger and fear will likely result in inappropriate responses with

640 negative or even dangerous consequences. From evolutionary perspective, it is also relevant for

641 humans to recognize emotions in other animals to some extent, but perhaps it is oftentimes

642 sufficient to know whether an animal is stressed and agitated as compared to relaxed and at ease.

643

644 The humans that we tested had no experience with chimpanzees whatsoever and it is possible

645 that accurate cross-species emotion recognition comes with experience and learning (Martin-

646 Malivel, & Okada, 2007). That said, there were no differences in attentional bias towards fearful

647 compared to angry stimuli. Both expressions attracted attention more than neutral ones (for

648 similar results, see de Valk et al., 2015). Most interestingly, this was also true for the chimpanzee

649 expressions: humans attended to those more readily than to images of chimpanzees in a relaxed,

650 neutral state. It is possible that had we added sound and dynamics to the stimulus material, naïve

651 humans would have also explicitly recognized the specific emotion in chimpanzees. The similar

652 attentional bias for human and chimpanzee expressions fits with the findings of a previous study

653 which also tested Darwin's emotional continuity hypothesis (Belin et al, 2008). In their study,

654 authors compared humans' perception of human and animal vocalisations on the explicit,

655 behavioural level and on the neurophysiological level. The results showed that although humans

656 failed to accurately discriminate rhesus macaques' and cats' affective vocalizations and whether

657 these were positive or negative, the fMRI results revealed successful discrimination, with the

658 patterns of neural activation mirroring those obtained for human affective vocalizations.

659 Possibly, this auditory activation pattern reflected low-level acoustical differences between the

660 vocalizations. Similarly in our study, structural differences related to arousal or valence that are

661 similar across humans and chimpanzees, might have accounted for the attentional bias towards

662 emotional expressions. Overall, this suggests an important degree of evolutionary continuity with

663 respect to the underlying mechanisms.

664

665 There is a large literature showing that emotional expressions of others may be processed

666 without awareness (e.g., Tamietto et al., 2009; Tamietto, & De Gelder, 2010). A predicition that

667 we therefore had and which was further based on a meta-analysis (Bar-Haim et al., 2007), was

668 that the predicted attentional bias towards emotions would be stronger when stimuli were

669 presented subliminally compared to supraliminally (e.g., when processed unconsciously

670 compared to consciously). This is not what we found. Presentation duration did not modulate the

671 relationship between the emotional content presented on the target image and reaction times on

672 touching the probe. Instead, presentation duration did have an effect on reaction times depending

673 on the emotion of the distracting image, and differentially so for human as compared to

674 chimpanzee expressions. The precise pattern is complex but it is potentially interesting to note

675 that it is exactly reversed for chimpanzee compared to the human expressions, while no such

676 reversal occurs for the neutral expressions. What this means exactly, needs to be determined in

677 future research.

678

679 Our study has several limitations. A limitation of this study is that the chimpanzees were captive

680 animals having interacted with humans throughout their lives. Although they might not have

681 seen human expressions of anger or fear that often, it is still possible that their reactions to

682 human emotion expressions are not generalizable to wild animals, who might have shown

683 different responses to stimuli of humans whom they have rarely encountered. Another limitation

684 is that our study did not have sufficient power to specifically compare biases towards anger as

685 compared to fear. Our study did not include a neutral-neutral condition. Future studies might

686 benefit from such an experimental condition, as this allows for the investigation of attentional

687   biases versus difficulties with disengaging from certain stimuli. Specifically, one can then

688   compare reaction times on threat-neutral trials with neutral-neutral trials (see Koster et al., 2004).

689   Previous research has shown that certain factors might modulate the effects obtained on the

690   emotional dot probe task, one of them being threat intensity (Koster et al., 2006; 2005; 2004;

691   Mogg et al., 2004). For example, Wilson and MacLeod (2003) found that both high and low trait

692   anxious individuals exhibited attentional biases towards highly threatening stimuli in the dot

693   probe task, though only high trait anxious individuals exhibited attentional biases towards mildly

694   threatening stimuli. Future studies should therefore aim to take these factors into account (for a

695   critical review on this task and further recommendations, see Cisler, Bacon, & Williams, 2009).

696

697   To conclude, applying well-established psychological paradigms to our closest relatives

698   represents a promising approach to providing insight into similarities and differences between

699   humans and apes. Over 500 articles have been published on the dot-probe task, showing that

700   humans have an attentional bias towards emotional expressions, especially to those representing

701   threats (for a review, see van Rooijen et al, 2017). For social species such as primates, efficiently

702   responding to others' emotions has great survival value. The present study applies a popular

703   psychological test to the chimpanzee and compares findings with humans. Even though the lack

704   of effects in the chimpanzee subjects requires further investigation, we demonstrate that humans

705   have heightened attention to emotional as compared to neutral individuals, independent of

706   whether these individuals are humans or chimpanzees, thus partly supporting evolutionary

707   continuity claims.

708

727 *Author contribution statement.* All authors contributed in designing the study. MEK and MA

728 were involved in data collection. MEK analyzed the data and wrote the article.

729

730

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A

| Submission | Display | Neutral |

Figure 1. A) Stimulus examples of chimpanzee expressions. **B)** Mother and son (Ai and Ayumu), separated by a glass panel, performing the task simultaneously.

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| Target Context | Presentation Duration | | | |
| | 33 ms | | 300 ms | |
	Mean	SE	Mean	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

Table 1. Results Study 1. SE = Standard Error of Mean; ms = miliseconds.

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A. Non-Scrambled

  Target
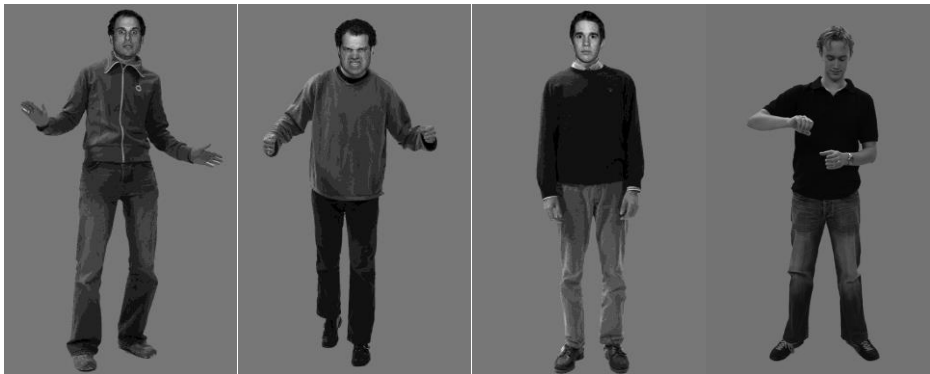
C.   Visual   Mask

(neutral body)

Figure 2 Stimulus examples of fearful, angry and neutral body postures

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	Chimpanzee Stimulus Presentation Duration				Human Stimulus Presentation Duration			
	33 ms		300 ms		33 ms		300 ms	
	Mean	SE	Mean	SE	Mean	SE	Mean	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

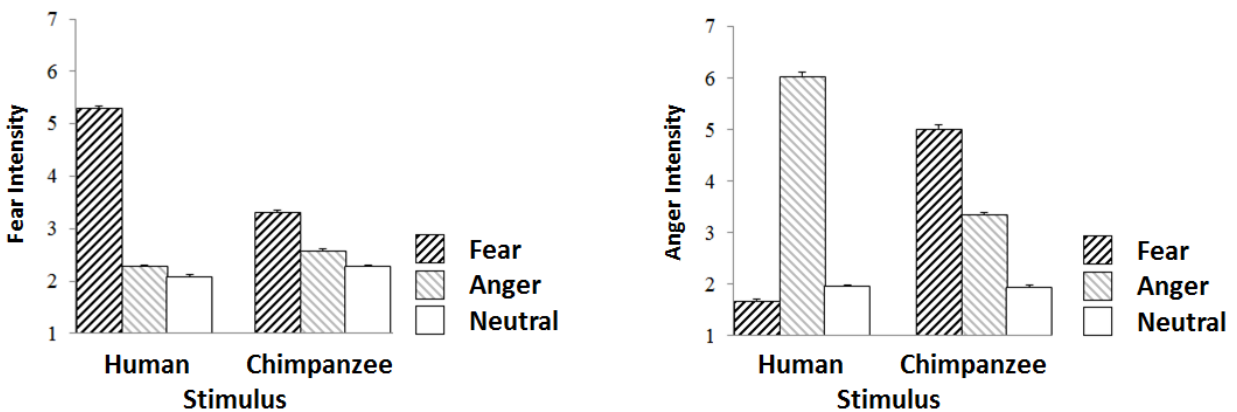**Table 2. Results Study 2.** SE = Standard Error of Mean; ms = miliseconds.

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	df1	df2	Sig.		
Corrected Model	4.972	18	16,966	0.000		
Stimulus Presentation Duration	7.741	1	16,966	0.005		
Distracting Emotion	3.994	2	16,966	0.018		
Target Emotion	5.115	2	16,966	0.006		
Species Stimulus	4.702	1	16,966	0.030		
Age of Subject	10.967		16,966	0.001		
Distracting Emotion * Stimulus Presentation Duration	8.304	2	16,966	0.000		
Target Emotion * Stimulus Presentation Duration	2.716	2	16,966	0.066		
Species Stimulus * Stimulus Presentation Duration	13.823	1	16,966	0.000		
Species Stimulus * Distracting Emotion	0.532	2	16,966	0.588		
Species Stimulus * Target Emotion	2.116	2	16,966	0.120		
Species Stimulus * Distracting Emotion * Stimulus	9.082	2	16,966	0.000		
					95% CI	
Random Factor	**Estimate**	**SE**	**Z**	**Sig.**	**Lower**	**Upper**
Variance	0.094	0.001	90.152	0.000	0.092	0.096
Var(Intercept)	0.076	0.004	17.856	0.000	0.068	0.085

Table 3. CI = confidence interval; SE = standard error

Species Stimulus	Stimulus Presentation Duration	Distracting Emotion	Contrast Estimate	Sig.
Chimpanzee	33	Fear vs. Anger	-20.772	0.002*
Chimpanzee	33	Neutral vs. Fear	26.065	0.001*
Chimpanzee	33 vs. 300	Neutral	31.44	0.000*
Chimpanzee	33 vs. 300	Anger	22.155	0.000*
Human	33	Neutral vs. Anger	23.629	0.000*
Human	33	Neutral vs. Fear	18.567	0.005
Human	300	Fear vs. Anger	-16.051	0.014
Human	33 vs. 300	Neutral	13.357	0.031
Human	33 vs. 300	Anger	-20.443	0.001*
Anger	33	Chimpanzee vs. Human	28.715	0.000*
Anger	300	Chimpanzee vs. Human	-13.883	0.024

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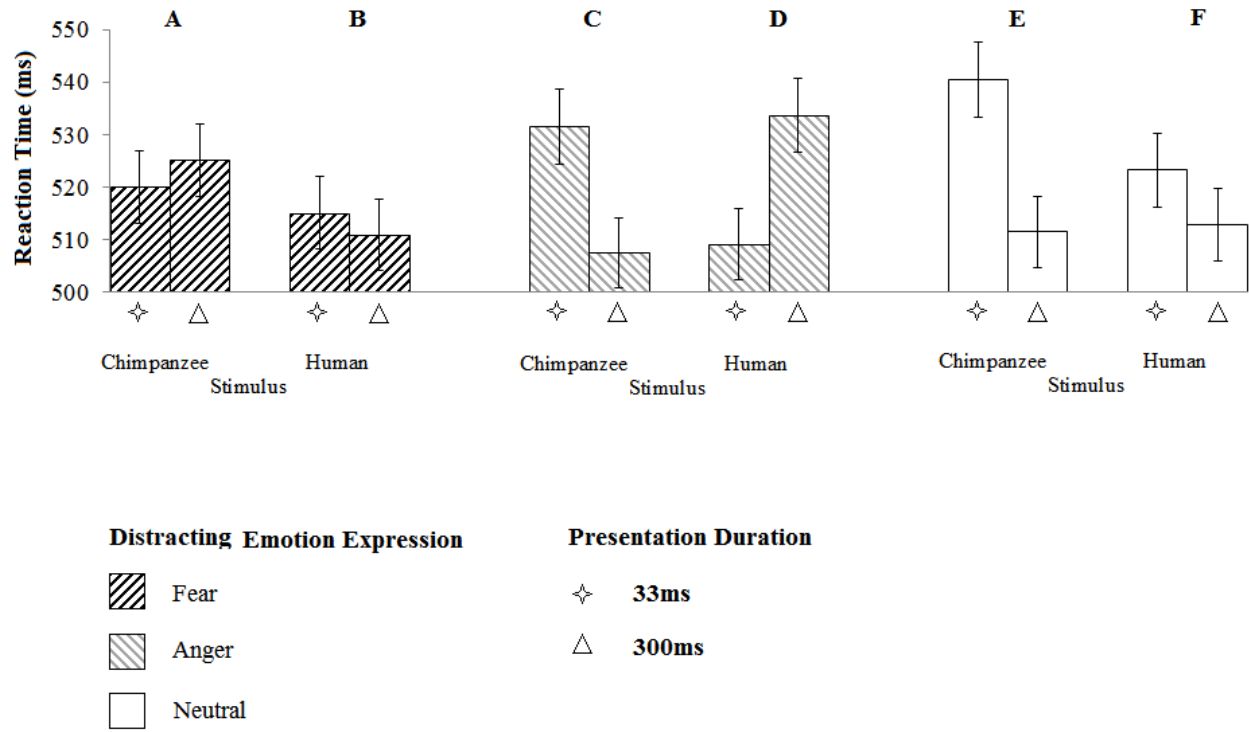
Figure 4. Emotional dot probe task in human observers. Visualization of three-way interaction between species stimulus * context emotion * stimulus presentation duration. Error bars represent the standard error of the means.

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