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**Infrared thermal imaging: Positive and negative emotions modify the skin
temperatures of monkey and ape faces**

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Short title: **Facial skin temperatures in nonhuman primates**

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17 **RESEARCH HIGHLIGHTS**

- 18 • The findings reveal that positive and negative emotions may induce distinctive facial
19 temperature changes in nonhuman primates, which are likely to reflect distinctive
20 physiological reactions of a primordial primate emotion system.
- 21 • Facial thermal imaging represents a promising physiologically-grounded technology to
22 noninvasively and continuously obtain reliable data on emotional states in nonhuman
23 primates.

24

25 **ABSTRACT**

26 Facial thermography has enabled researchers to noninvasively and continuously
27 measure the changes of a range of emotional states in humans. The present work used
28 this novel technology to study the effect of positive and negative emotions in nonhuman
29 primates by focusing on four facial areas (the peri-orbital area, the nose bridge, the nose
30 tip and the upper lip). Monkeys and apes were examined for positive emotions (during
31 interactions with toys and during tickling) and for negative emotions (during food delay
32 and teasing). For the combined toy and tickling conditions, the results indicated a drop in
33 the nose tip temperature and a tendency of an increase in the peri-orbital temperature.
34 For the combined food delay and teasing conditions, the results also revealed a rise in
35 the upper lip temperature of the subjects. These different effects on the facial
36 temperatures in monkeys and apes most likely reflect distinctive physiological reactions
37 of a primordial primate emotion system. We conclude that facial thermal imaging
38 represents a promising physiologically-grounded technology to noninvasively and
39 continuously obtain reliable data on emotional states in nonhuman primates, which may
40 help modernize research on emotions in nonhuman primates and enhance our
41 understanding of the evolution of human emotions.

42 **Key words: Thermography; physiological and behavioral responses; play;**
43 **deprivation; nonhuman primates.**

44

45 **INTRODUCTION**

46 The changes of emotional states are associated with alterations of the blood flow
47 underneath the facial skin, caused by stimulations of the sympathetic and the
48 parasympathetic nervous system which may increase and decrease the blood pressure
49 [Rubinstein & Sessler, 1990; Levenson, 1992; Kop et al., 2011]. The resulting rise and
50 drop of the facial skin temperature arguably stands in close relation with emotion-
51 grounded behavioral responses (e.g., facial expressions [Ekman et al., 1983; Levenson,
52 1992] and fight-flight reactions [Rubinstein & Sessler, 1990]). This physiological system
53 enables researchers to noninvasively capture changes of the inner states with infrared
54 thermal imaging, as carried out to study a range of emotions in humans (for a review on
55 facial thermal imaging research [Ioannou et al., 2014]). Facial thermal imaging used in
56 human research is sensitive enough to detect changes in affective states induced even
57 by images [Khan et al., 2009; Salazar-López et al., 2015], making this physiological
58 methodology, when applied to emotion research, comparable to more traditional ones,
59 such as facial EMG and skin conductance for example [Dimberg et al., 2000; Dezecache
60 et al., 2013]. With at least some human emotions (e.g., joy) having deep evolutionary
61 roots [Ledoux, 1998; Panksepp, 1998; Davila Ross et al., 2009; Davila-Ross et al., 2015],
62 facial thermal imaging could provide important insights to our understanding of emotions
63 in nonhuman primates. The current study, thus, used this methodology to examine
64 emotion-induced thermal changes in monkeys and apes.

65 So far, six facial thermography studies were conducted on nonhuman primates. Three of
66 them revealed a decrease on nasal skin temperatures from neutral states to fear, i.e., in
67 captive rhesus macaques [Nakayama et al., 2005; Kuraoka & Nakamura, 2011] and in
68 captive chimpanzees [Kano et al., 2016]. In a more recent study on wild chimpanzees, a
69 decrease in the nasal skin temperature and an increase in the ear temperature was found
70 in association with conspecific vocalizations [Dezecache et al., 2017]. Another study
71 showed an increment of the nasal skin temperature of only one laboratory rhesus
72 macaque, when being stroked (i.e., swept) by a human [Grandi & Heinzl, 2016].
73 Furthermore, a study on five rhesus macaques examined the temperatures of four facial
74 areas and compared them between a teasing context and a context including playful

75 interactions with toys (and feeding). At an individual level, the comparison showed a
76 higher peri-orbital temperature for teasing for 4 out of 5 individuals [Ioannou et al., 2015].
77 It, thus, remains to be tested to what extent positive and negative emotions may affect
78 the facial skin temperature in nonhuman primate species in general.

79 Regarding positive emotions, previous human studies revealed facial temperature
80 changes in opposite directions; four studies found a decrease: [Zajonc et al., 1989;
81 Nakanishi & Imai-Matsumura, 2008; Salazar-López et al., 2015; Cruz-Albarrán et al.,
82 2017] and three studies found an increase: [Zenju et al., 2004; Robinson et al., 2012;
83 Salazar-López et al., 2015]. Interestingly, one of the former studies showed a drop in
84 laughing infants [Nakanishi & Imai-Matsumura, 2008], which might be linked to a more
85 rudimentary physiological process, and a slight decrease in the nose tip was observed in
86 a previous study on children play, although no statistical significance was found [Ioannou
87 et al., 2013]. A comparable study on nonhuman primate positive emotional states, more
88 specifically emotions that reflect human joy, is likely to provide here more insight for a
89 reconstruction of a primordial emotion system. In addition, a study suggested that anger
90 induced facial temperature changes, but it did not use statistical tests to support these
91 statements ([Cruz-Albarrán et al., 2017]: increase in the forehead and decrease in the
92 nose and maxillary temperatures).

93 Emotion-induced increases and decreases in the facial skin temperature suggest
94 distinctive physiological activations in nonhuman primates, as found in humans,
95 activations that are under the control of the autonomic nervous system (ANS). These
96 thermal changes have often been associated with the activation of the sympathetic
97 nervous systems [Kreibig, 2010; Ioannou et al., 2014], leading to constrictions of the blood
98 vessels and the decrease of temperature in specific regions of the face. Other factors
99 may also affect the facial skin temperature. For instance, an increase in the breathing rate
100 may cool down the nasal area [Pavlidis et al., 2001]; it is, however, important to note that
101 an overall increase of the nose tip temperature may then nonetheless occur, as recently
102 found for crying [Ioannou et al., 2016]. Thermal changes result from the release of
103 distinctive neurotransmitters (e.g. norepinephrines) that trigger successive physiological
104 changes in the body [Levenson, 1988; Charkoudian, 2010]. For instance, heart rate

105 increase or decrease is the result of direct autonomic (sympathetic/parasympathetic)
106 stimulation [Cannon, 1929], which activates different β -adrenergic receptors in the body,
107 leading to its increase or decrease [Bers, 2002]. Positive emotions cover a range of
108 affective states in humans (e.g. joy, contentment) and imply different physiological
109 patterns [Kreibig, 2010]. For instance, joy is characterized by increased vagal control and
110 β -adrenergic and cholinergic neurotransmitter release, while contentment is
111 characterized by a decrease of α - and β -adrenergic and cholinergic activity along with
112 mild cardiac vagal activation [Wright, 1996]. Moreover, anger and frustration are
113 characterized by an increase in heart rate and α - and β -adrenergic influences [Vella &
114 Friedman, 2009].

115 In the current study, three monkey taxa and two ape taxa were examined during positive
116 and negative emotional states. It is important to note that we did not attempt to compare
117 across the five primate taxa of this study since potential differences here may be
118 explained by various factors other than phylogeny (e.g., different social group
119 constellations and rearing histories). Instead, the approach of this study was to capture
120 the diversity in the sample for stronger conclusions about the predicted thermal changes
121 in nonhuman primates. Playful interactions with a toy as well as tickling were both used
122 to induce positive emotional states [Davila Ross et al., 2009; Izzo et al., 2011; Griffis et
123 al., 2013]. Enrichment with toys has been previously found to positively affect both
124 physiological (i.e., diminution of cortisol level) and behavioural responses (i.e., increase
125 of normal behaviours) in nonhuman primates [e.g., Boinski et al., 1999]. Delays in
126 receiving food as well as teasing were used to induce negative emotional states, where
127 some level of frustration most likely was experienced during the waiting [Mischel et al.,
128 1972; Miller & Karniol, 1976], which may have even escalated into anger [Henna et al.,
129 2008]. The toy, tickling, food delay and teasing conditions were preceded by a neutral
130 baseline, where each subject was in a relaxed state.

131 Four facial areas (the peri-orbital area, the nose bridge, the nose tip and the upper lip)
132 were selected for the thermal analysis (according to their previously reported effects on
133 facial temperatures in primates [Nakanishi & Imai-Matsumura, 2008; Ebisch et al., 2012;
134 Ioannou et al., 2015]). Facial thermal analysis, in general, should include more than just

135 one area of interest, since the temperatures of specific facial areas may shift in opposite
136 directions within the same time period (e.g., startling decreases the cheek temperature
137 and increases the peri-orbital temperature: [Levine et al., 2001]; crying increases the
138 forehead, peri-orbital, cheek, nose and chin temperature and decreases the maxillary
139 temperature [Ioannou et al., 2016]; a decrease in the nose temperature and an increase
140 in the ear temperature may co-occur in wild chimpanzees hearing conspecific
141 vocalizations [Dezecache et al., 2017]). Facial skin areas are irrigated differently by the
142 many blood vessels that branch off from the facial artery and they are exposed to different
143 physiological processes [Kreibig, 2010; Ioannou et al., 2014]. For instance, the nose tip
144 was reported to provide particularly reliable data due to its rich blood supply [Bergersen,
145 1993], unlike the nose bridge, where the lateral nasal and inferior palpebral arteries show
146 poor blood supply [Ioannou et al., 2014; Ioannou et al., 2015]. Depending on the
147 experienced emotion, specific adrenergic pathways might be activated along the blood
148 vessels, consequently affecting the temperatures of the facial skin differently [Kreibig,
149 2010].

150 This study is the first to look at emotional responses using thermal imaging by including
151 different nonhuman primate taxa. The findings of this work could help evaluate the
152 application value of facial thermography as a technology to noninvasively capture reliable
153 emotion data on different nonhuman primates and, consequently, enhance the
154 understanding of the evolution of emotions. Importantly, it would also allow researchers
155 to continuously and quickly collect data on the inner states of monkeys and apes, while
156 other physiologically-grounded noninvasive approaches used in nonhuman primate
157 research are dependent on the collection of biological samples (e.g., faeces and saliva
158 samples). Consequently, this study examined the natural responses of nonhuman
159 primates in their everyday environments with a simple noninvasive approach by using
160 thermal imaging and behavioral observations. Based on the findings on macaques
161 [Ioannou et al., 2015], we hypothesized that positively grounded emotions related to
162 playful interactions with toys (and tickling) reduce the facial skin temperatures in
163 nonhuman primates, whereas negative emotional states, more specifically emotions that
164 are most likely to reflect anger or frustration, increase the facial skin temperature in
165 nonhuman primates.

166 **METHODS**

167 Research conducted within this study complied with protocols approved by Owl and
168 Monkey Haven and Port Lympne Wild Animal Park as well as the University of
169 Portsmouth's Animal Welfare and Ethical Review Body. All methods for this study
170 adhered to the legal requirements of the UK and the American Society of Primatologists'
171 Principles for the Ethical Treatment of Nonhuman Primates.

172 **Subjects and study sites**

173 Three monkey taxa and two ape taxa represented the study subjects: Common
174 marmosets (*Callithrix jacchus*), white-throated capuchins (*Cebus capucinus*), rhesus
175 macaques (*Macaca mulatta*), Bornean gibbons (*Hylobates muelleri*) and western lowland
176 gorillas (*Gorilla gorilla gorilla*). Nine subjects were tested for the toy or tickling condition
177 and ten subjects for the food delay or teasing condition. For the subject characteristics
178 and representation in the data, see Table I. All subjects except for the gorillas were
179 housed in the Owl and Monkey Haven (UK). The gorillas lived in Port Lympne Wild Animal
180 Park (UK). All subjects were habituated to human interactions, facilitating thus the data
181 collection. The data were collected when the subjects were in their social groups (groups
182 of twelve marmosets, three capuchins, five macaques, four gibbons, and four gorillas)
183 and in the enclosures where they stayed on a daily basis. All primates were outdoors
184 during the data collection, except the marmosets and gorillas, who were studied indoors.
185 The outdoor and indoor enclosures were equipped with climbing structures, and other
186 enrichment objects. The main feeding times were in the morning and afternoon for all
187 subjects (8am, 3pm and 5pm), except for the gorillas (12pm and 3pm). The subjects had
188 constant access to water. The monkeys and apes of this study are likely to represent
189 good candidates for facial thermal imaging research as the measured facial areas are
190 covered only with few hairs, with the exception of the upper lip.

191 --- Table I here ---

192

193 **Procedure and data collection**

194 Each subject was examined for at least one session, which included an experimental
195 condition (toy or tickling condition, or food delay or teasing condition), preceded by a
196 neutral condition. The sessions were at least 3 minutes apart.

197 Interactions with either toys or tickling were used to induce positive states. The
198 experimenter presented one-two toys (a baby rattle, a teddy bear or a doll purse) to a
199 subject, while playfully moving the toy, an approach which was expected to trigger
200 playfulness in the subjects, perhaps combined with curiosity. An exception here was
201 made for a gorilla who was known not to respond to toys; instead, the keeper tickled the
202 gorilla who initiated the tickle play by presented his back to be tickled. The toy and tickling
203 condition lasted up to 4 minutes, where the subjects occasionally took breaks of up to 10
204 seconds. The toy and tickling condition ended either when the subject left or stopped
205 facing the experimenter for more than 10 seconds or when a conspecific interfered. To
206 obtain mainly data on positive emotions for each toy and tickling session, a session was
207 included in the analyses only if the break(s) did not represent more than 20% of its total
208 duration.

209 In addition, food delay or teasing were used to induce negative states related to anger or
210 frustration. The experimenter presented to a subject food (crickets, mealworms or fruits)
211 that was out of reach for one minute. The experimenter held the food in the hand and if
212 the subject tried to reach for the food, the experimenter held the food further away.
213 Exceptions here were made for two gorillas as it would not have been safe to give them
214 the food directly from the hand. For the gorillas, a fruit bucket was placed on the ground
215 (out of reach). All subjects received the food after this condition ended. For the neutral
216 condition of this study, the subjects had to be calm (e.g., sitting in a relaxed way, with a
217 relaxed face and with no piloerection) for up to 10 seconds.

218 The testing took place after the subjects spontaneously separated from their social group
219 and approached the experimenter, without any group member interfering. Hence, during
220 the testing, the subjects could freely move in their enclosure and leave the experimental
221 area at any time. This prerequisite ensured that the subjects behaved naturally as well as
222 calmly during the neutral condition. Thus, not all nonhuman primates of each social group

223 approached the experimenter and became subjects of this study and the number of
224 sessions also varied between subjects.

225 Moreover, only sessions with thermal data obtained from both neutral and experimental
226 conditions were included for further analyses (Supplementary Material S1). A total of 33
227 sessions (19 for toy and tickling, 14 for food delay and teasing) were used for the analyses
228 (for an overview on the number of sessions, see Table I). The experimenter stood outside
229 of the enclosures, behind the meshes (behind the bars for the gorillas). The data collection
230 took place in October and November 2013 and in January and May 2014.

231 The thermal recordings were obtained by a recordist, who held a portable thermal camera
232 and tried to capture frontal shots of the face of the freely moving subject at a distance of
233 about one meter. For this study, the ThermoPro™ TP8 camera (© Wuhan Guide Infrared
234 Technology Co., Ltd, 2006, Wuhan, China; <http://www.guide-infrared.com/>) was used. It
235 has a resolution of 384 x 288 pixels, a temperature measurement accuracy of $\pm 1\%$ and
236 a thermal sensitivity of 0.08°C . These characteristics enable a similarly reliable data
237 collection across all taxa, regardless of the subject body size. Thermal cameras detect
238 the radiation emitted by organisms (and other matter) and convert it into electronic signals
239 that produce a thermal image. This image consists of different colors/shades, which refer
240 to distinctive temperatures (Fig. 1).

241

242 --- Figure 1 here ---

243

244 No direct sunlight affected the data collection as it was too cloudy for the sun to be visible
245 during the outdoor recordings. In addition, the recordist collected the thermal data
246 underneath a ceiling for all sessions, except the gibbon session. For an overview of the
247 enclosure temperatures during the recordings, see Table I. In addition, each subject was
248 video-recorded with a regular camera (JVC Everio) for the behavioral analysis. This
249 camera was placed about one meter outside of the enclosure.

250

251 **Thermal analysis**

252 For the thermal analysis, the subjects' facial skin temperatures were measured from
253 extracted picture frames every five seconds. For every picture frame, the mean
254 temperature of each of the four measured facial areas was obtained. A circular shape
255 was used to measure the temperature of the peri-orbital area, the nose bridge as well as
256 the nose tip, while a rectangular shape was used for the upper lip (Fig 1). To have all
257 facial areas sufficiently visible and measurable, a frame was only extracted if it showed
258 the frontal side of the subject face or up to a 45° angle sideways. If any facial area was
259 not fully visible (e.g., due to the enclosure meshes or bars), no thermal data were obtained
260 from this particular frame. For each of the four measured facial areas, the mean
261 temperatures of the neutral condition and the experimental condition were calculated per
262 session, respectively.

263 To ensure that the recording angle did not influence the thermal data, the frontal frames
264 (subject face turned towards the thermal camera) and the sideways frames (subject face
265 turned away from the thermal camera with an angle up to 45°) were statistically compared
266 within the neutral condition. The compared frames were no more than 10 seconds apart
267 from each other in order to avoid other factors having an impact.

268
269 The thermal analysis was carried out by one coder who was naïve about the hypotheses
270 and the different conditions. This coder was first trained by another researcher, who was
271 experienced with extracting such data from humans. To further ensure that the data were
272 reliably obtained, three sessions were then coded by both researchers and a full
273 agreement was reached. The program Launch Guide IR analyzer (© Wuhan Guide
274 Infrared Technology Co., Ltd, 2006, Wuhan, China; <http://www.guide-infrared.com/>) was
275 used.

276

277 **Behavioral analysis**

278 For the behavioral analysis, the intensities of bodily movements as well as the
279 presence/absence of facial expressions and calls were coded for every five-second
280 interval which preceded each thermal picture frame that was measured for the thermal

281 analysis. Only small bodily movements were observed during the test, and were coded
282 as either absent, slow (e.g., gently reaching for the toy or food) or rapid (e.g., quickly and
283 repeatedly grabbing for the toy or food). In addition, low and high level of behavioral
284 indicators of positive and negative emotional states were coded (for a list and description
285 of the behavioral indicators, see Table II; for video clips, see Supplementary Material S2).
286 The coding of behavioral indicators was meant to help find out if at least some of the
287 subjects experienced the relevant emotion tested for and, consequently, if the approach
288 to induce positive and negative emotional states, respectively, was successful.

289

290

--- Table II here ---

291

292 The behavioral analysis was conducted by two coders using Windows Media Player. The
293 main coder was then naïve about the use of all the behavioral data. The other coder
294 coded the capuchin and gorilla behaviors and was naïve about the use of the movement
295 and expression data.

296 **Statistics**

297 We used mean, median and standard error values to describe our thermal and behavioral
298 data. Due to our sample size, non-parametric tests were used. The Wilcoxon signed rank
299 test was performed to compare the neutral and emotional condition and compare frontal
300 and sideways frames. The Mann-Whitney U test was performed to test whether the bodily
301 movements and the air temperature could have been accounted for the thermal changes,
302 as well as whether the onset of behavioural indicator (low and high) differ when comparing
303 positive and negative emotion. For all tests, the level of significance was set at 0.05 and
304 the tests were one-tailed, unless indicated. For the behavioral analysis, an inter-coder
305 reliability test (Cohen's Kappa, $K=0.74$) was conducted based on 15 randomly selected
306 sessions (five subjects). For repeated statistical tests, α level adjustments were carried
307 out with Hommel-Hochberg corrections [Hochberg & Hommel, 1998]. The analyses were
308 computed with SPSS Statistics 23 (IBM, Chicago, IL, USA).

309

310 RESULTS

311 Thermal analysis

312 Five of the nine subjects tested with either the toy or tickling showed behavioral indicators
313 of positive emotional states (Table II). All of the ten subjects tested for food delay or
314 teasing showed behavioral indicators of negative emotional states (Table II). Behaviors
315 associated with positive state were absent during the food delay or teasing condition;
316 behaviors associated with negative state were absent during the toy or tickling condition.

317 For the combined toy and tickling condition, the thermal analysis showed a significant
318 decrease in the nose tip temperature of the subjects from the neutral condition to the
319 experimental condition (Wilcoxon signed rank test with Hommel-Hochberg corrections:
320 $z=-1.836$, $T=7$, $N=9$, $p<0.05$), but a tendency of an increase in the peri-orbital temperature
321 ($z=1.718$, $T=8$, $N=9$, $p=0.05$). No significant decreases were found for the nose bridge
322 ($z=0.296$, $T=20$, $N=9$, $p=0.410$) and for the upper lip ($z=-1.481$, $T=10$, $N=9$, $p=0.08$);
323 Figure 2. When including only the five subjects who showed behavioral indicators of
324 positive state, the thermal analysis showed a significant decrease in the nose tip
325 temperature ($z=-2.023$, $T=0$, $N=5$, $p<0.05$), and a significant increase in the peri-orbital
326 temperature ($z=-2.023$, $T=0$, $N=5$, $p<0.05$); the other two facial areas showed no
327 significant temperature changes (nose bridge: $z=-0.135$, $T=7$, $N=5$, $p=0.50$; upper lip: $z=-$
328 1.753 , $T=1$, $N=5$, $p=0.06$). Due to the difference between the toy and tickling conditions,
329 we decided to exclude the gorilla data (i.e., only tested in the tickling condition) from the
330 sample. We, then, assessed if the subjects who were tested in the toy condition showed
331 significant thermal changes. Such changes were not found for any of the four facial areas
332 when comparing the neutral to the experimental condition (Wilcoxon signed rank test with
333 Hommel-Hochberg corrections: peri-orbital: $z=-1.400$, $T=8$, $N=8$, $p=0.10$; nose bridge: $z=-$
334 0.140 , $T=17$, $N=8$, $p=0.47$; nose tip: $z=-1.540$, $T=7$, $N=8$, $p=0.07$; upper lip: $z=-1.120$,
335 $T=10$, $N=8$, $p=0.16$).

336

337

--- Figure 2 here ---

338

339 For the combined teasing and food delay condition, the analysis revealed a significant
340 increase in temperature from the neutral condition to the experimental condition in the
341 upper lip (Wilcoxon signed rank test with Hommel-Hochberg corrections: $z=-2.040$, $T=8$,
342 $N=10$, $p<0.05$). No significant difference was found when comparing neutral versus
343 combined food delay and teasing in the peri-orbital area ($z=-1.274$, $T=15$, $N=10$, $p=0.12$),
344 nose bridge ($z=-1.683$, $T=11$, $N=10$, $p=0.05$), and in the nose tip ($z=-0.357$, $T=24$, $N=10$,
345 $p=0.39$); Figure 3. Table III and the Supplementary Material S1 show the skin
346 temperatures of the monkeys and apes measured during the toy or tickling conditions and
347 the food delay or teasing conditions and their preceding neutral conditions for each facial
348 area. As for the positive emotion, due to the difference between the two negative
349 conditions, we decided to exclude the gorilla data (i.e., food delay condition) from the
350 sample. We, then, assessed if the individuals who were tested in the teasing condition
351 showed thermal changes. This analysis showed a significant increase in the upper lip
352 temperature when comparing the neutral to the teasing condition (Wilcoxon signed rank
353 test with Hommel-Hochberg corrections: $z=-1.752$, $T=5.50$, $N=8$, $p<0.05$). The other three
354 facial areas did not show any significant differences (peri-orbital: $z=-1.120$, $T=10$, $N=8$,
355 $p=0.16$; nose bridge: $z=-1.402$, $T=8$, $N=8$, $p=0.09$; nose tip: $z=-0.140$, $T=17$, $N=8$, $p=0.47$).

356

357 --- Figure 3 here ---

358

359 --- Table III here ---

360

361 Furthermore, for the facial areas that showed significant thermal changes in the main
362 analysis (i.e., the nose tip for the positive emotion and the upper lip for the negative
363 emotion), we tested whether this thermal change would already occur during the first 15
364 seconds of the experimental condition (Supplementary Material S3 for the subject-level
365 data). No such significant thermal changes were found (Supplementary Material S4 and
366 Fig. 4).

367

368 --- Figure 4 here ---

369

370 Additionally, it was tested if the recording angle could have had an impact on the thermal
371 data. No significant differences were found when comparing frontal and sideways frames
372 for any of the four facial areas of interest (Wilcoxon signed rank test with Hommel-
373 Hochberg corrections; two-tailed: peri-orbital area: $z=-0.431$, $T=8.5$, $N=8$, $p=0.78$; nose
374 bridge: $z=-1.491$, $T=7.5$, $N=8$, $p=0.16$; nose tip: $z=0.000$, $T=10.5$, $N=8$, $p=1$; upper lip: $z=-$
375 0.425 , $T=8.5$, $N=8$, $p=0.81$).

376 We also tested whether the air temperature might have had an impact on facial
377 temperature changes when comparing indoor and outdoor species. For the positive
378 emotion, we did not find any significant differences for any of the four facial areas when
379 comparing indoor and outdoor species (Mann-Whitney U test with Hommel-Hochberg
380 corrections; two-tailed: peri-orbital: $U=3$, $N_{\text{Indoor}}=4$, $N_{\text{Outdoor}}=5$ subjects, $p=0.11$; nose
381 bridge: $U=8$, $N_{\text{Indoor}}=4$, $N_{\text{Outdoor}}=5$, $p=0.73$; nose tip: $U=4$, $N_{\text{Indoor}}=4$, $N_{\text{Outdoor}}=5$, $p=0.19$;
382 upper lip: $U=5$, $N_{\text{Indoor}}=4$, $N_{\text{Outdoor}}=5$, $p=0.29$), Nor were such statistically significant
383 differences found for the negative emotions (peri-orbital: $U=5$, $N_{\text{Indoor}}=6$, $N_{\text{Outdoor}}=4$
384 subjects, $p=0.17$; nose bridge: $U=9$, $N_{\text{Indoor}}=6$, $N_{\text{Outdoor}}=4$, $p=0.57$; nose tip: $U=5$, $N_{\text{Indoor}}=6$,
385 $N_{\text{Outdoor}}=4$, $p=0.17$; upper lip: $U=7.5$, $N_{\text{Indoor}}=6$, $N_{\text{Outdoor}}=4$, $p=0.38$).

386

387 **Behavioral analysis**

388 We tested if bodily movements of the subjects as well as their facial expressions and
389 calls could have accounted for these resulting facial thermal changes. The skin
390 temperature of the four facial areas showed no significant difference between no/slow
391 bodily movements and rapid bodily movements when testing for the combined toy and
392 tickling condition (Mann-Whitney U test with Hommel-Hochberg corrections; two-tailed:
393 peri-orbital: $U=15$, $N_{\text{No/slow}}=9$, $N_{\text{Rapid}}=4$ subjects, $p=0.68$; nose bridge: $U=9$, $N_{\text{No/slow}}=9$
394 subjects, $N_{\text{Rapid}}=3$, $p=0.48$; nose tip: $U=16$, $N_{\text{No/slow}}=9$, $N_{\text{Rapid}}=4$, $p=0.83$; upper lip: $U=15$,
395 $N_{\text{No/slow}}=9$, $N_{\text{Rapid}}=4$, $p=0.60$) and for the combined food delay and teasing condition
396 (Mann-Whitney U test: peri-orbital: $U=15$, $N_{\text{No/slow}}=8$ subjects, $N_{\text{Rapid}}=5$ subjects, $p=0.52$;
397 nose bridge: $U=17$, $N_{\text{No/slow}}=7$, $N_{\text{Rapid}}=5$, $p=1$; nose tip: $U=19$, $N_{\text{No/slow}}=8$, $N_{\text{Rapid}}=5$, $p=0.94$;
398 upper lip: $U=17$, $N_{\text{No/slow}}=8$, $N_{\text{Rapid}}=5$, $p=0.72$). Only four subjects showed no/slow bodily

399 movements as well as rapid bodily movements when tested for toy or tickling and only
400 three subjects when tested for food delay or teasing. Furthermore, one subject produced
401 facial expressions and calls during testing (one gorilla produced play faces and laughter
402 during play).

403 For the positive emotion, the subjects showed 3.4 ± 0.6 (mean \pm SE) slow movements and
404 8 ± 3.5 rapid movements during the toy condition, and the gorilla tested during the tickling
405 condition showed 10 slow movements as well as 4 rapid movements. Regarding the
406 negative emotion, the subjects displayed 2 ± 0.2 slow movements as well as 2.5 ± 0.8 rapid
407 movements during the teasing condition, and the gorillas showed 5.5 ± 1.5 slow
408 movements, and only one subject showed 7 rapid movements. The number of
409 movements per session is presented in the Supplementary Material S1.

410 Regarding the behavioral indicators of the emotional state, low level of positively-related
411 behavioral indicators occurred 9.23 ± 2.11 seconds and five seconds after the beginning
412 of the toy condition and tickling condition, respectively. High level of positively-related
413 behavioral indicators occurred 26.25 ± 7.18 seconds and 15 seconds after the beginning
414 of the toy condition and the tickling condition (1 session), respectively. Low level of
415 negatively-related behavioral indicators occurred 5.71 ± 0.71 seconds and 5 ± 0.0 seconds
416 after the beginning of the teasing condition and food delay condition, respectively. High
417 level of negatively-related behavioral indicators occurred 5.83 ± 0.83 seconds and 40
418 seconds after the beginning of the teasing condition and the food delay condition,
419 respectively. When comparing the onset of the low level of behavioral indicators between
420 the negative and positive condition, no significant difference was found (Mann-Whitney U
421 test; two-tailed: $U=46.5$, $N_{\text{Positive}}=14$ sessions, $N_{\text{Negative}}=9$ sessions, $p=0.27$). Nor such
422 difference was found when excluding the gorilla data from the analysis ($U=33.5$,
423 $N_{\text{Positive}}=13$, $N_{\text{Negative}}=7$, $p=0.33$). Regarding the onset of the high level of behavioral
424 indicator, no significant difference was found between the negative and positive condition
425 ($U=8.5$, $N_{\text{Positive}}=5$, $N_{\text{Negative}}=7$, $p=0.13$). However, when excluding the gorilla data from the
426 analysis, the onset of high level of behavioral indicators occurred significantly faster within
427 the negative condition than within the positive condition ($U=3.5$, $N_{\text{Positive}}=4$, $N_{\text{Negative}}=6$,
428 $p<0.05$). We, then, tested whether there was a significant difference when comparing the

429 temperatures of the 15 seconds before and after the onset of the high level of behavioural
430 indicator for the positive emotion. No significant thermal changes were found for any of
431 the four facial areas (Wilcoxon signed rank test with Hommel-Hochberg correction: peri-
432 orbital: $z=-1.461$, $T=1$, $N=4$, $p=0.25$; nose bridge: $z=-0.000$, $T=3$, $N=3$, $p=1$; nose tip: $z=-$
433 0.552 , $T=3.50$, $N=4$, $p=0.75$; upper lip: $z=-1.461$, $T=1$, $N=4$, $p=0.25$).

434

435 **DISCUSSION**

436 The current study examined the facial skin temperatures in monkeys and apes associated
437 with positive and negative emotional states. We hypothesized that positively grounded
438 emotions related to playful interactions with toys (and tickling) reduce the facial skin
439 temperatures in nonhuman primates, whereas negative emotional states, more
440 specifically emotions that are most likely to reflect anger or frustration, increase the facial
441 skin temperature in nonhuman primates. Our results supported our two hypotheses to
442 some extent where only some facial areas showed significant thermal changes. The data
443 on behavioral indicators suggest that the approach to induce positive and negative
444 emotions in the studied nonhuman primates was in general successful, with five subjects
445 showing positive behaviors (e.g., playful head movements) and ten subjects showing
446 negative behaviors (e.g., display posture), respectively.

447 For the negative emotional states, the upper lip temperature of the monkeys and apes of
448 this study increased from the neutral condition to the experimental condition, when the
449 teasing data alone was examined and when it was combined with food delay data. These
450 findings on negative-induced increases of the facial skin temperature in nonhuman
451 primates support our hypothesis, which was based on our previous study on five rhesus
452 macaques [Ioannou et al., 2015]. The increased lip temperature during the negative
453 condition may have been the result of increased blood flow associated with an increase
454 of the heart rate as well as α - and β -adrenergic influences [Vella & Friedman, 2009].

455 Regarding the positive emotional states, the nose tip temperatures of the subjects
456 dropped from the neutral condition to the combined toy and tickling condition, but the peri-
457 orbital temperatures had a tendency of an increase. The nose tip data were consistent

458 with our previous macaque findings [Ioannou et al., 2015] and previous research on
459 human infant laughter [Nakanishi & Imai-Matsumura, 2008] and children play [Ioannou et
460 al., 2013] (cf. [Salazar-López et al., 2015]). The drop in the nasal temperature might have
461 resulted from the constriction of blood vessels innervating selectively this facial area (i.e.
462 arteriovenous anastomosis: [Bergersen, 1993]), an action mediated by the direct
463 sympathetic postganglionic neurons [Hales, 1985]. It is possible that an increased
464 breathing rate additionally contributed to cooling the nose [Pavlidis et al., 2001], but it may
465 have had a minor effect [Ioannou et al., 2016]. A temperature rise in the peri-orbital area
466 was previously also found for positive contexts in humans (positive self-sentiment:
467 [Robinson et al., 2012]) and might have resulted from an increased heart rate [Cannon,
468 1929] and increased blood flow to extra-ocular muscles [Ioannou et al., 2015]. Moreover,
469 blood may be redirected by other facial regions [Pavlidis et al., 2001].

470 Consequently, the temperature changes induced by positive emotions in this study did
471 not tend to occur in one collective direction for the four assessed facial areas, i.e., namely
472 the predicted overall decrease, a prediction which was based on our previous findings on
473 the peri-orbital temperature changes in rhesus macaques [Ioannou et al., 2015]. Such
474 opposite directions in temperature shifts are likely to present differing physiological
475 processes involved for the same emotion in nonhuman primates. They are consistent with
476 physiologically-grounded regional differences associated with the human facial skin (e.g.,
477 differences in the blood vessel innervations [Bergersen, 1993] and specific adrenergic
478 activations [Kreibig, 2010]), as well as previous thermal findings on humans [Levine et
479 al., 2001; Ioannou et al., 2016] and nonhuman primates [Dezecache et al., 2017]. Such
480 differences may also help to explain the discrepancies across empirical studies on facial
481 temperature changes. For positive emotions, humans showed, for instance, a decrease
482 in the forehead temperature [Zajonc et al., 1989; Nakanishi & Imai-Matsumura, 2008] and
483 an increase in the eye area temperature [Robinson et al., 2012].

484 Additionally, the discrepancies in the literature may also be explained by the different
485 uses of stimuli, such as play and pleasant touch [Nakanishi & Imai-Matsumura, 2008;
486 Salazar-López et al., 2015; Grandi & Heinzl, 2016]. When removing the gorilla data from
487 our sample, no thermal changes were found anymore for the positive emotion. It is

488 possible that different behavioral contexts may induce different physiological responses
489 due to the activation of a more specific emotion system associated with the context per
490 se [Kreibig, 2010]. By contrast, other researchers suggest that positive states are under
491 the control of a more general system resulting in similar physiological reactions regardless
492 of the context [Panksepp, 1998]. Future studies including different behavioral contexts to
493 induce positive emotions, as well as negative emotions, are needed to shed light onto this
494 disagreement.

495 While previous researchers suggested that thermal changes are detectable already within
496 the first 10 seconds after inducing an emotion state [Kuraoka & Nakamura, 2011; Ebisch
497 et al., 2012] and tendency for it was found also in the current study regarding the negative
498 condition, it is important to consider that some emotions may take longer to be induced
499 than others. Since negative states are associated with the fight-flight system, quick
500 behavioral responses to negative stimuli are generally predicted in comparison to
501 behavioral responses to positive stimuli [Levenson, 1992; Fredrickson, 2001]. This
502 pattern is consistent with our results, which revealed a particularly late onset for the
503 positively-related behavioral indicators, although significant thermal data changes
504 accompanying these primate behaviors could not be found. It is also noteworthy that the
505 onset of emotion-induced temperature changes in the facial areas of interest in this study
506 could have been at least to some extent affected by the subject's body size [Boyd & Silk,
507 2009] and, thus, their metabolic rate [Kleiber, 1932].

508 Although, the study presents some methodological issues regarding the uneven number
509 of sessions between the subjects and the small sample size, the nonparametric analyses
510 showed significant thermal changes, which revealed a reliable degree of statistical rigidity.
511 This study showed that positive and negative emotional states have a distinctive effect
512 on the facial temperatures in monkeys and apes. They might reflect distinctive
513 physiological reactions of a primordial emotion system, associated with the competing
514 subdivisions of the ANS [Wright, 1996; Vella & Friedman, 2009; Kreibig, 2010]. During
515 sympathetic arousal, they lead to heart acceleration and the constrictions of the blood
516 vessels whereas during parasympathetic activation, they lead to an inhibition of the
517 sympathetic axis and physiological restoration [Kreibig, 2010]. Both systems seem to play

518 an important role in the mediation of the different physiological actions that lead to the
519 release of specific neurotransmitters, such as adrenalin and acetylcholine, and to
520 changes in the blood flow [Kreibig, 2010], explaining the differences found for the
521 distinctive emotional states and their distinctive facial areas.

522 It is unlikely that the thermal results of this study were notably affected by bodily
523 movements of the monkeys and apes. Specifically, there was no indication in the data
524 that any rapid movement of the subjects resulted in higher facial skin temperatures than
525 slow movements and no movements. Nor could the production of facial expressions and
526 calls have notably affected the thermal results as these expressions were rare (produced
527 by one subject only). Previous findings similarly showed that locomotion in dogs [Travain
528 et al., 2015] and facial expressions in rhesus macaques [Nakayama et al., 2005] did not
529 account for facial temperature changes. In contrast, Kano and colleagues [2016] showed
530 that locomotive activity might affect the facial temperatures of chimpanzees. Perhaps
531 such differences in empirical findings depend on the intensity of movement of the
532 subjects. In our study, we did not observe any walking behaviors during the test and the
533 movement level seems to have been notably lower (e.g., touching the toy) than in the
534 study by Kano and colleagues [2016], where the chimpanzees showed high-arousal
535 behaviors, such as walking around in the test rooms.

536 Since facial thermal imaging can be applied to noninvasively, continuously and quickly
537 obtain data on positive and negative emotional states in a range of captive nonhuman
538 primates, this approach shows notable potential in helping to improve the primates' living
539 conditions and to monitor their states of wellbeing. However, to prevent variation in the
540 thermal data, this approach requires the conditions to follow immediately each other
541 allowing, therefore, to measure facial temperature changes across conditions. In future
542 thermal research on nonhuman primates, the peri-orbital area, the nose bridge, the nose
543 tip, and the upper lip need to be collectively closely examined as some areas may provide
544 more insight about the impact of the specific examined emotion than others. Overall, facial
545 thermography represents a promising physiologically-grounded technology that may help
546 enhance the understanding of the primate emotion systems.

547

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700

701

702 **Tables**703 **Table I. Overview of the subject representation in the data.**

Compared conditions	Taxon	Number of subjects	Number of sessions	Enclosure temperature (°C)
Neutral-Toy	Common marmosets	3	3	18-24
	White-throated capuchin	1	1	8-10
	Rhesus macaques	3	13	2-8
	Bornean gibbon	1	1	2-8
Neutral-Tickling	Western lowland gorilla	1	1	25-27
Neutral-Teasing	Common marmosets	4	6	18-24
	White-throated capuchin	1	1	8-10
	Rhesus macaques	3	5	2-7
Neutral-Food delay	Western lowland gorillas	2	2	25-27

704 For the tested conditions and taxa, the number of subjects and sessions and the
705 temperature of the enclosure during the data collection are provided.

706

707 **Table II. Overview of high level of behavioral indicators.**

Condition	Behavioral indicator	Description
Toy and tickling	Playful head movement	Head movement as observed in spontaneous play of nonhuman primates
	Play expression	Tickle-induced play faces in nonhuman primates and laughter in great apes (for a spectrogram on great ape laughter [Davila Ross et al., 2009])
	Inspecting	Touching, licking or smelling the toy in a relaxed or playful way
Food delay and teasing	Abrupt movement	Bodily movement, e.g., arm movement, that is abrupt and inferring aggression
	Aversive expression	Aversive open-mouth expression or vocalization in response to the food delay
	Display posture	Stiff posture that often is accompanied by piloerection and appears to show a larger body
	Lip pressing	Putting the lips tightly together

708 All behavioral indicators and their descriptions for the toy/tickling and the food
 709 delay/teasing conditions.

710

711 **Table III. Facial temperatures of the studied monkeys and apes.**

		Testing for positive emotional state		Testing for negative emotional state	
		Neutral condition	Toy and tickling condition	Neutral condition	Food delay and teasing condition
		median (\pm SE) temperature	median (\pm SE) temperature	median (\pm SE) temperature	median (\pm SE) temperature
Monkeys	Peri-orbital	34.4 (\pm 0.3)	34.8 (\pm 0.5)	33.8 (\pm 0.7)	33.7 (\pm 0.3)
	Nose bridge	26.8 (\pm 1.5)	26.5 (\pm 1.3)	27.1 (\pm 1.4)	27.5 (\pm 1.5)
	Nose tip	22.5 (\pm 2.0)	22.0 (\pm 1.8)	23.3 (\pm 1.6)	23.0 (\pm 1.7)
	Upper lip	26.5 (\pm 2.1)	25.7 (\pm 1.7)	26.9 (\pm 1.7)	28.0 (\pm 1.8)
Apes	Peri-orbital	35.0 (\pm 1.7)	32.9 (\pm 1.9)	35.6 (\pm 0.6)	36.0 (\pm 0.4)
	Nose bridge	28.6 (\pm 5.2)	28.1 (\pm 4.4)	32.2 (\pm 1.1)	32.4 (\pm 1.2)
	Nose tip	26.7 (\pm 7.6)	24.7 (\pm 5.9)	32.1 (\pm 2.1)	31.5 (\pm 3.1)
	Upper lip	30.8 (\pm 4.2)	29.4 (\pm 4.0)	34.1 (\pm 0.2)	34.4 (\pm 0.1)

712 Median (\pm SE) skin temperatures ($^{\circ}$ C) of the four measured facial areas in the monkey
 713 subjects and in the ape subjects when tested for the positive and negative emotions. The
 714 bold values represent the highest median temperatures for either the experimental
 715 condition or its preceding neutral condition.

716

717 **Figure Legends**

718 **Figure 1. Illustrations representing a white-throated capuchin and a Bornean**
719 **gibbon.** (a, d) Frontal photographs, (b, e) corresponding thermographic images and (c,
720 f) close-up thermographic images depicting the four facial areas of interest: peri-orbital
721 area, nose bridge, nose tip and upper lip. The white squares represent the regions of the
722 face to create the close-up image. The black circles refer to the peri-orbital area, the nose
723 bridge and the nose tip and the black rectangle refers to the upper lip. The colors of the
724 thermographic images refer to specific temperatures as indicated with the color bars and
725 temperature scales on the right side.

726
727 **Figure 2. Testing for facial temperature changes associated with positive emotion.**
728 Mean temperatures (°C) of the subjects from the neutral to the combined toy and tickling
729 condition (9 subjects) measured for four facial areas. The thick horizontal lines indicate
730 medians; the vertical length of the boxes corresponds to interquartile range; the thin short
731 horizontal lines indicate the minimum and maximum values. * $p < 0.05$. The two pictures
732 represent the thermal frames during the neutral and positive condition.

733
734 **Figure 3. Testing for facial temperature changes associated with negative emotion.**
735 Mean temperatures (°C) of the subjects from the neutral to the combined food delay and
736 teasing condition (10 subjects) measured for four facial areas. The thick horizontal lines
737 indicate medians; the vertical length of the boxes corresponds to interquartile range; the
738 thin short horizontal lines indicate the minimum and maximum values. * $p < 0.05$. The two
739 pictures represent the thermal frames during the neutral and negative condition.

740
741 **Figure 4. Time course of the facial temperature change from the neutral condition**
742 **to the experimental condition.** Mean temperatures (°C) per taxon of a) the nose tip
743 during the positive condition and b) the upper lip during the negative condition. Only the
744 last 5 seconds of the neutral condition (i.e., -5) and the first 15 seconds (i.e., 5, 10, and

745 15) of the experimental condition are depicted. The thin short horizontal lines represent
746 the error bars.

747

748 **Supporting Information**

749 S1. Dataset. Thermal data overview for testing positive and negative emotional state.

750 S2. Video clip.

751 S3. Time course dataset. Thermal data overview of the last 5 seconds of the neutral
752 condition and the first 15 seconds of the experimental condition for both positive and
753 negative emotion.

754 S4. Supplementary analysis.

755