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

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

KEYWORDS
deprivation, nonhuman primates, physiological and behavioral responses, play, thermography

1 | INTRODUCTION

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

Hélène Chotard and Marina Davila-Ross made an equal contribution to this work.

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So far, six facial thermography studies were conducted on nonhuman primates. Three of them revealed a decrease on nasal skin temperatures from neutral states to fear, that is, in captive rhesus macaques (Nakayama, Goto, Kuraoka, & Nakamura, 2005; Kuraoka & Nakamura, 2011) and in captive chimpanzees (Kano, Hirata, Deschner, Behringer, & Call, 2016). In a more recent study on wild chimpanzees, a decrease in the nasal skin temperature and an increase in the ear temperature was found in association with conspecific vocalizations (Dezecache, Zuberbühler, Davila-Ross, & Dahl, 2017). Another study showed an increment of the nasal skin temperature of only one laboratory rhesus macaque, when being stroked (i.e., sweeped) by a human (Grandi & Heinzl, 2016). Furthermore, a study on five rhesus macaques examined the temperatures of four facial areas and compared them between a teasing context and a context including playful interactions with toys (and feeding). At an individual level, the comparison showed a higher peri-orbital temperature for teasing for four out of five individuals (Ioannou, Chotard, & Davila-Ross, 2015). It, thus, remains to be tested to what extent positive and negative emotions may affect the facial skin temperature in nonhuman primate species in general.

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

Emotion-induced increases and decreases in the facial skin temperature suggest distinctive physiological activations in nonhuman primates, as found in humans, activations that are under the control of the autonomic nervous system (ANS). These thermal changes have often been associated with the activation of the sympathetic nervous systems (Ioannou et al., 2014; Kreibig, 2010), leading to constrictions of the blood vessels and the decrease of temperature in specific regions of the face. Other factors may also affect the facial skin temperature. For instance, an increase in the breathing rate may cool down the nasal area (Pavlidis, Levine, & Baukol, 2001); it is, however, important to note that an overall increase of the nose tip temperature may then nonetheless occur, as recently found for crying (Ioannou et al., 2016). Thermal changes result from the release of distinctive neurotransmitters (e.g., norepinephrines) that trigger successive physiological changes in the body (Charkoudian, 2010; Levenson, 1988). For instance, heart rate increase or decrease is the result of direct autonomic (sympathetic/parasympathetic) stimulation (Cannon, 1929), which activates different β-adrenergic receptors in the body, leading to its increase or decrease (Bers, 2002). Positive emotions cover a range of affective states in humans (e.g., joy, contentment) and imply different physiological patterns (Kreibig, 2010). For instance, joy is characterized by increased vagal control and β-adrenergic and cholinergic neurotransmitter release, while contentment is characterized by a decrease of α- and β-adrenergic and cholinergic activity along with mild cardiac vagal activation (Wright, 1996). Moreover, anger and frustration are characterized by an increase in heart rate and α- and β-adrenergic influences (Vella & Friedman, 2009).

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

Four facial areas (the peri-orbital area, the nose bridge, the nose tip, and the upper lip) were selected for the thermal analysis (according to their previously reported effects on facial temperatures in primates: Ebisch et al., 2012; Ioannou et al., 2015; Nakanishi & Imai-Matsumura, 2008). Facial thermal analysis, in general, should include more than just one area of interest, since the temperatures of specific facial areas may shift in opposite directions within the same time period (e.g., startling decreases the cheek temperature and increases the peri-orbital temperature: Levine, Pavlidis, & Cooper, 2001; crying increases the forehead, peri-orbital, cheek, nose, and chin temperature and decreases the maxillary temperature: Ioannou et al., 2016; a decrease in the nose temperature and an increase in the ear temperature may co-occur in wild chimpanzees hearing conspecific vocalizations: Dezecache et al., 2017). Facial skin areas are irrigated differently by the many blood vessels that branch off from the facial artery and they are exposed to different physiological processes (Ioannou et al., 2014; Kreibig, 2010). For instance, the nose tip was reported to provide particularly reliable data due to its rich blood supply (Bergersen, 1993), unlike the nose bridge, where the lateral nasal and inferior palpebral arteries show poor blood supply (Ioannou et al., 2014, 2015). Depending on the experienced emotion, specific adrenergic pathways might be activated along the blood vessels, consequently affecting the temperatures of the facial skin differently (Kreibig, 2010).

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

2 | METHODS

2.1 | Ethical statement

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

2.2 | Subjects and study sites

Three monkey taxa and two ape taxa represented the study subjects: Common marmosets (*Callithrix jacchus*), white-throated capuchins (*Cebus capucinus*), rhesus macaques (*Macaca mulatta*), Bornean gibbons (*Hylobates muelleri*), and western lowland gorillas (*Gorilla gorilla gorilla)*. Nine subjects were tested for the toy or tickling condition and 10 subjects for the food delay or teasing condition. For the subject characteristics and representation in the data, see Table 1. All subjects except for the gorillas were housed in the Owl and Monkey Haven (UK). The gorillas lived in Port Lympne Wild Animal Park (UK). All subjects were habituated to human interactions, facilitating thus the data collection. The data were collected when the subjects were in their social groups (groups of 12 marmosets, 3 capuchins, 5 macaques, 4 gibbons, and 4 gorillas) and in the enclosures where they stayed on a daily basis. All primates were outdoors during the data collection, except the marmosets and gorillas, who were studied indoors. The outdoor and indoor enclosures were equipped with climbing structures, and other enrichment objects. The main feeding times were in the morning and afternoon for all subjects (8 a.m., 3 p.m., and 5 p.m.), except for the gorillas (12 p.m. and 3 p.m.). The subjects had constant access to water. The monkeys and apes of this study are likely to represent good candidates for facial thermal imaging research as the measured facial areas are covered only with few hairs, with the exception of the upper lip.

2.3 | Procedure and data collection

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

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

In addition, food delay or teasing were used to induce negative states related to anger or frustration. The experimenter presented to a subject food (crickets, mealworms, or fruits) that was out of reach for 1 min. The experimenter held the food in the hand and if the subject tried to reach for the food, the experimenter held the food further away. Exceptions here were made for two gorillas as it would not have been safe to give them the food directly from the hand. For the gorillas, a fruit bucket was placed on the ground (out of reach). All subjects received the food after this condition ended. For the neutral condition of this study, the subjects had to be calm (e.g., sitting in a relaxed way, with a relaxed face, and with no piloerection) for up to 10 s.

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

Moreover, only sessions with thermal data obtained from both neutral and experimental conditions were included for further analyses (Supplementary Material S1). A total of 33 sessions (19 for toy and

TABLE 1 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

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

tickling, 14 for food delay and teasing) were used for the analyses (for an overview on the number of sessions, see Table 1). The experimenter stood outside of the enclosures, behind the meshes (behind the bars for the gorillas). The data collection took place in October and November 2013 and in January and May 2014.

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

No direct sunlight affected the data collection as it was too cloudy for the sun to be visible during the outdoor recordings. In addition, the recordist collected the thermal data underneath a ceiling for all sessions, except the gibbon session. For an overview of the enclosure temperatures during the recordings, see Table 1. In addition, each subject was video-recorded with a regular camera

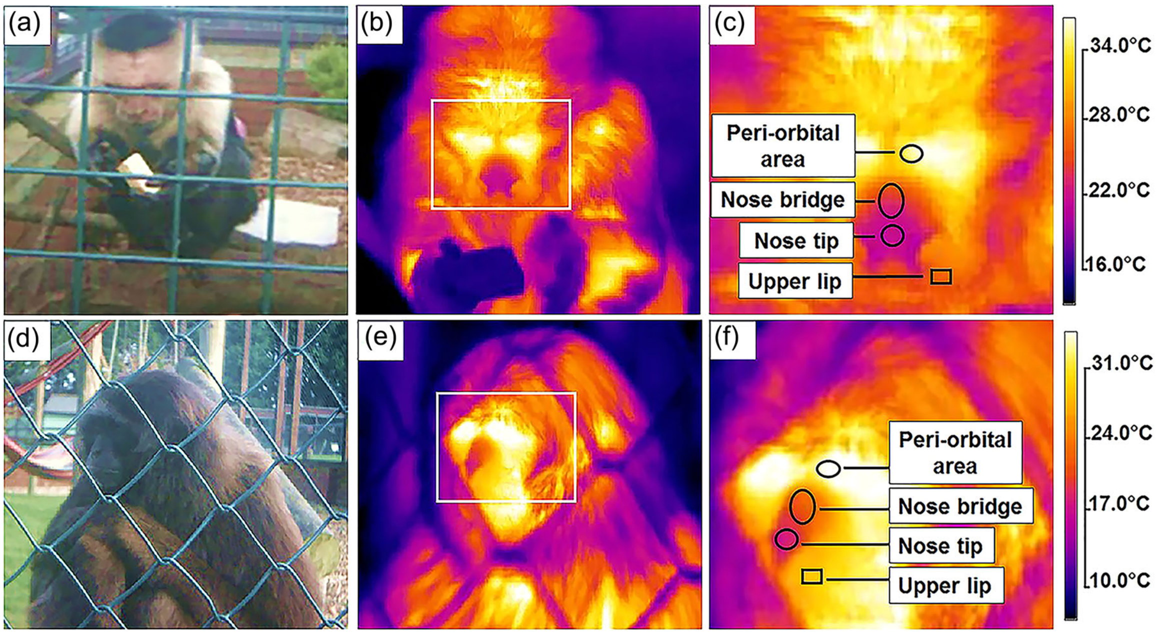

FIGURE 1 Illustrations representing a white-throated capuchin and a Bornean gibbon. (a and d) Frontal photographs, (b and e) corresponding thermographic images, and (c and f) close-up thermographic images depicting the four facial areas of interest: peri-orbital area, nose bridge, nose tip, and upper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

(JVC Everio) for the behavioral analysis. This camera was placed about 1 m outside of the enclosure.

2.4 | Thermal analysis

For the thermal analysis, the subjects' facial skin temperatures were measured from extracted picture frames every 5 s. For every picture frame, the mean temperature of each of the four measured facial areas was obtained. A circular shape was used to measure the temperature of the peri-orbital area, the nose bridge as well as the nose tip, while a rectangular shape was used for the upper lip (Figure 1). To have all facial areas sufficiently visible and measurable, a frame was only extracted if it showed the frontal side of the subject face or up to a 45° angle sideways. If any facial area was not fully visible (e.g., due to the enclosure meshes or bars), no thermal data were obtained from this particular frame. For each of the four measured facial areas, the mean temperatures of the neutral condition and the experimental condition were calculated per session, respectively.

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

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

2.5 | Behavioral analysis

For the behavioral analysis, the intensities of bodily movements as well as the presence/absence of facial expressions and calls were coded for every 5-s interval which preceded each thermal picture frame that was measured for the thermal analysis. Only small bodily movements were observed during the test, and were coded as either absent, slow (e.g., gently reaching for the toy or food) or rapid (e.g., quickly and repeatedly grabbing for the toy or food). In addition, low and high level of behavioral indicators of positive and negative emotional states were coded (for a list and description of the behavioral indicators, see Table 2; for video clips, see Supplementary Material S2). The coding of behavioral indicators was meant to help find out if at least some of the subjects experienced the relevant emotion tested for and, consequently, if the approach to induce positive and negative emotional states, respectively, was successful.

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

2.6 | Data analysis

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

TABLE 2 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 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

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

3 | RESULTS

3.1 | Thermal analysis

Five of the nine subjects tested with either the toy or tickling showed behavioral indicators of positive emotional state (Table 2). All of the 10 subjects tested for food delay or teasing showed behavioral indicators of negative emotional states (Table 2). Behaviors associated with positive state were absent during the food delay or teasing condition; behaviors associated with negative state were absent during the toy or tickling condition.

For the combined toy and tickling condition, the thermal analysis showed a significant decrease in the nose tip temperature of the subjects from the neutral condition to the experimental condition (Wilcoxon signed rank test with Hommel-Hochberg corrections: $z = -1.836$, $T = 7$, $N = 9$, $p < 0.05$), but a tendency of an increase in the peri-orbital temperature ($z = 1.718$, $T = 8$, $N = 9$, $p = 0.05$). No significant decreases were found for the nose bridge ($z = 0.296$, $T = 20$, $N = 9$, $p = 0.41$) and for the upper lip ($z = -1.481$, $T = 10$, $N = 9$, $p = 0.08$); Figure 2. When including only the five subjects who showed behavioral indicators of positive state, the thermal analysis showed a significant decrease in the nose tip temperature ($z = -2.023$, $T = 0$, $N = 5$, $p < 0.05$), and a significant increase in the peri-orbital temperature ($z = -2.023$, $T = 0$, $N = 5$, $p < 0.05$); the other two facial areas showed no significant temperature changes (nose bridge: $z = -0.135$, $T = 7$, $N = 5$, $p = 0.50$; upper lip: $z = -1.753$, $T = 1$, $N = 5$, $p = 0.06$).

Due to the difference between the toy and tickling conditions, we decided to exclude the gorilla data (i.e., only species tested in the tickling condition) from the sample. We then assessed if the subjects who were tested in the toy condition showed significant thermal changes. Such changes were not found for any of the four facial areas when comparing the neutral to the experimental condition (Wilcoxon signed rank test with Hommel-Hochberg corrections: peri-orbital: $z = -1.400$, $T = 8$, $N = 8$, $p = 0.10$; nose bridge: $z = -0.140$, $T = 17$, $N = 8$, $p = 0.47$; nose tip: $z = -1.540$, $T = 7$, $N = 8$, $p = 0.07$; upper lip: $z = -1.120$, $T = 10$, $N = 8$, $p = 0.16$).

For the combined food delay and teasing condition, the analysis revealed a significant increase in temperature from the neutral condition to the experimental condition in the upper lip (Wilcoxon signed rank test with Hommel-Hochberg corrections: $z = -2.040$, $T = 8$, $N = 10$, $p < 0.05$). No significant difference was found when comparing neutral versus combined food delay and teasing in the peri-orbital area ($z = -1.274$, $T = 15$, $N = 10$, $p = 0.12$), nose bridge ($z = -1.683$, $T = 11$, $N = 10$, $p = 0.05$), and in the nose tip ($z = -0.357$, $T = 24$, $N = 10$, $p = 0.39$); Figure 3. Table 3 and the Supplementary Material S1 show the skin temperatures of the monkeys and apes measured during the toy or tickling conditions and the food delay or teasing conditions and their preceding neutral conditions for each facial area.

Similarly to the positive conditions, we decided to exclude the gorilla data (i.e., only species tested in the food delay condition) from the sample due to the difference between the two negative conditions. We then assessed if the individuals who were tested in the teasing condition showed thermal changes. This analysis showed a significant increase in the upper lip temperature when comparing the neutral to the teasing condition (Wilcoxon signed rank test with Hommel-Hochberg corrections: $z = -1.752$, $T = 5.50$, $N = 8$, $p < 0.05$). The other three facial areas did not show any significant differences (peri-orbital: $z = -1.120$, $T = 10$, $N = 8$, $p = 0.16$; nose bridge: $z = -1.402$, $T = 8$, $N = 8$, $p = 0.09$; nose tip: $z = -0.140$, $T = 17$, $N = 8$, $p = 0.47$).

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

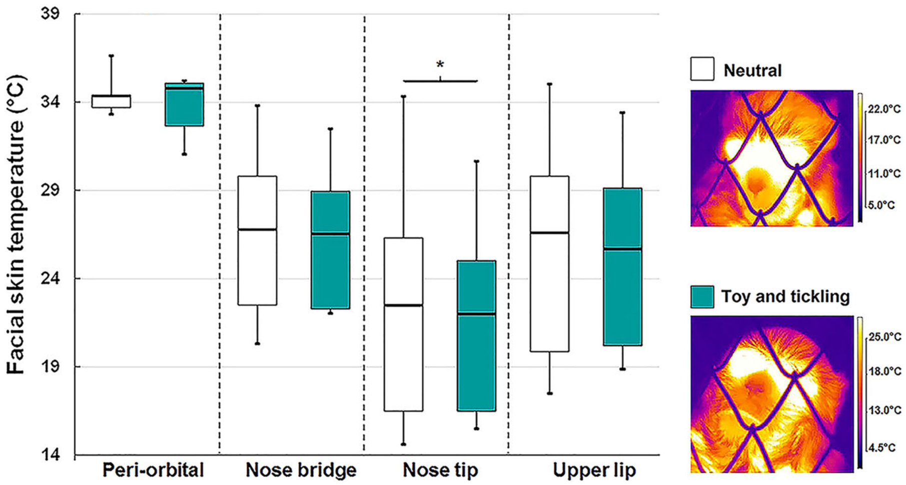

FIGURE 2 Testing for facial temperature changes associated with positive emotion. Mean temperatures (°C) of the subjects from the neutral to the combined toy and tickling condition (nine subjects) measured for four facial areas. The thick horizontal lines indicate medians; the vertical length of the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

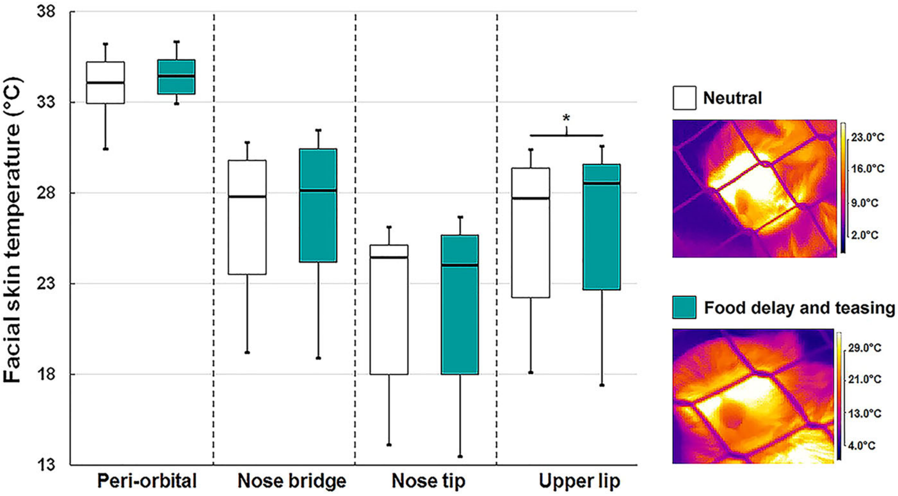

FIGURE 3 Testing for facial temperature changes associated with negative emotion. Mean temperatures (°C) of the subjects from the neutral to the combined food delay and teasing condition (10 subjects) measured for four facial areas. The thick horizontal lines indicate medians; the vertical length of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

Additionally, it was tested if the recording angle could have had an impact on the thermal data. No significant differences were found when comparing frontal and sideway frames for any of the four facial areas of interest (Wilcoxon signed rank test with Hommel-Hochberg corrections; two-tailed: peri-orbital area: $z = -0.431$, $T = 8.5$, $N = 8$, $p = 0.78$; nose 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: $z = -0.425$, $T = 8.5$, $N = 8$, $p = 0.81$).

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

3.2 | Behavioral analysis

Only four subjects showed no/slow bodily movements as well as rapid bodily movements when tested for toy or tickling and only

TABLE 3 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 (± SE) temperature	median (± SE) temperature	median (± SE) temperature	median (± SE) temperature
Monkeys				
Peri-orbital	34.4 (±0.3)	**34.8** (±0.5)	**33.8** (±0.7)	33.7 (±0.3)
Nose bridge	**26.8** (±1.5)	26.5 (±1.3)	27.1 (±1.4)	**27.5** (±1.5)
Nose tip	**22.5** (±2.0)	22.0 (±1.8)	23.3 (±1.6)	23.0 (±1.7)
Upper lip	**26.5** (±2.1)	25.7 (±1.7)	26.9 (±1.7)	**28.0** (±1.8)
Apes				
Peri-orbital	**35.0** (±1.7)	32.9 (±1.9)	35.6 (±0.6)	**36.0** (±0.4)
Nose bridge	**28.6** (±5.2)	28.1 (±4.4)	32.2 (±1.1)	**32.4** (±1.2)
Nose tip	**26.7** (±7.6)	24.7 (±5.9)	**32.1** (±2.1)	31.5 (±3.1)
Upper lip	**30.8** (±4.2)	29.4 (±4.0)	34.1 (±0.2)	**34.4** (±0.1)

Median (±SE) skin temperatures (°C) of the four measured facial areas in the monkey subjects and in the ape subjects when tested for the positive and negative emotions. The bold values represent the highest median temperatures for either the experimental condition or its preceding neutral condition.

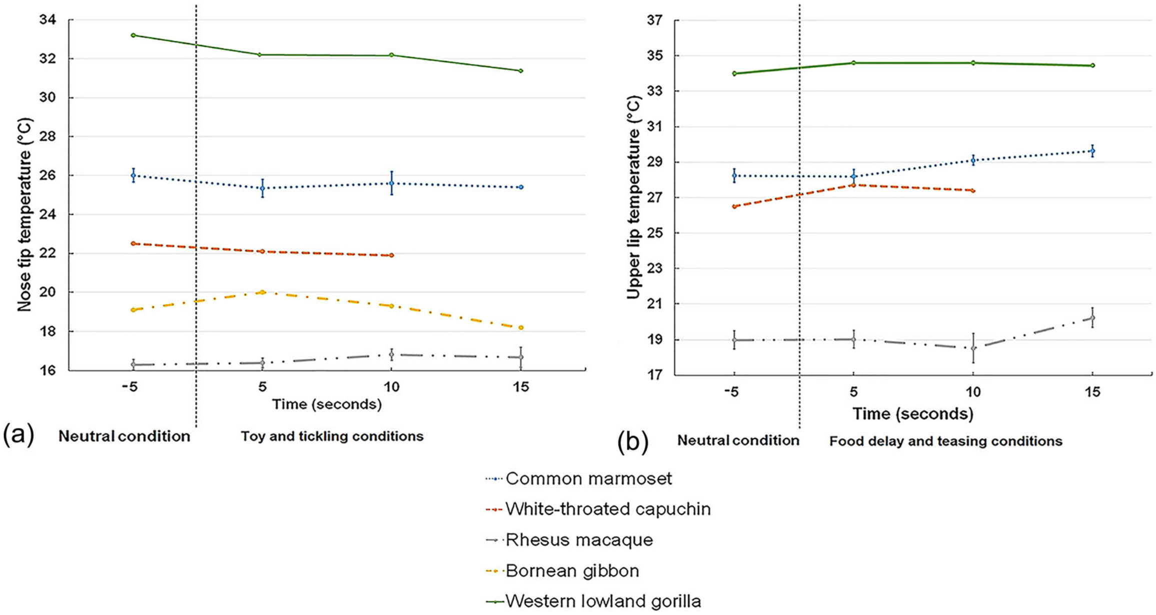

FIGURE 4 Time course of the facial temperature change from the neutral condition to the experimental condition. Mean temperatures (°C) per taxon of (a) the nose tip during the positive condition and (b) the upper lip during the negative condition. Only the last 5 s of the neutral condition (i.e., −5) and the first 15 s (i.e., 5, 10, and 15) of the experimental condition are depicted. The thin short horizontal lines represent the error bars

three subjects when tested for food delay or teasing. Furthermore, one subject produced facial expressions and calls during testing (one gorilla produced play faces and laughter during play). For the positive emotion, the subjects showed 3.4 ± 0.6 (mean ± SE) slow movements and 8 ± 3.5 rapid movements during the toy condition, and the gorilla tested during the tickling condition showed 10 slow movements as well as four rapid movements. Regarding the negative emotion, the subjects displayed 2 ± 0.2 slow movements as well as 2.5 ± 0.8 rapid movements during the teasing condition, and the gorillas showed 5.5 ± 1.5 slow movements, and only one subject showed seven rapid movements. The number of movements per session is presented in the Supplementary Material S1.

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

Regarding the behavioral indicators of the emotional state, low level of positively related behavioral indicators occurred 9.23 ± 2.11 (mean ± SE) seconds and 5 s after the beginning of the toy condition and tickling condition, respectively. High level of positively related behavioral indicators occurred 26.25 ± 7.18 s and 15 s after the beginning of the toy condition and the tickling condition (one session), respectively. Low level of negatively related behavioral indicators occurred 5.71 ± 0.71 s and 5 ± 0.0 s after the beginning of the teasing condition and food delay condition, respectively. High level of negatively related behavioral indicators occurred 5.83 ± 0.83 s and 40 s after the beginning of the teasing condition and the food delay condition, respectively. When comparing the onset of the low level of behavioral indicators between the negative and positive condition, no significant difference was found (Mann-Whitney U test; two-tailed: U = 46.5, $N_{\text{Positive}} = 14$ sessions, $N_{\text{Negative}} = 9$ sessions, $p = 0.27$). Nor such difference was found when excluding the gorilla data from the analysis (U = 33.5, $N_{\text{Positive}} = 13$, $N_{\text{Negative}} = 7$, $p = 0.33$). Regarding the onset of the high level of behavioral indicator, no significant difference was found between the negative and positive condition (U = 8.5, $N_{\text{Positive}} = 5$, $N_{\text{Negative}} = 7$, $p = 0.13$). However, when excluding the gorilla data from the analysis, the onset of high level of behavioral indicators occurred significantly faster within the negative condition than within the positive condition (U = 3.5, $N_{\text{Positive}} = 4$, $N_{\text{Negative}} = 6$, $p < 0.05$). We, then, tested whether there was a significant difference when comparing the temperatures of the 15 s before and after the onset of the high level of behavioral indicator for the positive emotion. No significant thermal changes were found for any of the four facial areas (Wilcoxon signed rank test with Hommel-Hochberg correction: peri-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 = −0.552, T = 3.50, N = 4, $p = 0.75$; upper lip: z = −1.461, T = 1, N = 4, $p = 0.25$).

4 | DISCUSSION

The current study examined the facial skin temperatures in monkeys and apes associated with positive and negative emotional states. We hypothesized that positively grounded emotions related to playful interactions with toys (and tickling) reduce the facial skin temperatures in nonhuman primates, whereas negative emotional states, more specifically emotions that are most likely to reflect anger or frustration, increase the facial skin temperature in nonhuman primates. Our results supported our two hypotheses to some extent where only some facial areas showed significant thermal changes. The data on behavioral indicators suggest that the approach to induce positive and negative emotions in the studied nonhuman primates was in general successful, with five subjects showing positive behaviors (e.g., playful head movements) and 10 subjects showing negative behaviors (e.g., display posture), respectively.

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

Regarding the positive emotional states, the nose tip temperatures of the subjects dropped from the neutral condition to the combined toy and tickling condition, but the peri-orbital temperatures had a tendency of an increase. The nose tip data were consistent with our previous macaque findings (Ioannou et al., 2015) and previous research on human infant laughter (Nakanishi & Imai-Matsumura, 2008) and children play (Ioannou et al., 2013) (cf., Salazar-López et al., 2015). The drop in the nasal temperature might have resulted from the constriction of blood vessels innervating selectively this facial area (i.e., arteriovenous anastomosis: Bergersen, 1993), an action mediated by the direct sympathetic postganglionic neurons (Hales, 1985). It is possible that an increased breathing rate additionally contributed to cooling the nose (Pavlidis et al., 2001), but it may have had a minor effect (Ioannou et al., 2016). A temperature rise in the peri-orbital area was previously also found for positive contexts in humans (positive self-sentiment: Robinson et al., 2012) and might have resulted from an increased heart rate (Cannon, 1929) and increased blood flow to extra-ocular muscles (Ioannou et al., 2015). Moreover, blood may be redirected by other facial regions (Pavlidis et al., 2001).

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

Additionally, the discrepancies in the literature may also be explained by the different uses of stimuli, such as play and pleasant touch (Grandi & Heinzl, 2016; Nakanishi & Imai-Matsumura, 2008; Salazar-López et al., 2015). When removing the gorilla data from our sample, no thermal changes were found anymore for the positive emotion. It is possible that different behavioral contexts may induce different physiological responses due to the activation of a more specific emotion system associated with the context per se (Kreibig, 2010). By contrast, other researchers suggest that positive states are under the control of a more general system resulting in similar physiological reactions regardless of the context (Panksepp, 1998). Future studies including different behavioral contexts to induce positive emotions, as well as negative emotions, are needed to shed light onto this disagreement.

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

Although, the study presents some methodological issues regarding the uneven number of sessions between the subjects and the small sample size, the nonparametric analyses showed significant thermal changes, which revealed a reliable degree of statistical rigidity. This study showed that positive and negative emotional states have a distinctive effect on the facial temperatures in monkeys and apes. They might reflect distinctive physiological reactions of a primordial emotion system, associated with the competing subdivisions of the ANS (Kreibig, 2010; Vella & Friedman, 2009; Wright, 1996). During sympathetic arousal, they lead to heart acceleration and the constrictions of the blood vessels whereas during parasympathetic activation, they lead to an inhibition of the sympathetic axis and physiological restoration (Kreibig, 2010). Both systems seem to play an important role in the mediation of the different physiological actions that lead to the release of specific neurotransmitters, such as adrenalin and acetylcholine, and to changes in the blood flow (Kreibig, 2010), explaining the differences found for the distinctive emotional states and their distinctive facial areas.

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

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

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SUPPORTING INFORMATION

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