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## **The use of infrared thermography to investigate emotions in common marmosets**

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1 The use of infrared thermography to investigate emotions in  
2 common marmosets

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21 Further information

22  
23 - Every figure should be in color  
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25  
26

27 **Abstract**

28

29 Measuring body surface temperature changes with infrared thermography has recently been put  
30 forward as a non-invasive alternative measure of physiological correlates of emotional  
31 reactions. In particular, the nasal region seems to be highly sensitive to emotional reactions.  
32 Several studies suggest that nasal temperature is negatively correlated with the level of arousal  
33 in humans and other primates, but some studies provide inconsistent results. Our goal was to  
34 establish the use of infrared thermography to quantify emotional reactions in common  
35 marmosets (*Callithrix jacchus*), with a focus on the nasal region. To do so we exposed 17  
36 common marmosets to a set of positive, negative and control stimuli (positive: preferred food,  
37 playback of food calls; negative: playback of aggressive vocalizations, teasing; control: no  
38 stimulus). We compared nasal temperature before and after the stimuli and expected that highly  
39 aroused emotional states would lead to a drop in nasal temperature. To validate the  
40 thermography measure, we coded piloerection of the tail as an independent measure of arousal  
41 and expected a negative correlation between the two measures. Finally, we coded physical  
42 activity to exclude its potential confounding impact on nasal temperature. Our results show that  
43 all predictions were met: the animals showed a strong decrease in nasal temperature after the  
44 presentation of negative arousing stimuli (teasing, playback of aggressive vocalizations).  
45 Furthermore, these changes in nasal temperature were correlated with piloerection of the tail  
46 and could not be explained by changes in physical activity. In the positive and the control  
47 conditions, we found systematic sex differences: in males, the preferred food, the playbacks of  
48 food calls, as well as the control stimulus led to an increase in nasal temperature, whereas in  
49 females the temperature remained stable (preferred food, control) or decreased (playback of  
50 food calls). Based on naturalistic observations that document higher food motivation and  
51 competition among female marmosets, as well as stronger reactions to separation from group  
52 members in male marmosets, these sex differences corroborate a negative correlation between  
53 arousal and nasal temperature. Overall, our results support that measuring nasal temperature  
54 by infrared thermography is a promising method to quantify emotional arousal in common  
55 marmosets in a fully non-invasive and highly objective way.

56

57 **Keywords**

58 Infrared thermography, Nasal skin temperature, Common marmosets, Emotions, Autonomic  
59 reaction, Piloerection, Arousal

60

## 61 1 Introduction

62

63 Identifying emotional states remains one of the big challenges in animal behavior research since  
64 in contrast to humans, animals cannot document their subjective experience in self-reports.  
65 However, in addition to subjective experiences, emotional states also correlate with behavioral  
66 and physiological responses that are accessible to empirical investigation in animals [1–3].

67 Physiological markers are particularly promising because they can be quantified  
68 objectively. Unfortunately, techniques to measure them tend to be invasive and restrict the  
69 movement of the subject. For example, EEG or fMRI can be used to measure brain activity  
70 patterns but require attaching electrodes or placing the subject in an fMRI tube [4]; changes in  
71 heart-rate can be assessed by electrocardiography that requires electrodes on the subjects body  
72 [5–7]; quantifying the galvanic skin response necessitates a finger transducer [8] and blood  
73 pressure is measured by a cuff or an arterial catheter [9,10].

74 The invasiveness of such methods limits their use to measure emotions, especially in  
75 animals. First, the measurement interferes with the behavior and is likely to produce a strong  
76 emotional reaction in itself. Furthermore, habituating the subject to the procedures is often time  
77 intensive or even impossible [1,6,11]. A fundamental limitation in the study of animal emotions  
78 is thus the scarcity of non-invasive methods to measure physiological reactions. This limitation  
79 is particularly striking when the goal is to quantify emotional arousal during naturalistic  
80 conditions or social interactions, which is an increasingly important domain of research [3,12].

81 In recent years, infrared thermography has been pioneered as a fully non-invasive,  
82 contact-free technique to examine emotional states. This technique measures emotion-related  
83 surface temperature changes [13]. Several studies have focused on temperature changes in  
84 highly exposed body regions such as the nose, fingers, paws or the tail of animals [3,6,14–16].  
85 The temperature of these areas seems to be highly sensitive to emotional changes. However,  
86 results are sometimes incongruent, and it is not yet clear which temperature reactions  
87 correspond to what kind of emotion and how sensitive such measures are.

88 In humans, first studies showed a trend to a decrease in temperature in peripheral body  
89 regions during negative, high-arousal states. Thus, a decrease in nasal or finger temperature has  
90 for example been observed in response to stimuli inducing mental stress [17], fear [16], guilt  
91 [14] or when experiencing empathy for a child in distress [18]. These temperature drops in  
92 peripheral body regions are mostly attributed to changes in subcutaneous perfusion that are  
93 controlled by the sympathetic branch (SNS) of the autonomic nervous system. The idea is that  
94 during the “fight or flight” response, the SNS induces peripheral vasoconstriction and hence a  
95 decrease in blood flow and cooling of the respective regions [13,14,19]. This mechanism is  
96 most likely caused by the immediate norepinephrine release by the sympathetic nervous system,  
97 that occurs within seconds after the presentation of stressful stimuli. Minutes later, especially  
98 with strong negative stimuli, the thermal signature could further change due the secretion of  
99 cortisol by the adrenal gland [20,21].

100 Peripheral temperature drops, however, appear to accompany arousal in general, and  
101 not only in combination with negative valence. In fact, various studies that examined thermal  
102 reactions to positive stimuli suggest that the respective impact of arousal on body temperature  
103 is independent of whether the emotion is of positive or negative valence. For instance,  
104 Kosonogov et al. [22] measured nasal temperature while human participants were watching  
105 standardized emotional pictures. They could show that arousal, but not valence, of the induced

106 psychological state had an effect on nasal temperature. Furthermore, Salazar-Lopez et al. [23]  
107 found that nasal temperature decreased during positive empathic reactions (empathic  
108 happiness). Another study found that playing and laughing, behaviors most likely linked to  
109 positive, high arousal emotions, evoked nasal temperature drops in human children [24].  
110 Consistent with this general effect of arousal, positive, relaxing situations were often linked to  
111 the opposite thermal reaction; an increase in peripheral body temperature. For example, human  
112 participants instructed to relax [25] or watching positive, relaxing video clips [26] showed an  
113 increase in finger temperature. Likewise, watching at and thinking about a beloved person  
114 evoked an increase in nasal and hand temperature in most and half of the participants,  
115 respectively [23].

116 Whereas the above findings match the suggested pattern of a negative correlation  
117 between arousal and the temperature of peripheral body regions in humans, a few studies have  
118 shown other reactions. For instance, sexual arousal was linked to an increase in nasal  
119 temperature although it is most likely not associated with a relaxed emotional state [27,28].  
120 Further, Salazar-López et al. [23] conducted an experiment in which human participants were  
121 exposed to IAPS images (International Affective Picture System: Lang et al. [29]) which  
122 elicited psychological states of varying valence and arousal levels. Positive images, both low  
123 and high arousal were linked to an increase in nasal temperature while for negative conditions,  
124 nasal temperature decreased in response to low arousal but increased in the case of high arousal.

125 In thermography studies with animals, most results support a general pattern of a  
126 negative relationship between arousal and the temperature of peripheral body regions. For  
127 example, macaques showed a decline in nasal temperature in response to a threatening person  
128 [19] or visual and vocal signals of aggressive conspecifics [8]. Kano et al. [6] found that the  
129 nose of chimpanzees became colder in response to playback calls and videos of fighting  
130 conspecifics. They validated their findings with behavioral but also additional physiological  
131 measurements. Most notably for one of the subjects they reported a decrease of the relative  
132 power of the high-frequency band of the heart rate variability spectrum, which is reported to be  
133 a reliable indicator of a highly aroused state. A further study [3] investigated thermal reactions  
134 of wild chimpanzees in response to naturally occurring species-specific vocalizations. They  
135 found that nasal temperature dropped significantly after aversive vocalizations while it stayed  
136 about the same after neutral ones. Intriguingly, they also report a significant increase in ear  
137 temperature in the neutral conditions but not in response to aversive vocalizations. Potentially  
138 underlying physiological mechanisms for these changes in ear temperature are not known. In  
139 fact, a different pattern was observed in rabbits and dogs where ear temperature decreased  
140 during stress or fear related situations [30,31]. Additionally, stress-related situations evoked a  
141 temperature drop in the tail and paws in rats [15].

142 In contrast to negative stimuli, much less research has been conducted to quantify  
143 thermal reactions to positive stimuli in animals. However, a macaque showed an increase in  
144 nasal temperature while it was stroked by a human, and the decrease in its heart rate suggested  
145 that the monkey became more relaxed during this procedure [32]. In addition, Chotard et al.  
146 [33] found a trend for a decrease in nasal temperature in non-human primates when the subjects  
147 were exposed to a toy, what was assumed to be positively arousing.

148 Another macaque study compared nasal temperature among three conditions that were  
149 assumed to be negatively or positively arousing: feeding with potential food competition,  
150 teasing with food, and playing with a toy. Nasal temperature was only significantly lower in

151 the feeding condition compared to the other two conditions, which did not show a significant  
 152 difference in nasal temperature among each other [11]. However, the conditions were not  
 153 compared to a “neutral” control or a baseline condition and no behavioral markers of arousal  
 154 were coded, which hampers the interpretation about the link between arousal and nasal  
 155 temperature. Table 1 summarizes the presented studies on humans and animals, classifying the  
 156 stimuli according to the suggested valence and arousal level as well as the corresponding  
 157 thermal reaction.

158  
 159 Table 1 | Summary of studies that examined the link between emotional states and thermal reactions in peripheral body regions  
 160 (nose, finger, tail or ears). We classified the emotions/psychological states according to the suggested valence and level of arousal  
 161 as well as the corresponding evoked peripheral temperature change. Some studies are mentioned several times as they examined  
 162 more than one emotion. The subscript letters indicate whether the emotion was examined in humans (H), non-human primates  
 163 (P) or other animals (A).

		Arousal	
		Increase	Decrease
Valence	Positive	<b>Temperature drop</b> - Empathic happiness [23] <sup>H</sup> - Joy [24] <sup>H</sup> - Playfulness [33] <sup>P</sup>  <b>Temperature rise</b> - Low and high, positive arousal due to exposure to IAPS images [23] <sup>H</sup> - Sexual arousal [27,28] <sup>H</sup>	<b>Temperature drop</b> - No studies  <b>Temperature rise</b> - Relaxing [25,26,32] <sup>H,P</sup> - Feeling love [23] <sup>H</sup>
	Negative	<b>Temperature drop</b> - Fear [16] <sup>H</sup> - Guilt [14] <sup>H</sup> - Negative empathy [18] <sup>H</sup> - Unpleasant arousal [22] <sup>H</sup> - Low negative arousal due to exposure to IAPS images [23] <sup>H</sup> - Stress, fear [3,6,8,11,15,19,30,31] <sup>P, A</sup> - Feeding with food competition (compared to teasing and playing) [11] <sup>P</sup>  <b>Temperature rise</b> - High negative arousal due to exposure to IAPS images [23] <sup>H</sup> - Teasing and Playing with a toy (compared to feeding with food competition) [11] <sup>P</sup>	No studies
	Neutral	<b>Temperature drop</b> - Mental Stress [17] <sup>H</sup>  <b>Temperature rise</b> - No studies	No studies

164  
 165 In contrast to humans, there are almost no results that contradict the proposed link  
 166 between arousal and a decrease in peripheral body temperature in animals. However, this could  
 167 be a simple artefact of the bias for studies about negative, high arousal emotions in animals.  
 168 Therefore, in order to reliably apply this method to assess the level of arousal in animal studies,  
 169 it is mandatory to investigate a variety of possible emotions that vary with both regard to  
 170 valence (positive/negative) and arousal.

171 A final issue in thermography studies, especially with animals, concerns the role of  
 172 physical activity [6,11,31]. An alternative explanation for thermal changes that accompany  
 173 arousal may be that higher arousal simply leads to higher physical activity that in turn influences  
 174 body temperature. Therefore, to verify the link between emotions and changes in peripheral  
 175 body temperature, it is important to examine this potentially confounding effect.

176 In this study we investigated the use of infrared thermography to infer emotional states  
 177 in common marmoset, a New World monkey species. Marmosets are increasingly used as

178 model species in social neurosciences and evolutionary anthropology [12,34–39] because of  
179 their high degree of sociality, cooperation and allomaternal care, which show striking  
180 similarities with humans [37,38]. Marmosets are small, highly active animals and do hardly  
181 ever stand still. This makes it difficult to reliably track the temperature of a respective region  
182 of interest, especially if its temperature is not very different from the surrounding area.  
183 However, the nasal region is prominently visible as a cold spot in the face and hence can be  
184 tracked reliably. We therefore decided to focus on nasal temperature as a first investigation  
185 about the use of infrared thermography in marmosets.

186 We experimentally examined nasal temperature changes in 17 common marmosets in  
187 five conditions that were supposed to induce psychological states of varying levels of arousal  
188 and valence: teasing with food, playback of aggressive vocalizations, preferred food, playback  
189 of food calls and control (no stimulus).

190 Based on previous studies, we expected a negative correlation between arousal and nasal  
191 temperature. We a priori assumed that teasing with food and the playback of aggressive  
192 vocalizations would evoke a negative, intermediate to high arousal state in the animals, whereas  
193 eating a preferred food item was assumed to be a positive, relaxing event. A similar reaction  
194 could be expected in response to playbacks of food calls given by group members because  
195 previous studies have shown that vocalization of familiar individuals can lead to a stress  
196 reduction (decrease in cortisol level) [40]. However, food calls mostly refer to the presence of  
197 preferred food items and encourage the animals to search for the food source [41,42]. Therefore,  
198 we expected that the food calls could also lead to a positive, but aroused rather than relaxed  
199 state. During the control condition, the experimenter turned away and no stimulus was given.  
200 This was assumed to be neither positive nor negative and thus not lead to a change in arousal.

201 Simultaneously to the presentation of the stimuli and the assessment of changes in nasal  
202 temperature, we quantified a behavioral marker of arousal throughout the experimental  
203 conditions (i.e. piloerection of the tail). This behavioral marker allowed us to validate the  
204 findings of the thermal reactions. Finally, we also quantified physical activity, to disentangle  
205 whether thermal reactions indeed capture emotional states rather than a mere consequence of  
206 physical activity.

207

208 **2 Methods**

209

210 **2.1 Subjects and housing**

211

212 We tested 17 adult common marmosets (*Callithrix jacchus*) (see supplementary material S.1  
213 for details about the subjects). They were all born and reared in captive family groups. The  
214 animals lived in different groups or pairs that were housed in adjacent enclosures and had only  
215 visual and olfactory contact with other groups.

216 The monkeys were housed in heated indoor enclosures that contained sleeping boxes,  
217 heated resting platforms as well as climbing and playing material like ropes and branches. The  
218 floor was covered with bark mulch. When weather conditions were suitable, the animals also  
219 had access to outdoor enclosures that could be reached via transparent tubes.

220 The marmosets were fed at least twice a day (porridge with vitamins at 8:30; fresh fruits  
221 and vegetables between 11:00 and 12:00) and water was continuously available. During the  
222 week they received an additional snack (mealworms, nuts etc.) in the afternoon. For this study  
223 the animals were neither food nor water deprived. The monkeys had already been involved in  
224 other behavioral experiments but had no previous experience with the current experimenter or  
225 a thermography camera.

226

227 **2.2 Ethics statement**

228

229 The experiments were approved by the Kantonales Veterinäramt des Kantons Zurich,  
230 Switzerland (license number 223/16) and classified as degree of severity = 0.

231

232

233 **2.3 Experimental procedure**

234

235 During the experiments the monkeys were separated in a testing compartment (60\*50\*50 cm)  
236 of a larger testing enclosure in a testing room. This helped to control for spatial variation in  
237 environmental conditions (light, temperature) and to reduce the monkey's ability to move  
238 around and interact with group members. The monkeys voluntarily entered the testing enclosure  
239 from their home cage via a tube system that could be opened and closed by the experimenter.  
240 Thus, no direct handling of the animals was required. At the front mesh of the testing enclosure  
241 we attached a perch that served as preferred sitting area for the monkeys. Two cameras were  
242 placed in front of the testing compartment, a thermography camera (FLIR, T620) and a  
243 camcorder (SONY, HDR-CX730E). Prior to the experiments, the animals were habituated to  
244 the testing enclosure over a period of several weeks, first with their family group, later alone.  
245 Subjects who failed to habituate were excluded from the experiment.

246 Before an experimental session started, the experimenter opened the entrance to the  
247 testing enclosure and allowed free access to all animals of the social group for about two  
248 minutes. After this settling-in period the experimenter separated the subject in the testing  
249 compartment and lured the other group members out of the testing room. The experimental  
250 session started when the subject was quietly sitting on the perch or clinging to the front mesh  
251 and did not show obvious signs of stress, such as escape attempts, excessive vocalization or  
252 running quickly back and forth.



253 Each experimental session was divided into a baseline, a stimulation and a post-  
254 stimulation phase. The baseline phase lasted for two to three minutes. During this phase the  
255 experimenter offered a mealworm or a small piece of nut cookie to the subject periodically  
256 (every 20 seconds) through the mesh with a tweezer. This procedure occupied the subject and  
257 kept its attention towards the direction of the camera. Although a potential effect of this feeding  
258 procedure on the emotional state could not be fully excluded, we expected it to be negligible,  
259 especially compared to the other stimuli, as it was only a small amount of food and the monkeys  
260 were already habituated to this procedure. More importantly, the procedure was identical for  
261 all conditions and could therefore not influence the main results, i.e. differential reactions  
262 depending on stimulus type during the stimulation phase.

263 The stimulation phase started 20 seconds after the last mealworm was handed over in the  
264 baseline. In this phase the subject was not offered food but was instead exposed to one of the  
265 five stimuli. The post-stimulation phase started right after the stimulus has ended. It was  
266 identical to the baseline and lasted for about three minutes.

267

## 268 **2.4 Stimuli**

269

270 We used 5 stimuli that were presented to the subjects in randomized order. Each subject was  
271 tested maximally once a day in one of the five conditions. To elicit an increase in negative  
272 arousal, we used teasing and a playback of aggressive vocalizations. To evoke positive  
273 emotions we used offering highly preferred food and a playback of food calls of familiar  
274 individuals. During the control stimulus the experimenter simply stopped interacting with the  
275 subject.

276 During the *teasing* condition, the experimenter showed the subject a defrosted cricket  
277 (*Acheta domesticus*) or a nut cookie, depending on what the respective subject preferred. The  
278 experimenter held the food item right in front of the mesh and pulled it away each time the  
279 subject tried to grab it. The teasing lasted maximally 60 seconds. However, the teasing was  
280 finished earlier when the subject showed increasing signs of stress (e.g. escape attempts,  
281 running back and forth).

282 The *playback of aggressive vocalizations (PB-)* consisted of aggressive calls of  
283 common marmosets that were given during intergroup visual contact. The calls were recorded  
284 with the Avisoft UltraSoundGate 116H laboratory software and a condenser microphone  
285 CM16/COMPA. For all the sessions we used the same recording which did not include calls from  
286 group members of any of the subjects. This stimulus lasted maximally 60 seconds but again it  
287 was terminated prematurely if the subject showed increasing signs of stress. The playback was  
288 broadcast using “iMovie” (Apple, Version 10.1.9) from a laptop (MacBook Pro, Apple) placed  
289 in the right or left neighboring compartment of the testing compartment.

290 In the *preferred food (food)* condition, a defrosted cricket (*Acheta domesticus*) was  
291 given to the subject by the experimenter with a tweezer through the mesh. The subject was  
292 allowed to eat the cricket in its entirety without any disturbance. During the feeding time, the  
293 experimenter turned to the camera and did not look at the monkey. The duration of this stimulus  
294 could not be controlled and depended on how long it took the animals to consume the food.

295 The *Playback of food calls (PB+)* consisted of food calls given by one to three members  
296 of the subjects social group. Each of the playbacks lasted for 45 seconds. The calls were again  
297 recorded with the Avisoft UltraSoundGate 116H laboratory software and a condenser

298 microphone CM16/CMPA and cut in “iMovie”. To imitate naturally sounding playbacks, the  
299 food calls were regularly interrupted by pauses that were similarly arranged for all the  
300 individuals. The calls were played back in the same way as the aggressive vocalizations.

301 Finally, we used a *control* stimulus that was assumed to not evoke a strong emotional  
302 reaction. The control stimulus was a continuation of the baseline condition with the exception  
303 that the experimenter no longer offered a mealworm every 20 sec. Instead, she turned her body  
304 to the camera and did not look at the subject. This stimulus lasted for about 45–60 seconds.

305 The exact durations of the stimuli are listed in table S.2 of the supplementary material.  
306

## 307 **2.5 Thermal measurement and coding**

308  
309 During the experiments the monkeys were constantly filmed with an infrared thermography  
310 camera of the model FLIR T620 (temperature sensitivity: 0.04 °C; resolution: 640 x 480 pixels;  
311 sampling rate: 30 fps). For acclimatization, the camera was located in the experimental room  
312 and turned on at least 15 minutes before the experiment started. The camera was placed on a  
313 tripod in front of the testing compartment about one meter from the mesh. It was controlled  
314 with the FLIR Tools+ software from a laptop. The room temperature and humidity were  
315 periodically recorded and entered into the camera while the emissivity was constantly set on  
316 0.98. To ensure an optimal and clear image, the orientation of the camera was manually adjusted  
317 towards the subject when it was climbing up or down. The focus of the camera was controlled  
318 by hand to prevent the autofocus from focusing on the mesh rather than the subject.

319 For the extraction of the nasal temperature data, we used a customized MATLAB  
320 (R2018b) script. To do so we manually placed an ellipse over the region of interest (nose) on  
321 the first appropriate frame in each two-second interval and exported the minimal temperature  
322 of this area automatically to an excel file. If a respective interval did not contain a useful  
323 frame it was omitted. Appropriate frames were selected based on the following criteria (see  
324 figure 1 for examples). (1) The subject had to be right behind the frontal mesh to ensure that  
325 its face was in the focus of the camera. (2) The subjects’ head had to be oriented straight  
326 toward the camera (maximum tilt angle of about 45°). (3) The nasal region was not covered  
327 by the mesh. (4) The nose was not blurred due to movements of the subject or the camera.  
328 Due to the resolution of the thermography camera, we were not able to recognize the tiny  
329 nostrils of the marmosets in the thermographic images. Therefore, we could not exclude  
330 potential effects of breathing patterns on individual raw data points. However, we reasoned  
331 that a potential change in temperature due to breathing would not influence our main results  
332 because it only leads to a change in the amplitude of the oscillation around a mean. This  
333 means that inhaling and exhaling compensate each other and hence potential changes in nasal  
334 temperature due to the experimental stimuli are still detectable.

335 20% of all thermography videos were analyzed by a second rater to assess inter-rater  
336 reliability. The videos could be coded with very high reliability, resulting in an intraclass  
337 correlation coefficient (ICC 3) of 1 with a confidence interval of 1 to 1.

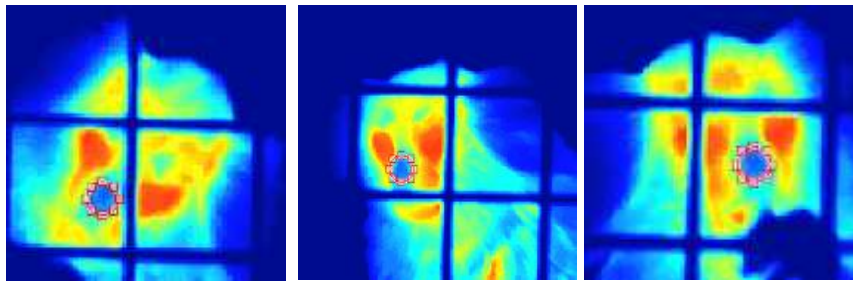


Figure 1 | Example of thermographic frames used to measure nasal temperature. The circles at the nasal region indicate the area from which the minimal temperature was measured

338

## 339 **2.6 Behavioral measurement and coding**

340

341 For the behavioral measurements we additionally filmed the animals with a camcorder (SONY,  
342 HDR-CX730E). The camcorder was placed on a tripod right next to the thermography camera.  
343 The behavioral analysis was conducted with the software INTERACT (MANGOLD GmbH,  
344 version 16).

345 We assessed piloerection of the tail as a signal of high arousal [43,44]. Therefore, we coded the  
346 level of piloerection of the tail every five seconds by assigning one of the three following levels:  
347 0 = no piloerection, 1 = half of the tail shows piloerection or the complete tail shows weak  
348 piloerection, 2 = the complete tail shows strong piloerection. If the state of piloerection was not  
349 visible at the respective time point, the time interval was extended by two seconds before it was  
350 coded as not available (N.A.). Piloerection was coded from 30 seconds before the stimulus  
351 onset until the stimulus offset. Finally, to estimate the change in the extent of piloerection  
352 during the stimulation phase we subtracted the mean of all scores collected during the baseline  
353 phase from the scores of the stimulation phase. For the coding of the piloerection, we reached  
354 an intraclass correlation coefficient (ICC 3) of 0.94 with a 95% confidence interval from 0.84  
355 to 0.98 (based on 20% of all the videos coded by two raters).

356 Finally, we coded the activity level of the monkeys to control for a potential impact of  
357 physical activity on nasal temperature. We counted the number of changes in position during  
358 the period of 30 seconds before the stimulus onset until 30 seconds after the stimulus had ended.  
359 A change in position was defined as the animal moving away all four limbs from the current  
360 position and moving at least one body length. Movements on the perch were not counted as  
361 changes in position because the perch was quite short (33 cm) and hence physical activity was  
362 highly restricted. When a subject changed between two positions via a third position that was  
363 occupied for less than ten frames (0.4 s), this was only counted as one change. For example,  
364 when a subject was hanging on the ceiling and jumped via the floor directly onto the perch it  
365 was counted as one change in position. We calculated a pre (30 seconds before stimulus onset)  
366 and a post (stimulus onset until 30 seconds after the stimulus) value by dividing the number of  
367 changes in position by the length of the respective period (in minutes) to get frequency measures  
368 of activity. For the activity measure, we reached an intraclass correlation coefficient (ICC 3) of  
369 0.96 with a 95% confidence interval from 0.88 to 0.99 (based on 20% of all the videos coded  
370 by two raters).

371

## 372 **2.7 Data analysis**

373

374 All statistical analyses were conducted in R 3.4.4. The assumption of homogeneous residuals  
375 and the absence of influential outliers were assessed by inspecting residual plots and cook's  
376 distances, respectively. Linear mixed models (LMM) were performed with the R function  
377 "lme" of the package "nlme". The models were built up in a step-forward procedure, starting  
378 with a null model that only included the random effect (random intercept) and adding all the  
379 fixed effects step by step (first all the main effects, then the interactions). To assess whether an  
380 added factor had a significant impact on the dependent variable, we always compared the  
381 respective model to the previous one (the one that did not include the respective factor) by a  
382 likelihood ratio test (R function "anova"). If a fixed factor or an interaction did not lead to an  
383 improvement of the model it was excluded from the final model if its higher-order interactions  
384 were also non-significant [45].

385

### 386 **2.7.1 Nasal thermal reaction**

387

388 To assess temporal changes in nasal temperature, we compared the temperature measures taken  
389 during the last 30 sec of the baseline condition (pre) to the measures taken 30 secs after the  
390 stimulus onset (post). With this protocol, we would most likely capture the immediate stress  
391 response (norepinephrine based "fight or flight" reaction) rather than a slower, potential  
392 increase in cortisol [20,21].

393

394 Since we were interested in temperature changes relative to baseline, rather than in  
395 absolute temperature, we calculated a centered temperature measure, by subtracting the  
396 individual mean temperature of the baseline from all temperature measures of the respective  
397 session.

397

398 To examine the effect of the different stimuli on changes in nasal temperature we  
399 conducted a LMM (model 1) on the centered nasal temperature. We set condition (food, teasing,  
400 PB-, PB+ and control), phase (pre and post), sex (male, female) as well as all two- and three-  
401 way interactions as fixed effects. Further, we added the subject as random effect to control for  
402 the repeated measures within a session.

402

403 To assess in more detail how males and females reacted to the different stimuli, we  
404 compared least square means of nasal temperature between pre and post phase per condition  
405 and sex based on the final model. Finally, to investigate the thermal reactions on the individual  
406 level, we performed Mann-Whitney U tests that compared nasal temperature between the pre  
407 and post-phase separately within each session (see supplementary S.3, table S.3).

407

### 408 **2.7.2 Piloerection**

409

410 First, we assessed the effect of the different stimuli on piloerection of the tail by calculating a  
411 LMM (model 2) on the extent of piloerection of the tail that included condition, sex as well as  
412 their interaction as fixed effect and subject as random effect. Based on the final model we  
413 compared least square means among the conditions.

414

415 To examine the link between the nasal thermal reaction and the piloerection, we set up  
416 a LMM (model 3) on the temperature data of the post-phase. We included the extent of  
piloerection of the tail, sex and their interaction as fixed effect and subject as random effect.

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### **2.7.3 Physical activity**

First, we assessed whether the stimuli had an effect on physical activity. Therefore, we ran a LMM (model 3) on physical activity (frequency of changes in position) that included condition, phase, sex as well as all their interactions as fixed effects and the subject as random effect. Based on the final model, we compared least square means between the phases within each condition.

In a second step we examined whether the observed temperature changes could be mere artefacts of changes in body temperature due to physical activity. First, we examined whether changes in temperature were better explained by experimental condition, physical activity, or piloerection of the tail. We therefore compared the AIC values of three LMMs that we conducted on nasal temperature of the post phase (the data of one male marmoset (Merkur) in the food call condition was excluded as no piloerection data was available) that each included one of the three fixed factors of interest. Subject was always set as random effect.

Second, we looked for each experimental condition separately if there was a link between physical activity and nasal temperature. We thus ran five separate LMMs, one for each condition. We used nasal temperature of the post-phase as dependent variable while physical activity (post value), sex as well as their interaction were set as fixed effects and the subject as random effect.

## **3 Results**

### **3.1 Nasal thermal reaction**

The best model to explain nasal temperature included the factors condition, phase, sex as well as all their two- and three-way interactions (see table 2, model 1). We used pairwise comparisons of least square means of nasal temperature between the pre and post phase per condition and sex to disentangle these effects (table 3 and figure 2). In the negative conditions (teasing and playback of aggressive vocalizations), both males and females showed a strong decrease in nasal temperature in response to the stimulus. The temperature drops were more pronounced in females than males. In the positive conditions (preferred food and playback of food calls), males and females reacted differently. Males showed an increase in both conditions, whereas females showed no change in temperature after eating a preferred food item and a decrease in temperature after the playback of food calls. In the control condition, finally, females showed no significant change in temperature whereas males showed a modest increase. See supplementary S.3 for an overview over the results at the individual level, separately for each condition.

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Table 3 | Pairwise comparisons of least square means of nasal temperature between pre and post per condition and sex. Bold *p*-values indicate a significant result (< 0.05).

Final model: Nasal temperature ~ Condition*Phase*Sex + Subject (random effect)							
Contrast	Condition	Sex	Estimate (°C)	**SE (°C)	df	t-value	<i>p</i> -value
Pre to Post phase	Teasing	Male	-0.524	0.082	1012	-6.361	< <b>0.0001</b>
		Female	-0.832	0.068	1012	-12.188	< <b>0.0001</b>
	PB-	Male	-0.215	0.073	1012	-2.936	<b>0.003</b>
		Female	-0.926	0.073	1012	-12.703	< <b>0.0001</b>
	Food	Male	0.202	0.076	1012	2.650	<b>0.008</b>
		Female	0.028	0.083	1012	0.342	0.733
	PB+	Male	0.244	0.083	1012	2.935	<b>0.003</b>
		Female	-0.238	0.084	1012	-2.820	<b>0.005</b>
	Control	Male	0.174	0.079	1012	2.196	<b>0.028</b>
		Female	-0.143	0.082	1012	-1.744	0.081

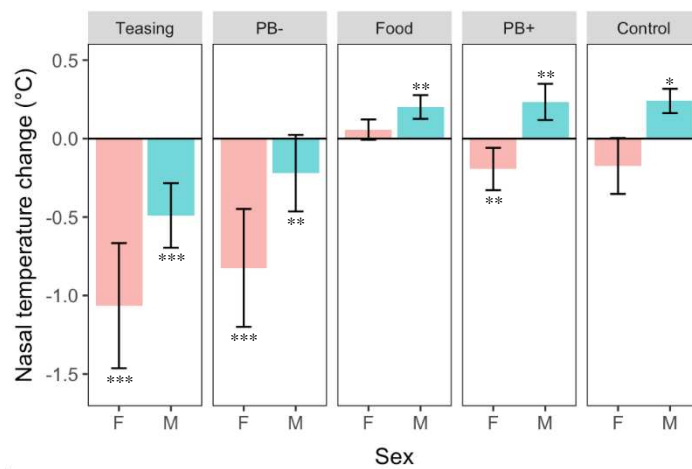


Figure 2 | Grand mean of nasal temperature changes (temperatures of post phase) during the five different stimuli separately for each sex (error bars indicate SE). Significant changes are indicated by asterisks (\*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ )

### 458 3.2 Piloerection

459

460 First, we examined how the extent of piloerection differed between the conditions and the sexes.  
 461 The respective LMM (see table 2, model 2) showed a significant effect of condition on the  
 462 extent of piloerection, whereas sex and the interaction of sex and condition were not significant.  
 463 Based on the final model, pairwise multiple comparisons of least square means of piloerection  
 464 among the conditions (see table 4 and figure 3) revealed that in the negative conditions, the  
 465 teasing and the playback of aggressive vocalizations, the monkeys showed significantly more  
 466 piloerection than in the other conditions. Between the two negative conditions the extent of  
 467 piloerection was not significantly different.

468

Table 4 | Multiple pairwise comparisons of least square means of the extent of piloerection among the conditions. Bold *p*-values indicate a significant differences (< 0.05)

Final model: Extent of piloerection ~ Condition + Subject (random effect)						
Contrast		Estimate	SE	df	t-value	<i>p</i> -value*
Teasing	PB-	-0.023	0.154	43	-0.150	1.000
	Food	0.619	0.159	43	3.883	<b>0.003</b>
	PB+	0.544	0.171	43	3.183	<b>0.022</b>
	Control	0.658	0.163	43	4.038	<b>0.002</b>
PB-	Food	0.642	0.154	43	4.168	<b>0.001</b>
	PB+	0.567	0.166	43	3.417	<b>0.012</b>
	Control	0.681	0.158	43	4.320	<b>0.001</b>
Food	PB+	-0.075	0.171	43	-0.436	0.992
	Control	0.039	0.163	43	0.237	0.999
PB+	Control	0.113	0.174	43	0.649	0.966

\* *p*-values adjusted by tukey method

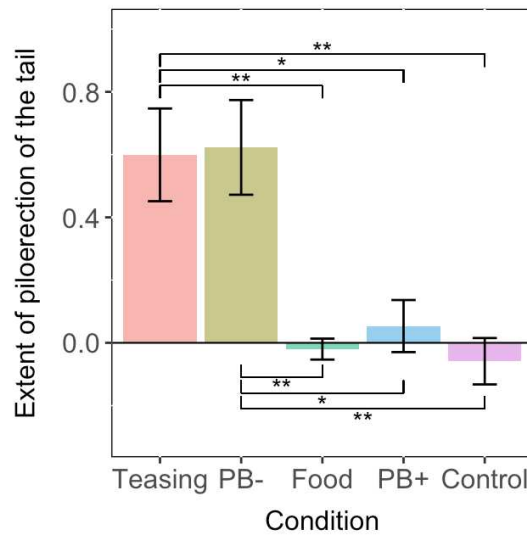


Figure 3 | Mean of the extent of piloerection of the tail for all the different conditions. Significant differences between the conditions are indicated by asterisks (\*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ ).

471 To validate the findings of the thermoimaging data, we tested whether there was a link  
 472 between the extent of piloerection and the change in nasal temperature. A LMM (table 2,  
 473 model 3) conducted on nasal temperature revealed that the extent of piloerection is a  
 474 significant predictor of the change in nasal temperature: more piloerection of the tail was  
 475 linked to a stronger decrease in nasal temperature (see figure 4). Although sex did  
 476 significantly improve the model, which was expected given model 1, the interaction of the  
 477 extent of piloerection and sex was not a significant predictor of the thermal reaction.

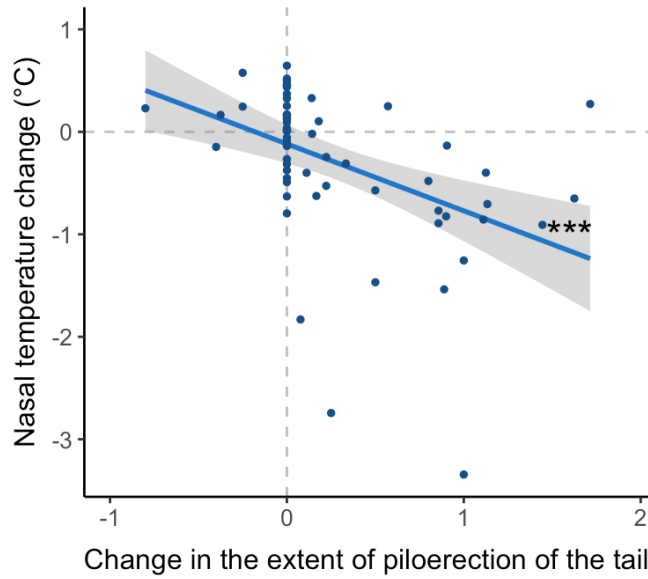


Figure 4 | Relationship between piloerection of the tail and nasal thermal reaction. Each point indicates the mean data of one session (one subject in one condition). X-values less than zero indicate a decrease while positive values indicate an increase in piloerection of the tail from the baseline to the stimulation phase. The grey band represents the standard error and the significance is indicated by asterisks (\*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ ).

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### 481 3.3 Physical activity

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483 In a first analysis we examined whether the experimental stimuli had an influence on physical  
 484 activity. We found that condition, phase and their interaction had an effect, whereas sex as well  
 485 as all its interactions were no significant predictors for physical activity (table 2, model 4).  
 486 Based on the final model, we compared least square means of nasal temperature between the  
 487 pre and post phase within each condition (table 5, figure 5) and found a significant increase in  
 488 physical activity during the playback of aggressive vocalizations, but no change in any of the  
 489 other conditions.

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491

Table 5 | Comparisons of least square means of physical activity between pre and post within each condition. Bold  $p$ -values indicate a significant result ( $< 0.05$ ).

Final model: Physical activity ~ Condition*Phase + Subject (random effect)						
Contrast	Condition	Estimate	SE	df	t-value	p-value
Pre to Post phase	Teasing	1.369	0.990	112	1.385	0.169
	PB-	<b>4.606</b>	0.925	112	4.980	<b>&lt;.0001</b>
	Food	-0.481	0.990	112	- 0.487	0.627
	PB+	1.264	1.068	112	1.183	0.239
	Control	1.642	1.026	112	1.601	0.112

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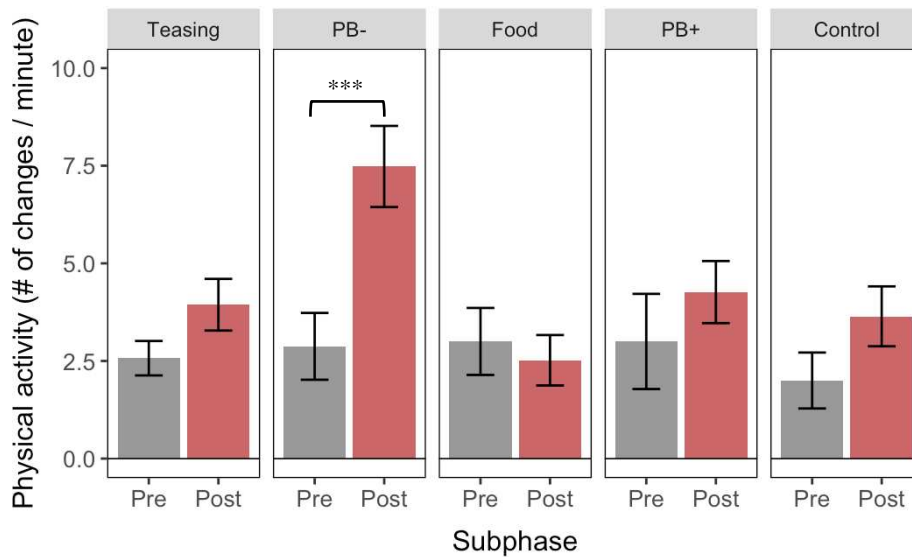


Figure 5 | Mean of physical activity for the pre and post phase for each condition (error bars indicate SE). Significant changes are indicated by asterisks (\*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ )

493 Second, we were interested in the impact of physical activity on nasal temperature. We  
 494 thus analyzed whether the change in nasal temperature was better explained by mere physical  
 495 activity rather than the emotional state. Based on the findings above, emotional state was  
 496 proxied by experimental condition and piloerection of the tail. The comparison of the AIC  
 497 values of the three LMMs revealed that the thermal reaction was explained worst by physical  
 498 activity, better by piloerection, and best by condition (table 6).

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Table 6 | Comparison of the relative impact of the fixed factors condition, extent of piloerection and physical activity on nasal temperature by AIC values.

Dependent variable	Fixed factor	$\Delta$ AIC
Nasal temperature (Post phase, all conditions)	Condition	0
	Extent of piloerection	76.265
	Activity (post value)	135.3

501 Finally, we quantified the effect of physical activity on nasal temperature for each condition  
 502 separately with LMMs (table 2, model 5 a–e; figure 6). There was no consistent relationship  
 503 between physical activity and nasal temperature among the different conditions, except in the  
 504 aggressive playback condition, where higher physical activity was significantly correlated with  
 505 a stronger decrease in nasal temperature.

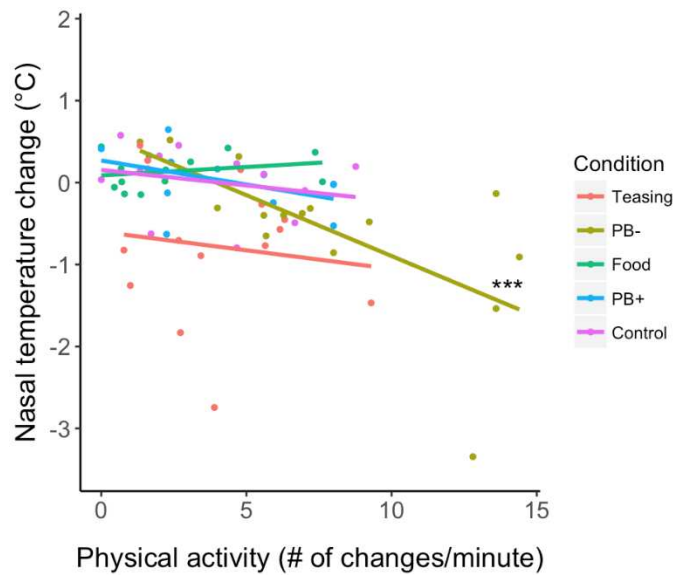


Figure 6 | Relationship between physical activity (post value) and nasal thermal reaction in each condition. Each point indicates the mean data of one session (one subject in one condition). Significant relationships are indicated by asterisks (\*  $p \leq 0.05$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ ).

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Table 2 | Summary of all linear mixed models. The df,  $\chi^2$  and p-values resulted from the respective model comparisons by likelihood ratio tests. The order in which the different fixed factors were added to the model corresponds to the order in which the factors are listed here. In all the models, subject was set as random factor.  
 Bold p-values indicate significant results (< 0.05)

Model	Dependent variable	Fixed factor / effect	df	$\chi^2$	p-value	
<b>1</b>	Nasal temperature (Pre and Post phase; all conditions)	Condition	4	119.907	< <b>0.0001</b>	
		Phase	1	83.200	< <b>0.0001</b>	
		Sex	1	4.983	<b>0.026</b>	
		Condition*Phase	4	172.789	< <b>0.0001</b>	
		Condition*Sex	4	2.348	0.672	
		Phase*Sex	1	65.729	< <b>0.0001</b>	
		Condition*Phase*Sex	4	15.134	<b>0.004</b>	
<b>2</b>	Extent of piloerection (all conditions)	Condition	4	30.888	< <b>0.0001</b>	
		Sex	1	1.433	0.231	
		Condition*Sex	4	2.621	0.623	
<b>3</b>	Nasal temperature (Post phase, all conditions)	Extent of piloerection	1	110.794	< <b>0.0001</b>	
		Sex	1	4.927	<b>0.026</b>	
		Extent of piloerection*Sex	1	0.551	0.458	
<b>4</b>	Activity (Pre and Post phase; all conditions)	Condition	4	12.447	<b>0.014</b>	
		Phase	1	14.400	<b>0.000</b>	
		Sex	1	0.669	0.413	
		Condition*Phase	4	15.285	<b>0.004</b>	
		Condition*Sex	4	2.756	0.600	
		Phase*Sex	1	1.288	0.256	
		Condition*Phase*Sex	4	1.599	0.809	
<b>5</b>	a) Teasing	Nasal temperature (Post phase; Teasing)	Physical activity (post value)	1	0.248	0.619
	b) PB-	Nasal temperature (Pre and post phase; PB-)		1	9.572	<b>0.002</b>
	c) Food	Nasal temperature (Pre and post phase; Food)		1	0.769	0.380
	d) PB+	Nasal temperature (Pre and post phase; PB+)		1	2.494	0.114
	e) Control	Nasal temperature (Pre and post phase; Control)		1	0.832	0.362

## 520 **4 Discussion**

521

522 Our goal was to evaluate the usefulness of infrared thermography as a non-invasive and  
523 objective measure of emotional reactions in common marmosets. More precisely, we focused  
524 on how nasal temperature changed in response to different stimuli that were chosen to induce  
525 varying types of emotional reactions. As predicted, we found that nasal temperature dropped  
526 significantly in situations that were assumed to be highly arousing. To validate whether the  
527 drop in nasal temperature indeed reflected arousal, we first analyzed whether it was correlated  
528 with an independent behavioral measure of arousal in marmosets, namely piloerection of the  
529 tail. We found such a correlation, which was a first indication that a decrease in nasal  
530 temperature indeed reflects arousal. However, an alternative possibility is that the decrease in  
531 nasal temperature is the result of an increase in physical activity, rather than a marker of arousal  
532 per se. To exclude this alternative, we also measured the individuals' activity. Our results show  
533 that there was no consistent relationship between physical activity and the thermal response  
534 across conditions. In fact, we only found a significant correlation between these two measures  
535 in the aggressive playback condition. Even though in principle, activity in this condition may  
536 be responsible for the decrease in nasal temperature, the lack of such a correlation in all other  
537 conditions suggest that the temperature change cannot be solely explained by activity. Most  
538 likely, the negative stimulus in the aggressive playback condition led to an emotional reaction  
539 reflected in nasal temperature changes and a behavioral reaction (increased activity). The latter  
540 may also have influenced nasal temperature and therefore, the observed thermal signature may  
541 indicate the result of both internal and behavioral (activity) consequences of arousal. Finally,  
542 there was no increase in physical activity in the teasing condition, where we observed the  
543 strongest decrease in nasal temperature, corroborating that most variation in nasal temperature  
544 is independent of activity.

545 Accordingly, changes in nasal temperature were far better explained by the stimulus type  
546 (condition) or by piloerection rather than by activity. It is thus unlikely that changes in nasal  
547 temperature were a mere reflection of physical activity, at least in the current setting.  
548 Admittedly, in more naturalistic settings with freely moving individuals, such as in the wild,  
549 variation in activity will be much greater and may well have a stronger influence on nasal  
550 temperature. Nevertheless, these results support that infrared thermography is a reliable and  
551 valid measure of arousal in captive common marmosets that are tested under controlled  
552 conditions.

553 The negative stimuli, i.e. teasing and a playback of aggressive vocalizations, elicited the  
554 most obvious thermal responses. These two stimuli were a priori assumed to be perceived as  
555 negative in valance and highly arousing. In both conditions nasal temperature decreased  
556 significantly after the stimulus. This result was true for most of the individuals and although  
557 females reacted more strongly, the effect was present in both sexes. Furthermore, the amplitude  
558 of the thermal responses was relatively large compared to the ones in the other conditions. In  
559 addition to the thermal reaction, piloerection of the tail was significantly more prevalent in the  
560 two negative conditions compared to the others. This indicates that the teasing and the playback  
561 of aggressive vocalizations were indeed more arousing than the other conditions. Furthermore,  
562 there was also a negative correlation between the extent of piloerection of the tail and nasal  
563 temperature. Overall, these observations are consistent with the pattern found in other non-

564 human primates, namely that high negative arousal is accompanied by a decrease in nasal  
565 temperature [3,6,8,11,19].

566 In contrast to the negative conditions, the temperature responses to the two positive and  
567 the control stimulus were less pronounced, suggesting that these stimuli had a smaller impact  
568 on the emotional state. The piloerection data was fully consistent with this idea: while  
569 piloerection was abundant in the negative conditions, it was almost absent in the positive and  
570 the control conditions, without any sex differences. The behavioral data would thus suggest no  
571 emotional reaction in the positive and the control conditions, but the thermal data revealed a  
572 more fine-grained pattern: an increase in nasal temperature was only observed in the males,  
573 whereas there was no effect (preferred food and control condition) or even a temperature  
574 decrease (food calls condition) in the females. The patterns observed in the positive conditions  
575 as well as the slight sex differences in the negative conditions (females showed a stronger  
576 temperature decrease) go in line with the predicted link between arousal and nasal temperature  
577 if we consider behavioral sex differences in marmosets. In general, female common marmosets  
578 seem to be more interested and motivated than males in situations where food is involved. They  
579 are faster and more persistent when they have to search for food [46] or when they have to solve  
580 a food-related task [43,47] and they are more likely to aggressively defend their food against  
581 group members [48]. Further females show higher intra-sexual competition and are more  
582 involved in between-group aggression [49,50].

583 The lack of an increase in nasal temperature following the food stimulus may thus indicate that  
584 the females were slightly aroused by the anticipation of food competition, which overrode the  
585 relaxing effect of the food per se. In addition, the temperature decrease in the food call condition  
586 in females may simply reflect the excitement about the presence of high-quality food as  
587 announced by the food calls. The higher food motivation may also explain the stronger decrease  
588 in temperature in females during the teasing. On the other hand, the stronger reaction of the  
589 females in the aggressive playback condition may be caused by the fact that they were more  
590 aroused due to potential encounters with same-sex competitors.

591 In the males, there appeared to be a consistent overall pattern in the two positive and the control  
592 conditions: males tended to have higher nasal temperatures after all these stimuli. This could  
593 suggest that the males were more likely to be not fully habituated to the situation by the start of  
594 the experiment and would have needed more time to calm down at the start of an experimental  
595 session. This is not unlikely since among callitrichids, males are known to be the more vigilant  
596 sex and they are more responsible for the detection of potential dangers to their group [51,52],  
597 what could explain a higher level of arousal and hence a slower habituation during the  
598 separation procedure. However, additional analyses suggest that this explanation doesn't hold,  
599 because males did not show a steeper positive increase in nasal temperature during the baseline  
600 than females (see supplementary materials S.4 for more details). Therefore, a more plausible  
601 explanation would be that males perceive these three stimuli as relaxing. This was expected for  
602 the food and the food calls playback condition but not for the control condition. However,  
603 during the control condition, the baseline phase where the experimenter interacted with the  
604 subject by giving him a mealworm every 20 seconds was followed by the stimulus phase where  
605 the experimenter directed her attention away from the subject and instead watched at the  
606 camera. It is possible that this removal of attention from the experimenter reduced tension and  
607 thus arousal in the males. In fact, this would be consistent with a previous study that showed  
608 that male marmosets are more emotionally aroused than females when confronted with a human

609 experimenter [43]. Whether the increases in nasal temperature in the two positive conditions  
610 were indeed evoked by the stimuli itself or were again caused by the distance to the  
611 experimenter is not clear. However, both possibilities support that a reduction of the arousal  
612 level is linked to an increase in nasal temperature.

613 Despite the clear sex differences in the overall data, some individual females showed  
614 the male pattern of thermal changes, and some individual males showed the female pattern (see  
615 supplementary material S.3). This suggests that in addition to systematic sex differences,  
616 individual differences exist with regard to how a specific situation is perceived. Importantly,  
617 these could only be made visible with thermo-imaging but not with measuring piloerection of  
618 the tail, a traditionally used behavioral indicator of arousal. Thermography thus appears to be a  
619 particularly sensitive measure of arousal in marmosets. High sensitivity of thermography to  
620 quantify arousal had previously been proposed for humans by Kosonogov et al. [22]. They  
621 compared nasal temperature changes with the skin conductance response and also found that  
622 the thermal reaction was more sensitive to arousal than the other measure. Nevertheless, since  
623 interindividual differences in physiological and behavioral responses to emotions are possible,  
624 it is most desirable to code several indicators of emotional arousal simultaneously.

625 We only focused on the nasal region due to its clear visibility in the thermal images,  
626 which made the tracking of the respective temperature highly reliable. However, in future  
627 studies, the thermal reactions of additional body parts could be investigated. Results in humans  
628 and other primates indeed suggest that combinations of different thermal reactions can  
629 distinguish between different emotions in more detail [3,13,33,53]. Next to measuring  
630 peripheral body regions, one promising area are the eyes, that have been shown to change their  
631 temperature during emotional reactions in humans and different animals [20,54–57].

632  
633 Overall, the current experiment supports that in common marmosets nasal temperature is  
634 sensitive to emotional changes, and that infrared thermography is an appropriate, highly  
635 objective and non-invasive method to infer these thermal reactions. In fact, this method appears  
636 to be more sensitive than the traditional behavioral marker of arousal, i.e. piloerection.  
637 Furthermore, our continuous graphical representations of marmoset thermal reactions (see  
638 supplementary material S.3, figure S.1) provide useful benchmarks about onset latencies and  
639 the amplitude of the thermal reaction for future studies.

640 Mirroring the literature, particularly consistent results were achieved with highly  
641 arousing, negative stimuli, most likely because they are perceived in the same way by all  
642 individuals. Equally universal positive stimuli are more difficult to identify, and even the  
643 presentation of highly preferred food may result in negative arousal if individuals anticipate  
644 food competition. The measurement of valence independently of arousal thus continues to be a  
645 challenge.

646

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648

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653

654 **Data accessibility**

655

656 Data can be accessed from the Mendeley Data repository [58].

657

658 **Competing interests**

659

660 We declare we have no competing interests.

661

662

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841 S.1 List of subjects

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Table S.1: Families of the tested marmosets with information about sex, status and age. The subjects that were used in the experiments are marked in black, while grey and cursive indicate family members that were excluded due to their age or insufficient habituation to the experimental set-up.

<b>Group</b>	<b>Subject</b>	<b>Sex</b>	<b>Status</b>	<b>Birth date</b>
1	Mina	f	breeder	10.07.06
	John	m	breeder	10.03.07
	Merkur	m	helper	11.07.12
	Manuka	f	helper	04.05.15
	<i>Mojita</i>	<i>f</i>	<i>immature</i>	<i>04.05.15</i>
2	<i>Marvin</i>	<i>m</i>	<i>breeder</i>	<i>03.10.06</i>
	Jet	m	helper	03.04.09
	Jupie	f	helper	29.08.09
	Joyce	f	helper	29.08.09
	<i>James</i>	<i>m</i>	<i>helper</i>	<i>21.04.13</i>
	<i>Jamaica</i>	<i>f</i>	<i>immature</i>	<i>10.11.15</i>
3	<i>Jambi</i>	<i>m</i>	<i>immature</i>	<i>10.11.15</i>
	Tabor	m	-	30.10.08
4	Thilo	m	-	06.03.08
	Jaja	f	breeder	29.08.09
	<i>Membo</i>	<i>m</i>	<i>breeder</i>	<i>17.06.09</i>
	Jandira	m	helper	27.01.15
	Jala	f	helper	27.01.15
	<i>Jelly</i>	<i>f</i>	<i>helper</i>	<i>01.07.16</i>
5	Jam	m	helper	01.07.16
	Lancia	f	breeder	26.08.02
	Lexus	m	breeder	19.07.03
	<i>Lotus</i>	<i>m</i>	<i>helper</i>	<i>03.07.12</i>
6	<i>Lola</i>	<i>f</i>	<i>helper</i>	<i>29.03.13</i>
	Vesta	f	-	05.10.04
7	<i>Vito</i>	<i>m</i>	<i>-</i>	<i>30.05.06</i>
	<i>Lea</i>	<i>f</i>	<i>breeder</i>	<i>18.08.07</i>
	Kyros	m	breeder	03.01.08
	<i>Lima</i>	<i>f</i>	<i>helper</i>	<i>15.02.15</i>

846 S.2 Durations of the stimuli

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Table S.2: Lengths of the stimuli used for all the sessions

Stimulus	Subject	Duration (s)	Stimulus	Subject	Duration (s)
Control	Jaja	60	PB-	Jala	45
	Jala	48		Jam	45
	Jet	59		Jandira	45
	Joyce	46		Jet	60
	Jupie	49		John	47
	Kyros	60		Joyce	45
	Lancia	59		Jupie	45
	Lexus	58		Kyros	42
	Merkur	60		Lancia	45
	Mina	45		Lexus	51
	Tabor	45		Manuka	45
	Thilo	45		Merkur	45
Vesta	60	Mina	45		
Food	Jala	48	Tabor	54	
	Jam	29	Thilo	45	
	Jet	103	Vesta	48	
	John	128	Teasing	Jala	42
	Joyce	31		Jam	46
	Jupie	32		Jet	47
	Kyros	45		John	30
	Lancia	51		Joyce	46
	Lexus	25		Jupie	60
	Merkur	59		Kyros	44
	Mina	54		Lancia	40
	Tabor	38		Lexus	44
Thilo	21	Manuka		47	
Vesta	52	Mina		59	
PB +	Jala	45		Tabor	55
	Jet	45	Thilo	49	
	John	45	Vesta	60	
	Joyce	45			
	Jupie	45			
	Lexus	45			
	Manuka	45			
	Merkur	45			
	Mina	45			
	Tabor	45			
Thilo	45				
Vesta	45				

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### S.3 Individual information about the thermal reaction and the state of piloerection

Table S.3 | Information about the thermal reaction and the extent of piloerection for each individual in the five different conditions. The results of the Mann-Whitney U tests show whether there was a significant temperature change from pre to post within a single individual.

Sex	Subject	Nasal temperature change*	p-value of Mann-Whitney U test	Direction of temperature change	Extent of piloerection
<b>Control</b>					
F	Jaja	-0,796	0.000	Decrease	0
	Jala	-0,097	0.065	None	0
	Joyce	-0,626	0.006	Decrease	0,167
	Jupie	-0,491	0.012	Decrease	0
	Lancia	0,23	0.004	Increase	-0,800
	Mina	0,103	0.351	None	0,180
	Vesta	0,454	0.002	Increase	0
M	Jet	0,137	0.025	Increase	0
	Kyros	0,576	0.000	Increase	-0,250
	Lexus	0,196	0.352	None	0,100
	Merkur	0,325	0.001	Increase	0
	Tabor	0,035	0.384	None	0
	Thilo	0,168	0.004	Increase	0
<b>Food</b>					
F	Jala	0,329	0.001	Increase	0,140
	Joyce	0,124	0.142	None	0
	Jupie	0,009	0.659	None	0
	Lancia	0,018	0.645	None	0
	Mina	0,008	1	None	0
	Vesta	-0,147	0.043	Decrease	-0,400
M	Jam	0,37	0.100	Increase	0
	Jet	-0,057	0.775	None	0
	John	0,437	0.008	Increase	0
	Kyros	-0,138	0.315	None	0
	Lexus	0,422	0.011	Increase	0,200
	Merkur	0,169	0.045	Increase	0
	Tabor	0,252	0.010	Increase	0
	Thilo	0,155	0.020	Increase	0
<b>Playback of food calls</b>					
F	Jala	-0,63	0.000	Decrease	0
	Joyce	0,166	0.003	Increase	-0,375
	Jupie	0,094	0.556	None	0
	Manuka	-0,02	0.864	None	0,143

	Mina	-0,334	0.010	Decrease	0,222
	Vesta	-0,246	0.008	Decrease	0,222
M	Jet	0,246	0.012	Increase	-0,250
	John	0,25	0.117	None	0,571
	Lexus	-0,026	0.786	None	0
	Merkur	0,412	0.000	Increase	NA
	Tabor	-0,126	0.330	None	0
	Thilo	0,646	0.000	Increase	0
	<b>Playback of aggressive vocalizations</b>				
F	Jala	-0,4	0.010	Decrease	0,111
	Jandira	-3,345	0.000	Decrease	1
	Joyce	-0,315	0.005	Decrease	0
	Jupie	-0,48	0.001	Decrease	0,800
	Lancia	-0,309	0.000	Decrease	0,333
	Manuka	-0,908	0.006	Decrease	1,444
	Mina	0,021	0.913	None	0
	Vesta	-0,856	0.000	Decrease	1,111
M	Jam	-0,134	0.100	None	0,905
	Jet	0,496	0.030	Increase	0
	John	-0,376	0.012	Decrease	0
	Kyros	-0,651	0.000	Decrease	1,625
	Lexus	0,318	0.000	Increase	-1,114
	Merkur	-1,537	0.000	Decrease	0,889
	Tabor	-0,399	0.002	Decrease	1,125
	Thilo	0,519	0.000	Increase	0
<b>Teasing</b>					
F	Jala	-1,468	0.001	Decrease	0,500
	Joyce	-0,266	0.000	Decrease	0
	Jupie	0,454	0.000	Increase	0
	Lancia	-0,892	0.000	Decrease	0,857
	Manuka	-2,744	0.000	Decrease	0,250
	Mina	-1,831	0.001	Decrease	0,077
	Vesta	-0,705	0.000	Decrease	1,133
M	Jam	-0,452	0.001	Decrease	0
	Jet	-0,824	0.000	Decrease	0,900
	John	-1,256	0.001	Decrease	1
	Kyros	0,271	0.002	Increase	1,714
	Lexus	0,158	0.222	None	0,500
	Tabor	-0,755	0.017	Decrease	0,857
	Thilo	-0,571	0.050	Decrease	0,500

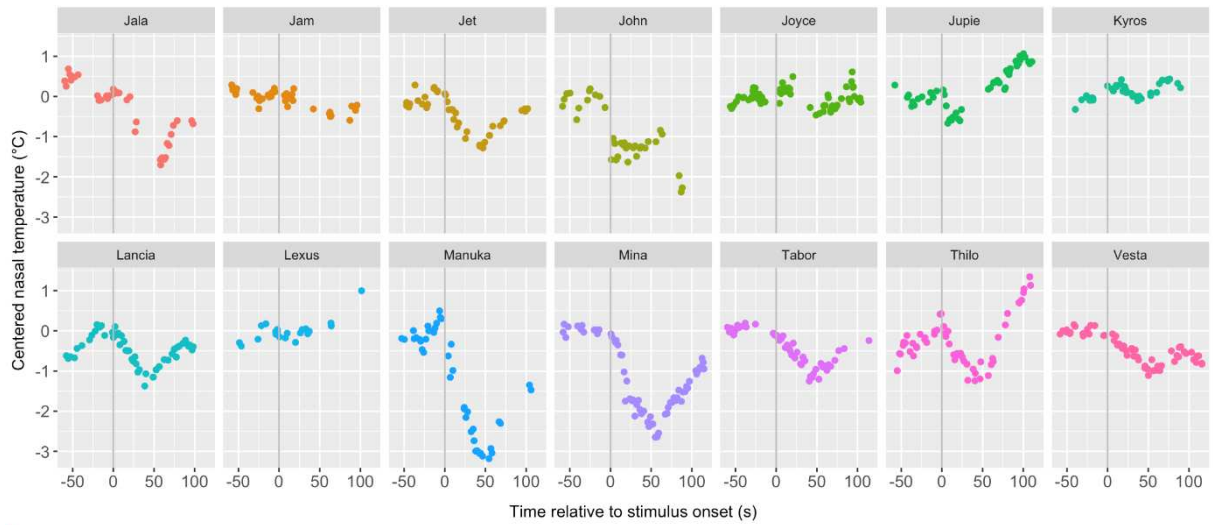
\* Average nasal temperature of subphase 5

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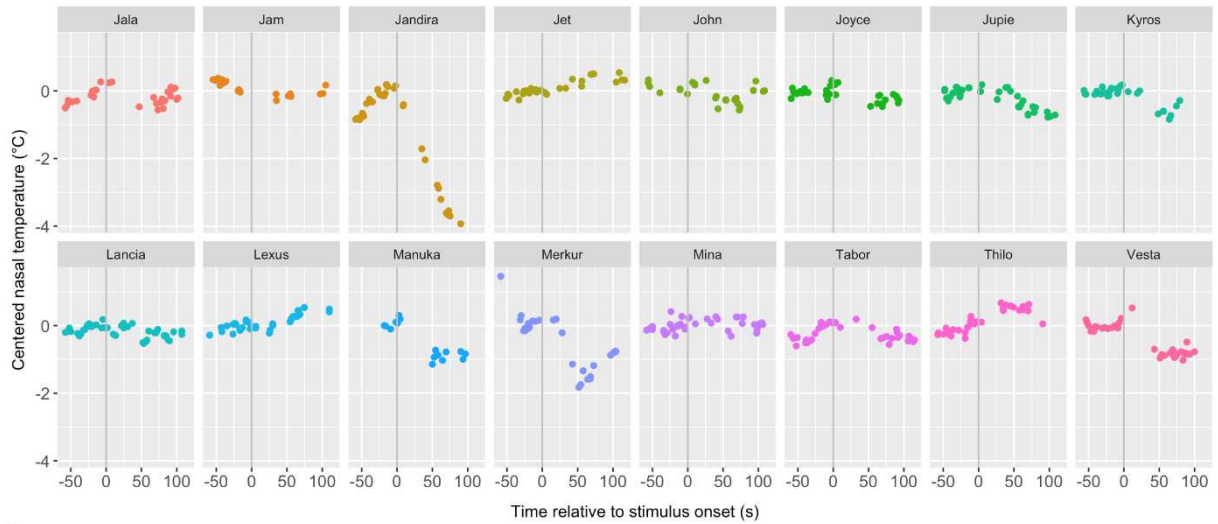
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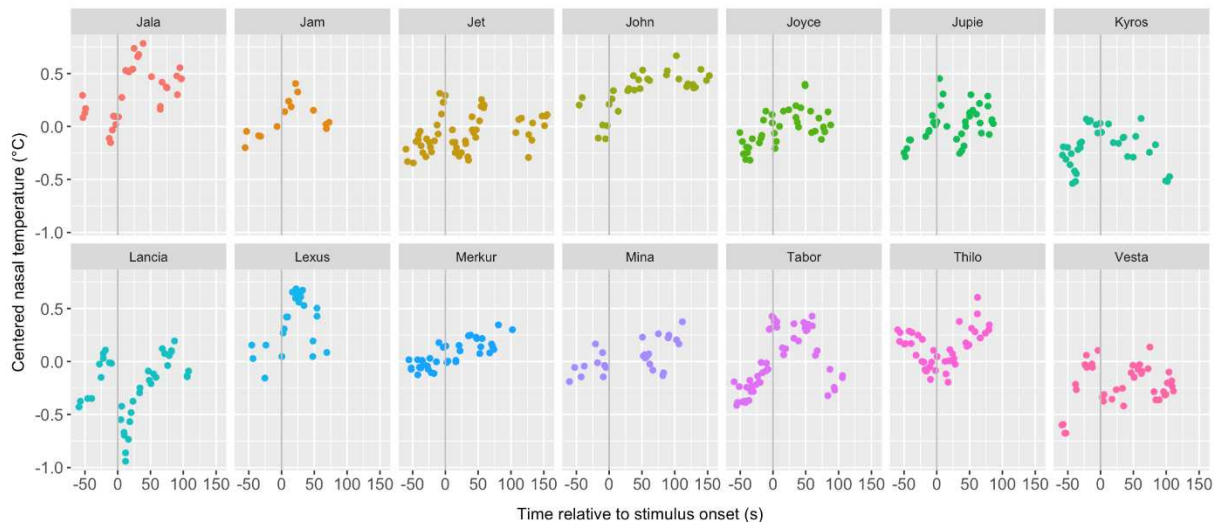
### Teasing condition



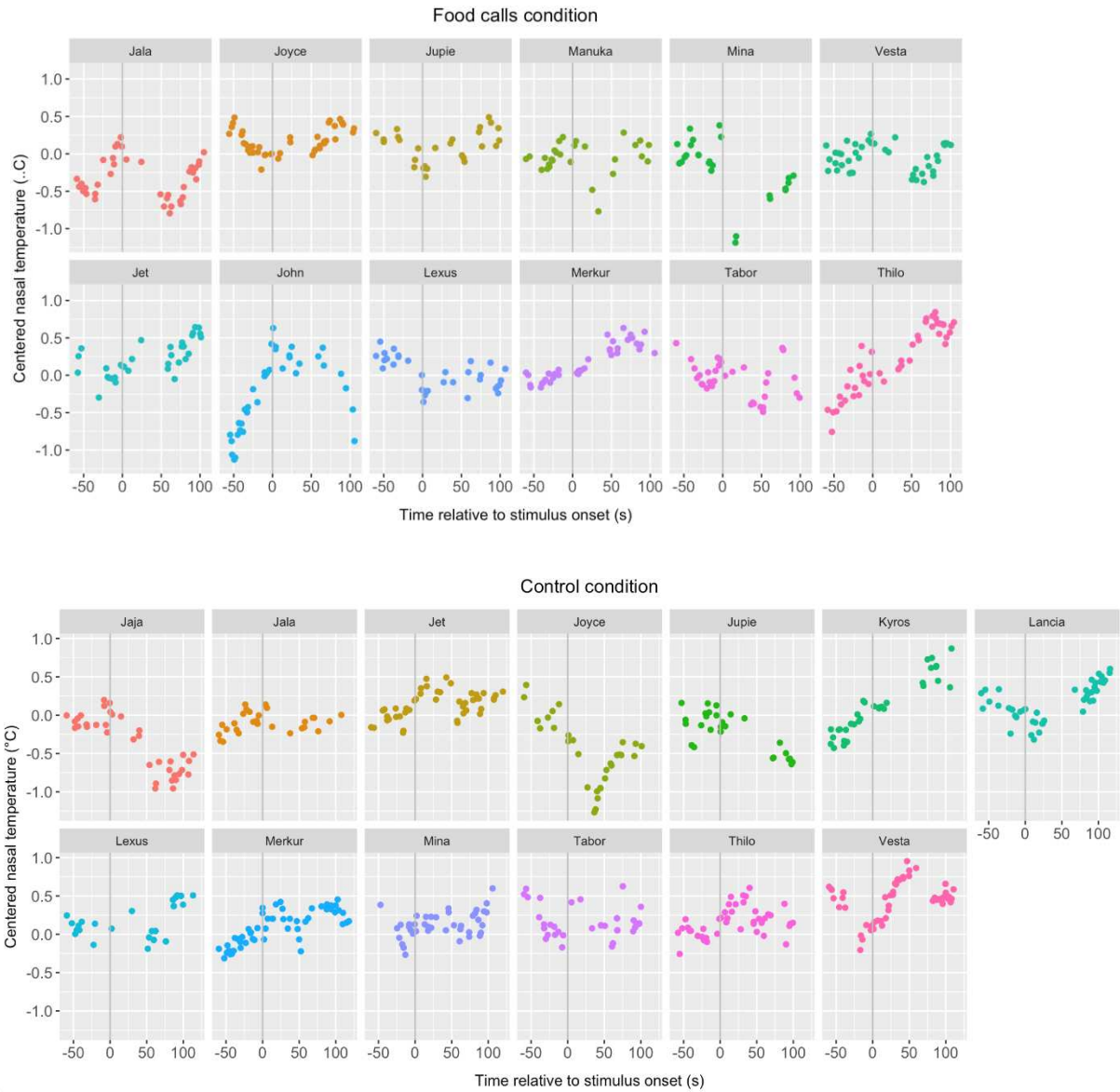
### Aggressive playback condition



### Food condition







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Figure S.1 | Nasal temperature course over time for each individual in each condition. The stimulus onset at time 0 is indicated by a vertical line.

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## 863 S.4 Analysis of nasal temperature during baseline

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865 Over all the male monkeys there was a significant increase in nasal temperature in the two positive and the control condition.  
866 To test the hypothesis that this pattern could be an artefact of an insufficient habituation to the experimental set-up, we  
867 examined nasal temperature during the baseline only in more detail. We were interested in whether males showed a stronger  
868 increase in nasal temperature during the baseline (60 seconds before the stimulus started) supporting the hypothesis that they  
869 were still habituating. Therefore, we conducted a LMM on the correlation coefficient of the relationship between time and  
870 nasal temperature in the baseline of each session. We set sex as fixed effect and subject as random effect.

871 According to this analysis, sex was not a significant predictor of the correlation coefficient ( $\chi^2(2) = 0.901, p = 0.637$ ). This  
872 means that males did not show a significantly steeper increase in nasal temperature during the baseline what speaks against  
873 the hypothesis that males needed longer to habituate.

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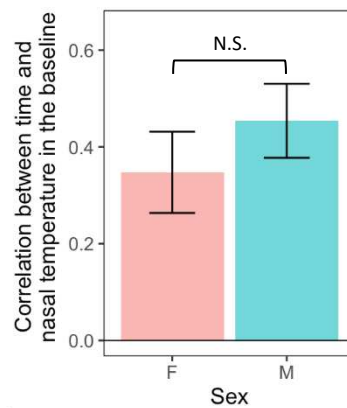
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886 Figure S.2 | Individual correlation coefficients between  
887 time and nasal temperature during the baseline, split up  
888 by males and females.

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