Spontaneous attention and psycho-physiological responses to others' injury in chimpanzees

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Abstract

Previous studies have shown that humans experience negative emotions when seeing contextual cues of others' pain, such as injury (i.e., empathic pain), even without observing behavioral expressions of distress. However, this phenomenon has not been examined in nonhuman primates. We tested six chimpanzees (*Pan troglodytes*) to experimentally examine their reactions to others' injury. First, we measured viewing responses using eye-tracking. Chimpanzees spontaneously attended to injured conspecifics more than non-injured conspecifics, but did not do so in a control condition in which images of injuries were scrambled while maintaining color information. Chimpanzees did not avoid viewing injuries at any point during stimulus presentation. Second, we used thermal imaging to investigate chimpanzees' physiological responses to others' injury. Previous studies reported that reduced nasal temperature is a characteristic of arousal, particularly arousal associated with negative valence. We presented chimpanzees with a realistic injury: a familiar human experimenter with a prosthetic wound and artificial running blood. Chimpanzees exhibited a greater nasal temperature reduction in response to injury compared with the control stimulus. Finally, chimpanzees were presented with a familiar experimenter who stabbed their (fake) thumb with a needle, with no running blood, a situation that may be more challenging in terms of understanding the cause of distress. Chimpanzees did not physiologically distinguish this condition from the control condition. These results suggest that chimpanzees inspect others' injuries and become aroused by seeing injuries even without observing behavioral cues, but have difficulty doing so without explicit (or familiar) cues (i.e., open wound and blood).

Keywords *Pan troglodytes* · Injury · Pain · Attention · Skin temperature · Emotion

Introduction

Caring for injured or weak members is common among humans. This behavior appears to have an ancient evolutionary origin in Homo, and fossil records indicate that Neanderthal individuals with severe injuries and disabilities survived for relatively long periods, suggesting that they routinely received care from community members (Spikins et al. 2018). Although such routine care may be less frequent in nonhuman animals (Turner et al. 2014), some species have been observed to show affiliation and offer help to distressed conspecifics (e.g., rodents: Burkett et al. 2016; ravens: Fraser and Bugnyar 2010, wolves: Palagi and Cordoni 2009; great apes: de Waal and van Roosmalen 1979; dolphins: Warren- Smith and Dunn 2006; elephants: Plotnik and de Waal 2014). One proposed psychological mechanism underlying these behaviors is empathy for others in distress (e.g., Decety et al. 2016; Frank and Linsenmair 2017; de Waal 2008). The term "empathy" involves multi-faceted phenomena, ranging from reflexive or automatic matching with others, such as emotional contagion and behavioral mimicry, to more cognitively controlled or sympathetic behaviors, such as consolation and targeted helping (e.g., de Waal and Preston 2017; Heyes 2018; Seyfarth and Cheney 2013; Yamamoto 2016). Empathy is reported to be modulated by observers' individual traits, such as previous knowledge or experience (e.g., Sato et al. 2015), and the social relationships between the sufferers and the observers, such as familiarity and kinship (e.g., Burkett et al. 2016).

Empathetic responses to others in distress can either be based on the sufferer's behavioral expressions, such as screaming or distressed facial expressions, or contextual cues, such as injury or inability to escape from a trap (Goubert et al. 2005, 2009). A variety of species have been reported to show affiliation to injured conspecifics after fights or accidents (e.g., monkeys:

Campbell et al. 2016; Clyvia et al. 2014; Dittus and Ratnayeke 1989; dolphins: Warren-Smith and Dunn 2006; elephants: Douglas-Hamilton et al. 2006). Chimpanzees are one of the species in which this behavior has been most frequently documented. For example, chimpanzees have often been observed to inspect, groom, or lick their groupmates' injuries (Boesch 1991, 1992; Goodall 1986; Nishida and Hiraiwa-Hasegawa 1985). In addition, a group of chimpanzees was observed to wait for an injured individual who was left behind when the group traveled to another location (Boesch 1992). Moreover, an adolescent male chimpanzee was observed to help carry an infant when the mother chimpanzee was injured (Pruetz 2011). Finally, an adult male chimpanzee was observed to help remove a snare from a trapped groupmate (Amati et al. 2008; also see Tokuyama et al. 2012 for a similar behavior in bonobos).

These observations are informative because they suggest that chimpanzees respond to others' distress not only when seeing a behavioral cue (based on a specific emotion possibly developed for species-typical communication) but also when seeing a contextual cue (based on understanding a cause of distress); both observations together provide more stringent evidence for empathy in chimpanzees. However, for the latter observations, previous studies have mainly documented behaviors rather than internal responses. Thus, it remains unclear whether chimpanzees experience negative emotions in response to others' injuries while offering affiliation/help to them. Previous studies with human participants have reported that humans experience negative emotion (i.e., empathetic pain) when observing "painful" situations in which other individuals accidentally harm themselves or undergo injury (Goubert et al. 2005, 2009; Kupfer 2018). This line of studies has utilized a variety of physiological measures to evaluate participants' internal responses, such as heart rate (Preis and Kroener-Herwig 2012), skin conductance (Forgiarini et al. 2011; Hein et al. 2011), pupil diameter (Azevedo et al. 2013), and skin temperature changes (Salazar-López et al. 2015).

However, these methods have rarely been used in studies of chimpanzees. As a notable exception, Parr (Parr 2001; Study 1) examined decreases in finger skin temperature as an index of physiological arousal among chimpanzees when they were observing video clips depicting conspecifics being injected with a hypodermic needle. Chimpanzees were found to exhibit a temperature decrease in response to the video clip. However, they responded similarly to a control video clip depicting a hypodermic needle alone. Thus, it remains unclear whether chimpanzees empathized with conspecifics in distress, or simply responded to the hypodermic needle as an aversive stimulus. Therefore, further studies are necessary to elucidate this issue. Such studies could provide important evidence regarding the question of whether nonhuman animals exhibit empathic responses in the absence of sufferers' behavioral cues, and also could help to establish an experimental approach that is similar to the research paradigms used with human participants.

However, at least two major methodological challenges are involved in performing such studies. First, the contextual cues that elicit emotional responses in chimpanzees in a laboratory setting are currently unclear. Given that the video of a needle injection used by Parr (2001) was somewhat ambiguous in terms of the aversive value of a needle, it may be useful to conduct exploratory experiments to examine this issue. Second, it is practically challenging to measure physiological responses in large-bodied animals such as chimpanzees because untrained chimpanzees typically do not accept the use of electrodes, which are necessary for most physiological measurement techniques. However, recent advances in thermal imaging techniques provide a promising avenue for research because the technique does not require direct contact (e.g., Ioannou et al. 2014; Sato et al. 2018).

Thermal imaging has been used to measure physiological changes of an animal by observing changes in skin temperature. For example, Kuraoka and Nakamura (2011) reported that conspecific screams (behavioral cues of dis- tress) induced changes in skin conductance and a decrease in nasal skin temperature in rhesus monkeys. Following this previous study, Kano et al. (2016) reported that conspecific screams induced changes in heart rate variability and a drop in nasal skin temperature in chimpanzees. Additionally, Dezecache et al. (2017) reported similar results in a field setting. These studies provide evidence that monkeys and chimpanzees respond emotionally to behavioral cues, such as others' distress calls, but it remains unclear if they do so in response to contextual cues, such as others' injury.

Therefore, based on the previous studies discussed above, particularly Parr (2001), Kano et al. (2016), and Dezecache et al. (2017), the current study sought to experimentally investigate chimpanzees' physiological responses to others' injury using thermal imaging techniques. In addition, we used eye-tracking to examine chimpanzees' gaze behavior in response to others' injury. The purpose of the eye-tracking experiment was to confirm previous reports of chimpanzees spontaneously inspecting others' injuries (e.g., Boesch 1991; Goodall 1986; Nishida and Hiraiwa-Hasegawa 1985). If chimpanzees both visually inspect and physiologically react to others' injury, these observations together would strengthen the notion that they inspect injured others not only out of interest but also out of empathy.

Study 1

Chimpanzees have been observed to gently inspect conspecifics' injuries (e.g., Boesch 1991; Goodall 1986; Nishida and Hiraiwa-Hasegawa 1985). An interesting aspect of this behavior is that chimpanzees tend to spontaneously approach others' injuries, rather than being afraid of or avoiding them. This is an important characteristic of these responses, because it may differentiate an other-regarding affective response or sympathetic concern from a personal fear or disgust. In Study 1, we examined how chimpanzees allocated their attention when they viewed pictures of conspecifics with and without injuries. We predicted that chimpanzees would attend to the conspecifics' injuries throughout the presentation time (i.e., chimpanzees would not show avoidance at any point during the presentation). We also predicted that chimpanzees would not attend to others' injuries simply because the injury had a conspicuous color (i.e., red). We tested this prediction in a control condition.

Methods

Participants

Six chimpanzees (*Pan troglodytes*; five females and one male, 15.3 ± 6.0 years old, mean ± SD) living at Kumamoto Sanctuary, Wildlife Research Center, Kyoto University, participated in this study. Details of the participants are shown in Table S1, and are available in the Great Ape Information Network (https://shigen.nig.ac.jp/gain/index.jsp). At the time of the experiment, these six chimpanzees lived in a social group adjacent to neighboring chimpanzee groups, with visual access between groups. Four of the chimpanzees were reared by their biological mothers, while the others (Mizuki and Hatsuka) were partially reared by human caretakers (and partially by their biological mothers and conspecific peers) following rejection by their biological mothers (Idani and Hirata 2006).

Ethics statement

Chimpanzees were fed with a variety of vegetables, fruits, nuts, and monkey chow three times a day. Water was avail- able ad libitum. The chimpanzees typically spent the day- time in three outdoor enclosures connected to each other (approximately 300 m^2 in total). The outdoor enclosures were furnished with small trees, platforms, pieces of fire hose, or hammocks, providing complex three-dimensional environments in which chimpanzees could actively exercise. Additional enrichment items (e.g., pieces of jute bags) were provided daily. The indoor enclosures also contained pieces of fire hose, hammocks, and wooden stages, where the chimpanzees could comfortably rest and sleep. Neither food nor water was deprived for the purpose of the experiments, and participation in the experiments was voluntary. As predicted, we confirmed that chimpanzees were not fearful of the images of injured conspecifics, and did not avoid the experiments. Animal husbandry and study protocols complied with the Guide for Animal Research Ethics pro- vided by the Wildlife Research Center, Kyoto University (No. WRC-2018-KS008A).

Apparatus

Participants were invited from the outdoor enclosures into an indoor experimental booth (3.0 m × 3.0 m × 2.0 m). Eye- gaze was measured using an infrared head-free eye-tracker (Tobii X300, Tobii Technology AB, Stockholm, Sweden). Visual stimuli were presented on a 23-inch LCD monitor with a resolution of 1280 × 768 pixels, at a viewing distance of approximately 70 cm (40° × 23°). The eye-tracker and monitor were placed outside the experimental booth. Participants in the experimental booth viewed stimuli on the monitor through a transparent 1-cm polycarbonate panel. Each day before testing, we sprayed anti-fog spray on the panel to prevent condensation from chimpanzees' breath obscuring their view and recording of their eye movement through the panel. During the test, we allowed participants to sip grape juice from a nozzle attached to the panel from a custom-made juice dispenser hanging from the ceiling. In addition, an experimenter lightly held the head of some participants. We employed these procedures to encourage chimpanzees to remain focused on the monitor throughout testing (note that the eye-tracker did not require participants' heads to be firmly fixed). In the first session, we conducted two- point automated calibrations for each participant, in which we showed a small object or movie clip on each reference point. We manually checked the accuracy of the calibration before each session and repeated

the calibration whenever necessary. With these calibration procedures, we confirmed that the recorded error (the distance between the target and the recorded gaze positions) were typically within a degree (Kano et al. 2011). The calibration, presentation of stimuli, and eye-movement recordings were controlled in Tobii Studio software (version 3.4.8).

Stimuli and procedure

The experiments were conducted each day for approximately 15 min between 11 a.m. and 1 p.m., from November to December 2017. When two chimpanzees were invited together (the two mother–offspring pairs), one chimpanzee was distracted while the other was tested. The experiment consisted of two conditions, a test condition and a scramble condition (which served as a control condition) with a within-subject design. In the test condition, we presented eight image pairs. Each pair consisted of two images (i.e., the preferential looking paradigm). Images were 600 × 600 pixels (21° × 21°) in size, and were positioned 40 pixels apart from each other with a gray-scale background (Fig. 1a). One image depicted a chimpanzee with a bleeding injury either on their head, limb, or genital region, and the other image of each pair depicted a different individual of the same sex with no injury. All images depicted chimpanzees that were unfamiliar to the participants. Two of eight image pairs depicted female chimpanzees. The configuration of the scenes, such as the depicted chimpanzees' body parts and body postures, was matched as closely as possible between the two images in each pair. The backgrounds were blurred. We conducted image processing using Adobe Photoshop CC 2017. In the scramble condition, we used the same eight image pairs, but with pixel-scrambled masks. Specifically, in each pair, we used the scramble-filter function in Photoshop to scramble the pixels of the rectangular areas surrounding the injury of the depicted chimpanzee on one image, and those of the corresponding size-matched areas on the other image (Fig. 1b). This eliminated all of the form information within the rectangular areas, but kept the color and luminance of each image. The side of presentation of the injured chimpanzee (and the corresponding injury-scrambled chimpanzee) in each pair was counterbalanced between the participants. On a trial, each image pair was presented for 6 s. At the beginning of each trial (before presenting each image pair), a small animation (illustration of a nonhuman animal) was presented at the center of the screen as an attention-getting stimulus (1.5 s). Each condition (test and scramble) contained two blocks (four blocks in total), each with 4 trials (16 trials in total). Each day, one or two blocks were presented, depending on participants' willingness to continue the experiment, which took 3 or 4 days in total. One participant (Misaki) did not view the images in one trial, and this was treated as a missing trial. The order of presentation of conditions was counterbalanced between participants. The order of presentation of each trial within a block was counterbalanced between participants.

Data analysis

Eye-movement data were filtered with a default Tobii Fixation Filter. We defined areas of interest (AOIs) for the whole image (640 × 640 pixels), which were slightly larger than the image size (600 × 600 pixels) to accommodate minor errors in the recorded gaze. We also defined AOIs for injured body parts of injured chimpanzees and corresponding body parts of uninjured chimpanzees. The size of AOIs varied across image pairs, but was consistent within an image pair, occupying 9.87 ± 9.97% (mean ± SD) of the AOIs for the whole picture (i.e., 640 × 640 pixels).

To examine chimpanzees' bias in looking at either of the two images in each pair, we calculated the proportion of looking time directed to the image depicting an injured chimpanzee. Thus, we divided the time spent looking at the injury image by the total time spent looking at the two images in each trial (presenting each image pair). A higher score corresponded to a longer time spent looking at the injury image. This score was compared between two conditions (test vs. scramble) for each participant using a paired t test. When significant differences were found, we compared the score with the chance level, 0.5, using a one-sample t test. To examine the time course of the looking bias, we divided the 6 s of presentation time of an image pair into three 2-s time-bins, and calculated the proportion of looking time to the injury image for each time-bin. We then subjected the scores to a repeated-measures analysis of variance (ANOVA) with condition (test vs. scramble) and time-bin (0–2, 2–4, and 4–6 s) as within-subject factors. All statistical tests were two-tailed and the significance level was set at $\alpha = 0.05$. As effect sizes, Cohen's d and generalized eta squared were reported for the paired *t* test and ANOVAs, respectively. Statistical analyses were performed in R (version 3.4.2).

Results

Chimpanzees viewed both images of each pair for 4.73 ± 0.92 s in the test condition and 3.96 ± 1.00 s in the scramble condition, respectively (hereafter, the data are presented as mean ± SD). The looking time for both images was marginally longer in the test condition than in the scramble condition (paired t test: t [5] = 2.50, p = 0.054). This result was expected, because the scrambled mask covered certain attention-attracting features of images (e.g., injury, chimpanzees' face). In the test condition, chimpanzees viewed the image of the injured chimpanzees for 2.73 ± 0.69 s (during which they viewed the injury AOI for 1.29 ± 0.66 s) and those of the uninjured chimpanzee for 2.01 ± 0.43 s (during which they viewed the corresponding AOI for 0.80 ± 0.25 s). In contrast, in the scramble condition, chimpanzees viewed the images of injured chimpanzees for 2.18 ± 0.71 s (during which they viewed the scrambled-injury AOI for 0.56 ± 0.25 s) and those of uninjured chimpanzees for 1.78 ± 0.63 s (during which they viewed the corresponding AOI for 0.45 ± 0.20 s).

The proportion of time spent looking at the image of an injured chimpanzee was higher in the test condition com- pared with the scramble condition (t [5] = 2.65, p = 0.045, d = 1.08; Fig. 2a). In addition, the proportion of time spent looking at the injury image was above chance in the test condition, whereas it was not above chance in the scramble condition (test condition: t [5] = 3.15, p = 0.025; scramble condition: t [5] = 1.43, p = 0.212). The time-bin analysis yielded no significant interaction and no significant main effect (condition × time-bin: F [2, 10] = 0.26, p = 0.775, η^2_G = 0.02; condition: F [1, 5] = 1.66, p = 0.253, η^2_G = 0.03; time-bin: F [2, 10] = 0.72, p = 0.510, η^2_G = 0.07; Fig. 2b).

Regarding the other behavioral responses, chimpanzees did not show any fearful expressions (e.g., grimacing) or aversive postures (e.g., moving away from the screen) during the presentation of stimuli in either condition.

Discussion

Chimpanzees attended to injured conspecifics for longer than they attended to uninjured conspecifics and they did not avoid viewing injuries at any point during the stimulus presentation. In addition, we found that this phenomenon was not simply driven by the conspicuous color of the injury (i.e., red color). From the results of this experiment, we were unable to exclude the possibility that chimpanzees viewed others' injuries because of their novelty (or the relatively unfamiliar nature of injured skin compared with intact skin). These possibilities were addressed in Study 2. At minimum, however, the results of Study 1 revealed that chimpanzees exhibited a tendency to look at injured conspecifics spontaneously, rather than exhibiting fear or seeking to avoid them.

Study 2

Recent reviews concluded that empathy for pain in humans is triggered by both behavioral cues, such as sufferers' emotional expressions, and contextual cues, such as injury (Goubert et al. 2005, 2009). Following this line of research, in Study 2, we examined whether chimpanzees would be physiologically aroused when viewing others' injuries with- out seeing pain-related behavioral cues. We used infrared thermal imaging to measure changes in nasal skin temperature in chimpanzees. Decreases in nasal skin temperature have been observed when both human and nonhuman primates are aroused, either positively or negatively, but a stronger response tends to be observed during negative arousal (Chotard et al. 2018; Dezecache et al. 2017; Ioannou et al. 2014, 2015; Kano et al. 2016; Kuraoka and Nakamura 2011; Nakayama et al. 2005). This physiological response is likely to be caused by the activation of sympathetic nervous system activity, which subsequently triggers a constriction of arteriovenous anastomosis in the nasal area (Ioannou et al. 2014). In Study 1, we observed that chimpanzees attended more to injured than uninjured conspecifics. Thus, to control for the possibility that an increased level of attention caused stronger physiological responses to the stimuli, we attempted to equalize the looking time for the stimuli, by presenting attention-grabbing stimuli in the control conditions.

Prior to Study 2, we conducted two unsuccessful experiments, which may have failed for several potential reasons (see online Supplementary Materials for the details). In brief, in the first experiment, we presented chimpanzees with still images of either injured conspecifics (test condition) or uninjured conspecifics (control condition), as in Study 1. However, chimpanzees did not physiologically distinguish between the two conditions. This result suggests that chimpanzees viewed injured conspecifics for longer than uninjured conspecifics simply out of interest but not out of empathy in Study 1. However, it remains unclear whether the still images were sufficiently realistic or powerful to elicit emotional responses. Therefore, in the second experiment, we presented video clips of conspecifics being injected with a hypodermic needle (test condition), as in Parr (2001), and video clips of conspecifics being touched softly by a familiar human experimenter (control condition). Again, we found no difference between conditions (except

for confounding variables, see Supplementary Materials). We suspect that these negative results may be partly due to methodological factors, such as low baseline nasal temperature. We also suspect that more realistic situations are important to reveal subtle emotional reactions in chimpanzees, because presenting an image of an injury on a monitor is already a somewhat artificial or unfamiliar situation for chimpanzees.

In Study 2, we, therefore, presented chimpanzees with a realistic demonstration by a human experimenter, as previously employed in experiments with human children (e.g., Gill and Calkins 2003; Zahn-Waxler et al. 1992). We assumed that a real-life theatrical demonstration would pro- vide a more familiar and thus more powerful stimulus for eliciting emotions in chimpanzees. We also assumed that a familiar human could substitute for a conspecific model in this experiment, because all of our chimpanzee participants had extensive experience interacting with humans since their youth (Idani and Hirata 2006). We presented chimpanzees with a familiar human who accidentally cut his palm, while alone (i.e., not social aggression). As a control condition, we presented chimpanzees with a seemingly equally interesting event, during which the same experimenter accidentally made his hands dirty (with bananas) and subsequently washed them with soap.

Methods

Participants

The same group of chimpanzees from Study 1 also participated in Study 2.

Apparatus

Participants were invited from the outdoor enclosures to an indoor sleeping room (7.5 m × 3.0 m × 3.5 m) equipped with metal mesh (instead of polycarbonate panels, because infrared light is reflected by polycarbonate panels). Nasal temperature was non-invasively measured with an infrared thermo-camera (T650sc, FLIR Systems Japan K.K., Tokyo, Japan), with a resolution of 640 × 480 pixels and a frame rate of 30 Hz (Fig. 3a). The emissivity was set at the default value of 0.95. The thermo-camera was installed on a tripod and positioned approximately 1 m from the metal mesh. The thermo-camera was aimed at the participant chimpanzee's face, and the angle and position of the camera were adjusted carefully in real time according to the participant's postural changes. According to the manufacturers' recommendations, the thermo-camera was switched on a minimum of 15 min before the start of the experiment. A video camera was set in front of the participant to record their looking behavior.

Stimuli

Study 2 involved two conditions. A familiar experimenter (YS), who had been working with the participants for approximately 1 year, presented chimpanzees with two types of demonstration: artificial wound and hand-washing in the test and the control conditions, respectively. In the test condition, the participant was exposed to an experimenter with a prosthetic wound and artificial blood on his right palm. The prosthetic wound was created from skin- colored wax painted with reddish eye-shadow and artificial blood (Fig. 4a). In addition, a tube was hidden under the right sleeve, through which fake blood was pumped over the wound. At the beginning of the demonstration, the experimenter picked up a banana and attempted to cut it with a knife (with the prosthetic wound hidden in his hand). He slipped with the knife, appearing to cut his right palm, put the banana and knife down, showed the wound to the participant chimpanzee, and let the fake blood run by quickly removing the stopper from the tube. The experimenter then used tissues to wipe the blood from the wound, and maintained this action until 180 s had passed since the beginning of the demonstration. The experimenter's gaze was kept on the wound throughout the demonstration. After the demonstration, the experimenter swiftly exited the area so that he was no longer visible to the participants. It should be noted that the experimenter did not show any behavioral signs of pain (e.g., facial/ bodily expression or vocalization) during and after the demonstration. In the control condition, the experimenter performed the same actions as in the test condition, but cut the banana with the knife (instead of slipping and cutting his palm) during which he made his hands dirty with the banana, and put the banana and knife down. He then put soap on his left palm from a soap dispenser placed on the floor, rubbing his hands, and picked up a plastic bottle filled with water placed on the floor to rinse his hands (both items were also present on the floor in the test

condition). The experimenter then rubbed his hands, rinsed his hands with water from a plastic bottle, put his wrist- watch back on, and used tissues to wipe the water from his hands and watch. He maintained this action until 180 s had passed since the beginning of the demonstration, then swiftly exited the area.

Procedures

The general procedures followed those described by Kano et al. (2016). We conducted testing between 11:30 a.m. and 1:30 p.m. in May and June 2018. Chimpanzees participated in one trial per testing day and two trials for each condition, a total of four trials. The room temperature and humidity (mean ± SD) at the time of testing were 23.6 ± 0.7 °C and 69.8 ± 8.8%, respectively. The two mother–offspring pairs were invited to the test area together, and the remaining two participants were invited alone. The mother and offspring in each pair sat next to each other and viewed the same stimuli together. This was due to the difficulty distracting one chimpanzee while showing interesting stimuli to the other. How- ever, we confirmed that the results of chimpanzees which participated as a pair did not differ from the results of other chimpanzees, and therefore, this factor was not considered further in the main analyses.

Participants sat in front of the metal mesh (each grid was 5 cm × 5 cm in size) so that we could measure their nasal temperature through the openings of the grid. According to recommendations by Ioannou et al. (2014) and Kano et al. (2016), we employed an acclimatization period: after the entrance to the sleeping room from the outdoor compound, the chimpanzees sat still for approximately 1–5 min until the nasal temperature became stable (the temperature typically increased sharply at the beginning). During this acclimatization period, an experimenter gave the chimpanzees small pieces of food (peanuts or grapes), and another experimenter checked changes in nasal temperature visually on the monitor of the thermo-camera. We avoided giving a large amount of food as gastrointestinal activity can affect peripheral skin temperature (van Baak 2008; Kano et al. 2016). We then started the test recordings, which consisted of a stimulus presentation period (180 s), plus the preceding 3-min and subsequent 3-min recording periods (to accommodate the 180-s post-stimulus period). Kano et al. (2016) reported that chimpanzees' nasal temperature dropped immediately after stimulus onset, continued to drop for up to 2 min, and recovered to baseline within 1 min after stimulus offset. To encourage participants to stay in front of the thermo- camera, we allowed them to sip tepid juice (grape or apple) diluted with roughly the same amount of water throughout the trial. We used identical juice dispensers to those used in Study 1. Chimpanzees could sip the juice approximately at 0.5–1.5 ml/s. Thus, chimpanzees were not distracted by the presentation of small pieces of food during the demonstration (Sato et al. 2018). When a participant walked away from the juice dispenser during stimulus presentation, we called their name to encourage them to come back, and later coded these events from the video recordings. This occurred in three trials for one male chimpanzee (Zamba; first trial of test condition: 31.3 s; first trial of control condition: 28.8 s; second trial of test condition: 8.3 s) and one trial for a female chimpanzee, albeit only briefly (Misaki; first trial of test condition: 4.9 s). Kano et al. (2016) reported that nasal temperature decreased to a greater extent as chimpanzees walked for a longer period. This effect was not considered in the current study because walking was relatively infrequent, and the duration of walking (which approximately equaled our measure of the time for which the individual left the juice dispenser) did not differ substantially between conditions.

Data analysis

We used Research IR thermal-image analysis software to analyze the temperature data. We defined the AOI as a circle approximately 1 cm in size (measured as the relative size compared with the 5 × 5 cm grid) on the participant's nasal tip, and extracted the average temperature of the AOI every 20 s (Fig. 3b). In accord with the recommendation by Kano et al. (2016), each recording time point accommodated ± 5 s to avoid inappropriate frames in which the participant's face quickly moved (thereby causing a motion blur) or was angled at more than 45°. The missing values comprised 2.3% of the whole data set, and were linearly interpolated in the analysis. We assessed the inter-coder reliability of temperature extraction: another coder who was blind to the condition coded one trial for each participant (for the whole stimulus period and the first 2 min of post-stimulus period, resulting in 96 data points) and we computed the intraclass correlation coefficient based on a single rater, with an absolute-agreement, two-way random-effects model (Koo and Li 2016) using the R package, irr. This analysis yielded an acceptable level of reliability, 0.87 (95% CI = [0.02, 0.96]). The baseline was set at the onset of the demonstration. The demonstration lasted for 180 s. We also included in the analysis the following 180 s as the post-demonstration period, in which the temperature was expected to recover. We subtracted the baseline value from the following 360 s; 18 data points (i.e., 20, 40, …, 360 s from the stimulus onset).

Statistical analyses were based on linear mixed-effect models (LMMs) to analyze the time-series data. For the response variable, temperature data (the changes from base-line) were used. For the explanatory variables, we used condition (test vs. control), trial (first vs. second), time, and the square of time, $time^2$, as well as interactions between condition, trial, and time, and interactions between condition, trial, and $time^2$. We included $time^2$ into the model because we expected a recovery in temperature after the offset of the demonstration. We also included the random effects of participants, including both the random intercept and random slopes for each variable. However, the random slope for the three-way interaction was dropped in the final model because the model failed to converge with it.

Using the video recordings (30 Hz), chimpanzees' looking behaviors during the demonstration were coded offline. During the 180-s demonstration, participants' looking at the stimulus was defined when participants looked at either the demonstrator's hand or the blood on the floor. We also coded instances in which chimpanzees moved away from the juice dispenser, as noted earlier. Additionally, within a certain time frame, looking could not be coded because the eyes were obstructed by the metal grids or the demonstrator's body or hand. In the test condition, this occurred for 11.73 ± 12.72% in the first trial and for 8.17 ± 9.37% in the second trial, respectively (mean ± SD). In the control condition, this occurred for 27.97 ± 18.79% in the first trial and for 20.91 ± 26.37% in the second trial, respectively (mean ± SD). Thus, the items we coded included: (1) looking at stimulus, (2) leaving juice dispenser, and (3) not clearly seen (Table S2). Behavioral coding was performed using BORIS software (version 6.3.7 and 7.4: Friard and Gamba 2016). In the software, we replayed the video at a slower speed than the normal speed, and coded the onset/offset of each behavior using a key press. We then calculated the pro-portion of looking time in relation to the total observation time: [(1)/(180 s − (2) − (3))]. We compared the proportion of looking duration between conditions using a repeated-measures ANOVA with trial (first vs. second) and condition (test vs. control) as within-subject factors.

Results

Chimpanzees exhibited a greater decrease in nasal temperature in the test compared with the control condition (see Fig. 5 for the mean of each trial, and Fig. 6 for the individual data and the model fits). The model revealed significant main effects of condition (β ± SE = 0.33 ± 0.12, df = 9.40, t = 2.81, p = 0.019), time (β ± SE = − 0.14 ± 0.02, df = 19.70, t = − 8.63, p < 0.001), and $time^2$ (β ± SE = 0.00 ± 0.00, df = 13.90, t = 4.72, p < 0.001). The main effect of trial was not significant. We found no significant interaction effects. Regarding the looking data, no significant effect was found (condition × trial: F [1, 5] = 0.85, p = 0.399, η^2_G = 0.07; condition: F [1, 5] = 1.18, p = 0.326, η^2_G = 0.06; trial: F [1, 5] = 1.14, p = 0.334, η^2_G = 0.06), indicating that chimpanzees' attention was attracted to the demonstration to a similar degree across conditions (Fig. S1a).

For the other behaviors, we observed that the three adult females and one adult male interrupted their juice sipping and looked at the injury for several seconds to several tens of seconds at the beginning of the demonstration. We did not observe other identifiable behaviors, including facial and vocal expressions, in those chimpanzees.

Discussion

The results suggest that chimpanzees were aroused by seeing a familiar human injuring themselves. Importantly, the human demonstrator did not present any behavioral signs of pain, and chimpanzees viewed the demonstration for similar durations in both conditions. Thus, although the visual novelty could potentially have explained the observed responses of chimpanzees in Study 1, this was not the case in Study 2. Regarding behavioral responses, we did not observe any conspicuous behavioral signs of fear or distress in chimpanzees. However, we observed that three adult females and one adult male interrupted their juice sipping at the beginning of the demonstration, suggesting that they were prepared to incur at least some cost to inspect the injury.

The finding that chimpanzees were physiologically aroused while not showing any clear emotional expression suggests that the injury event was only moderately arousing. This finding also suggests that chimpanzees can be physiologically aroused without expressing emotion explicitly. This means that the absence of conspicuous emotional expression in chimpanzees does not necessarily indicate the absence of arousal, highlighting the importance of physiological measurement in experiments.

Somewhat unexpectedly, chimpanzees exhibited decreased nasal temperature in both the test and control conditions, although the response was stronger in the test condition. This result may suggest that the stimulus presented in both conditions was arousing for chimpanzees to some extent. Importantly, we suspect that procedural factors may have also been involved. For

example, it is possible that giving a sip of juice during the demonstration (to encourage chimpanzees to remain in front of the thermo-camera) caused a decrease in nasal temperature. It has been previously reported that gastrointestinal activity can cause a drop in nasal temperature due to activation of the sympathetic nervous system at the initial stages of ingestion (van Baak 2008; Kano et al. 2016). Unfortunately, we were unable to exclude this potential confound in the current experiment. Kano et al. (2016) observed this phenomenon when chimpanzees ate a large amount of food at once (e.g., a whole banana) but not when they ate small pieces of food periodically (e.g., one small cut piece of grape per 10 s). There- fore, future studies should use the latter option (giving small pieces of fruit), instead of giving juice, to avoid this potential confound. In the current experiment, most importantly, we confirmed that chimpanzees exhibited a greater decrease in nasal skin temperature in the test compared with the control condition. It should be noted that three adult females ceased juice sipping when they saw the injury. However, such interruptions in juice sipping would be expected to have no effect on the nasal temperature, and therefore, do not explain the larger temperature decrease in the test condition.

Although our sample size was not sufficient to formally analyze individual differences, the results suggested potential individual differences, with three adult females exhibiting clearer results than the other chimpanzees. As previous reviews have discussed, both direct and indirect experiences of pain can strengthen the response toward others' pain in humans (e.g., Goubert et al. 2005, 2009, 2011). Likewise, it is possible that previous experiences of being injured or witnessing injured conspecifics affected the results. Future studies should address this possibility with a larger number of chimpanzees.

Study 3

Previous studies have suggested that empathy involves at least two types of processes: automatic, reflexive, and bottom-up processes; and more cognitively controlled, top-down processes (Heyes 2018; de Waal and Preston 2017; Yamamoto 2016). Empathizing with others based on contextual cues presumably requires both processes; that is, to empathize with others' pain based on the observation of contextual cues, the observer needs to understand the cause of pain. In Study 2, we presented chimpanzees with an injury involving an open wound and running blood. Although chimpanzees were given only contextual cues but not behavioral cues (e.g., emotional expressions) in Study 2, the cognitive demand involved in understanding the cause of pain must have been relatively low because chimpanzees experience such injuries regularly in fights with groupmates. In many previous related studies with humans, the stimulus was a needle poking or penetrating a part of the body (e.g., Azevedo et al. 2013). The cognitive demand involved in understanding the cause of pain may be relatively high in this situation because needle penetration is only indicative of pain because of the nature of the needle and the body. Participants in these previous studies may have needed to infer the cause of pain based on inference from similar experiences (e.g., an injection with a hypodermic needle). In Study 3, therefore, we tested whether chimpanzees would show a similar physiological response to that observed in Study 2, even when we eliminated explicit cues such as an open wound, or blood.

Methods

The general procedures were identical to those of Study 2 except for the demonstrations/stimuli. The room temperature and humidity (mean ± SD) were 25.6 ± 1.0 °C and 80.8 ± 8.8%, respectively. The missing values for nasal temperature comprised 2.5% of the whole data set, and were linearly interpolated in the analysis.

For this demonstration, a familiar experimenter (FK), who had been working with the participants for longer than 3 years, acted out either stabbing a fake thumb with a needle in the test condition, or stabbing a piece of wood with a needle in the control condition. In the test condition, the experimenter was wearing a fake thumb made of plastic and painted with skin-colored powder (Fig. 4b). The experimenter wore fingerless gloves on both hands to hide the joints between the skin and the fake thumb. At the beginning of the demonstration, the experimenter picked up a piece of wood and attempted to stab it with a fat needle (15 cm in length and 0.3 cm in diameter) but slipped and stabbed his thumb. He then wiggled the needle and finally removed it from his thumb. The experimenter repeated this action twice and stopped the second demonstration when 180 s had passed since the beginning of the demonstration. He then swiftly left the area, so that he was no longer visible to the participants. It should be noted that, as in Study 2, the experimenter did not show any behavioral signs of pain during and after the demonstration. In the control condition, the experimenter started performing the same actions as in the test condition, but stabbed the piece of wood (instead of slip- ping and stabbing his thumb). He then wiggled the needle and finally removed it from the piece of wood. He repeated these actions twice, stopped the second demonstration when 180 s had passed since the beginning of the demonstration, and then swiftly left the area.

As in Study 2, we coded the looking behaviors from the video recordings. We were unable to code looking behavior in some of the recording period because of obstructions; in the test condition, this occurred for 13.64 ± 16.92% of the first trial, and for 6.02 ± 5.71% of the second trial, respectively (mean ± SD). In the control condition, this occurred for 3.23 ± 2.92% of the first trial and for 3.76 ± 3.46% of the second trial, respectively (mean ± SD).

For the statistical analysis of temperature data, we used the same model as in Study 2. The random slope of the three-way interaction was dropped from the model because the model failed to converge with it.

Results

Chimpanzees did not exhibit changes in nasal temperature over time in any of the trials/conditions (see Fig. 7 for the mean of each trial, and Fig. 8 for the individual data and the model fits). The LMM did not reveal any significant effects (Table S4).

For the looking data, no significant effect was found (condition × trial: F [1, 5] = 3.98, p = 0.103, η^2_G = 0.06; condition: F [1, 5] = 2.21, p = 0.198, η^2_G = 0.22; trial: F [1, 5] = 5.08, p = 0.074, η^2_G = 0.22), indicating that their attention was attracted to the demonstration to a similar degree across conditions (Fig. S1b).

For the other behavior, we observed that two adult females (Misaki and Mizuki) squinted their eyes at the very moment the needle penetrated the finger in the test condition, but not in the control condition.

Discussion

Chimpanzees did not physiologically distinguish between the conditions in which a needle penetrated a familiar experimenter's finger or an inanimate object. This result may indicate that chimpanzees had difficulty in under- standing others' pain without seeing familiar cues, such as a wound and blood. An alternative but related possibility is that direct experience is important to elicit empathic responses, as discussed in previous reviews (e.g., Goubert et al. 2005, 2009). Further studies will be needed to clarify this issue by adopting more stringent control of experiences.

It is also possible that chimpanzees exhibited subtle responses that could not be captured by the thermal imaging technique. This speculation is based on the observation that a female adult (Mizuki) exhibited reduced nasal temperature at the very moment the needle penetrated the finger (and recovered immediately after). Note that we did not expect such a brief change, and thus our model did not fit the observed decrease (Fig. 8). To capture such a subtle and short change, a measure of skin conductance may be more appropriate. Thus, future tests should consider the use of this technique. However, skin conductance measures should be used complementarily with thermal imaging because both techniques have strengths and limitations (c.f., Kuraoka and Nakamura 2011).

General discussion

In previous studies, chimpanzees have been observed to spontaneously show affiliation and offer help to injured conspecifics (e.g., Boesch 1991; Goodall 1986; Nishida and Hiraiwa-Hasegawa 1985). Some researchers have pro- posed that such behaviors can be considered as manifestations of empathy (e.g., de Waal 2008). The current study adds to these previous observations by showing that chimpanzees attend to injured conspecifics more than uninjured conspecifics (Study 1) and that they exhibit physiological arousal when seeing a familiar experimenter's injury with an open wound and running blood (Study 2). Importantly, we controlled for the conspicuousness of the images (i.e., the redness of the injury) in Study 1, excluding the possibility that chimpanzees only attended to conspicuous cues. We then controlled for the level of attention to the events in Study 2, suggesting that an additional psychological factor caused chimpanzees' physiological responses. In Study 3, no chimpanzee showed a similar level of physiological arousal when seeing a familiar experimenter stabbing his finger with a needle (without an open wound or blood), suggesting that explicit or familiar cues are necessary to elicit chimpanzees' physiological responses. Taken together, these results suggest that chimpanzees inspect others' injuries not only out of interest, but also out of empathy—at least in some familiar situations, as in Study 2 (but not in an unfamiliar situation, as in Study 3).

It could be argued that the chimpanzees may have been scared of, or disgusted with, an injury, rather than empathizing with the injured individual. However, taking the results of all experiments together, the current findings do not support this possibility. In Study 1, chimpanzees spontaneously attended to injuries rather than avoiding them, and we did not observe any conspicuous behavioral signs of distress (e.g., a fear grimace) throughout our experiments. In previous studies with humans, negative responses to images of injury are sometimes interpreted as an expression of disgust (e.g., Calvo and Lang 2004; Shenhav and Mendes 2014). However, it should be noted that the stimuli used in such studies are typically graphic, and some researchers have intentionally dissociated them from the images of "painful-injury" when selecting the stimuli (Shenhav and Mendes 2014). The stimuli in Study 2 were depictions of an injury that was similar to the injuries that chimpanzees occasion- ally observe after fights with groupmates. A recent study with human participants reported that people distinguish images of injuries from those of pathogen-related items, and that the images of injuries tended to be associated with a feeling of empathic pain rather than disgust (Kupfer 2018). It could also be argued that chimpanzees might have associated the presence of injury with aggression based on past experiences, and consequently exhibited excitement to the potential initiation of a fight rather than empathy for the injured experimenter in Study 2. This explanation may be consistent with the results of Study 3, which showed that chimpanzees did not physiologically respond to the injury when neither an open wound nor blood was present. However, this interpretation cannot explain chimpanzees' behavioral responses toward others' injuries in the previous observations and in our experiments. In particular, in previous observations, chimpanzees have been observed to gently inspect conspecifics' injuries, and in the current experiments, chimpanzees did not exhibit the kind of excitement

that is typically displayed when witnessing fighting (e.g., body swaying, emitting pant-hoots or alarm calls; c.f., Kano et al. 2016). However, to completely rule out this possibility, it will be necessary to further explore what contextual cues could cause physiological arousal in the absence of explicit cues, such as blood.

The current findings make two key contributions to previous research, one theoretical and the other methodological. First, previous studies have tended to focus on the behaviors rather than internal states when reporting chimpanzees' responses to others' injuries. The current findings revealed that chimpanzees exhibited physiological arousal when seeing others' injuries. This finding corroborates the idea that chimpanzees can empathize with distressed others, even without behavioral cues such as emotional expressions, which may motivate chimpanzees to inspect injured groupmates.

Second, we provided a new method for studying animal empathy using a cutting-edge thermal imaging technique in combination with a real-life theatrical demonstration of an accident. Thermal imaging can provide an effective approach for studying animal emotion experimentally, particularly with large-bodied animals such as great apes (Chotard et al. 2018; Kano et al. 2016). Although our main aim was to study the effect of injury (but not behavioral cues) on chimpanzees' responses, the same method can be applied to situations involving behavioral cues in future studies. Moreover, our method showed that a theatrical demonstration of an accident is effective in experiments with chimpanzees, as in previous experiments with human children (e.g., Gill and Calkins 2003; Zahn-Waxler et al. 1992). However, it should be noted that real-life demonstration may be necessary for testing chimpanzees because our initial attempts using still images or video footage did not elicit physiological reactions to the stimuli among chimpanzees. This could be partly due to artifacts (see Supplementary Materials) but could also have occurred because the visual representation of injury was not sufficiently powerful to elicit emotion in chimpanzees.

One weakness of the current study is that the number of chimpanzees tested was relatively small, making it difficult to identify individual differences in chimpanzees' responses to others' injury. Further studies are thus necessary to test a larger number of chimpanzees using the same methods. Such studies could be useful for revealing the structure of individual differences in the observed responses, and could extend understanding of their cognitive and emotional underpinnings. Based on the current results, individual traits that should be considered in future studies include sex, age, relationship quality between the demonstrator and the observer, past experiences with the object causing pain, and cognitive ability to understand the cause of pain. Other potential factors of interest include social competence (Webb, Romero, Franks, and de Waal 2017) and emotional regulation (Clay and de Waal 2013), which are thought to be related to consolation behavior in great apes.

In conclusion, the current findings revealed that chimpanzees spontaneously attended to conspecifics' injuries and were physiologically aroused when seeing an injured human experimenter. These findings are consistent with the notion that chimpanzees have the capacity to empathize with the distress of an injured individual. However, individual differences and the underlying cognitive mechanisms should be further explored to elucidate the precise nature of this response in future studies.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All procedures performed in studies involving ani- mals were in accordance with the ethical standards of the institution or practice at which the studies were conducted.

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Fig. 1 a A stimulus used in the test condition. **b** The corresponding stimulus in the scramble condition
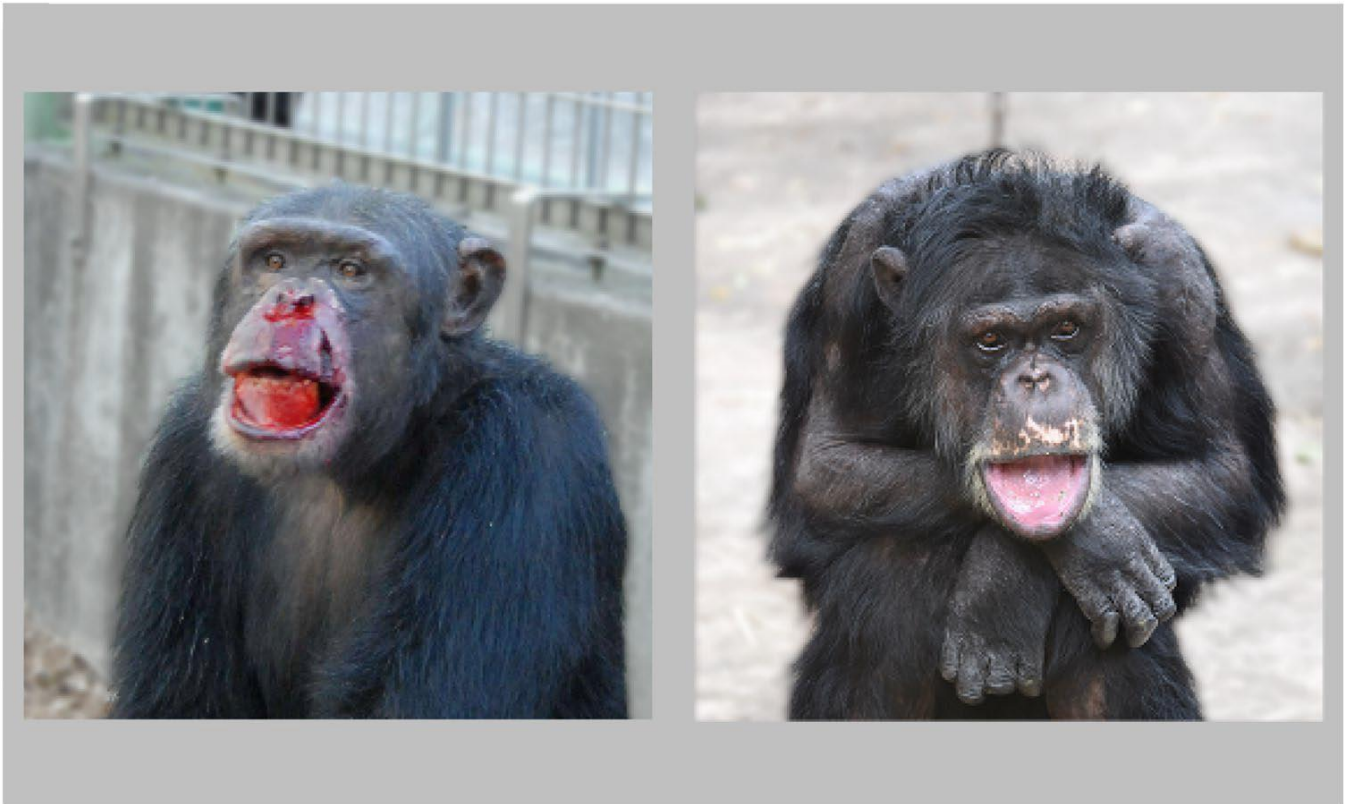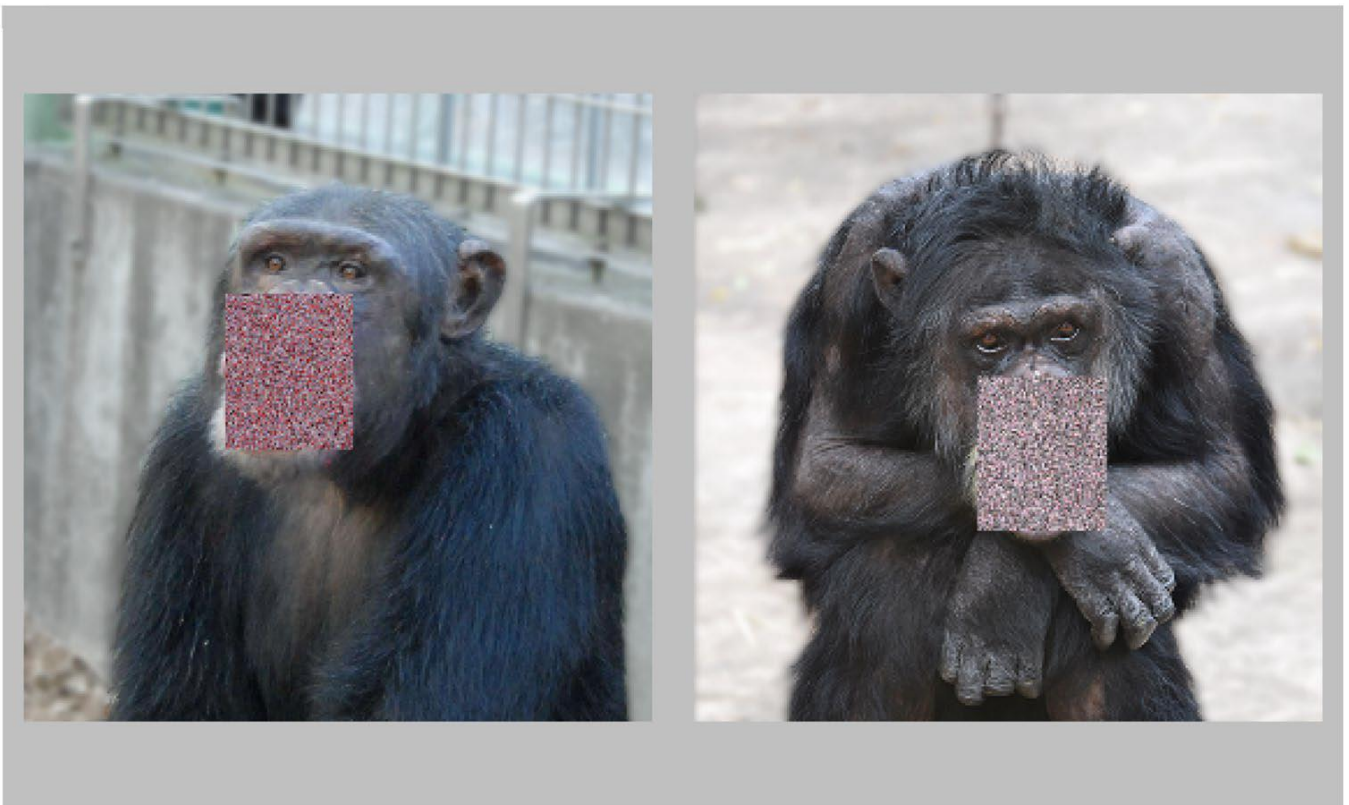
Fig. 2 a Proportion of time spent looking at injured chimpanzees (mean ± SEM, $n = 6$). Gray dots show each participant's data. The broken line indicates the chance level. **b** Proportion of looking time on injured chimpanzees in three time-bins ($n = 6$). The upper and lower ends of the box show the third- and first-quartiles, respectively. The thick line inside indicates the median. Whiskers indicate the maximum and minimum value. *: $p < 0.05$
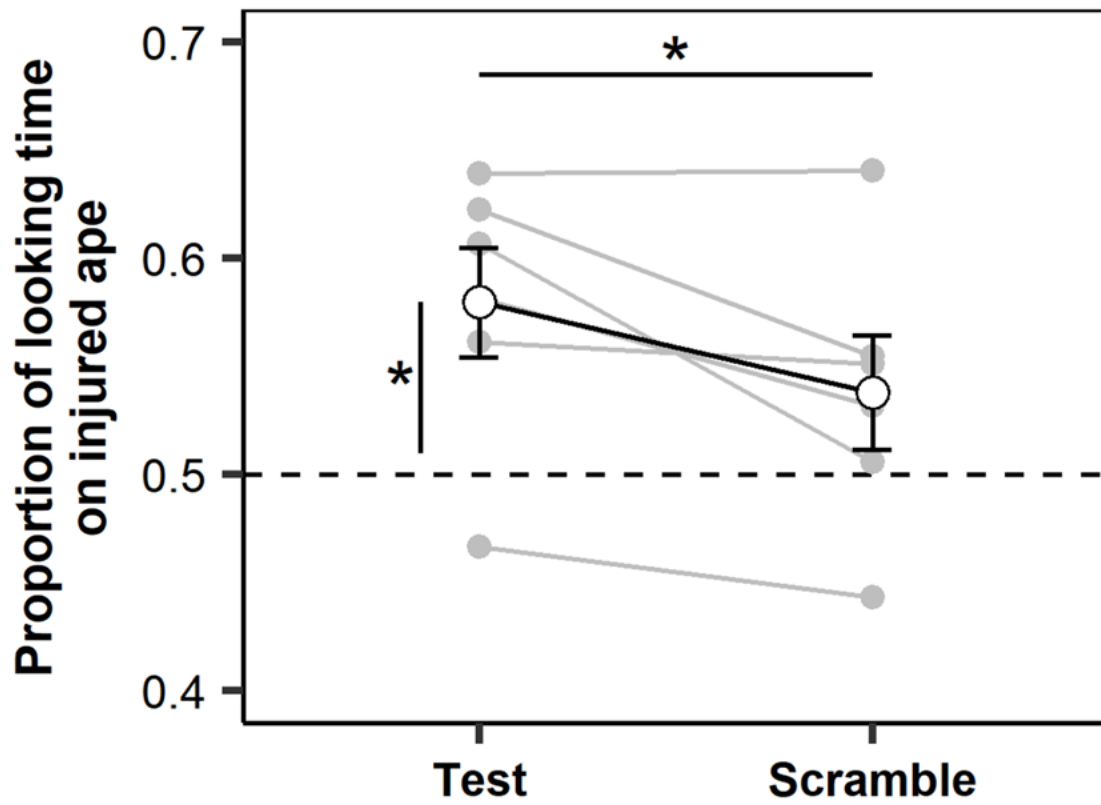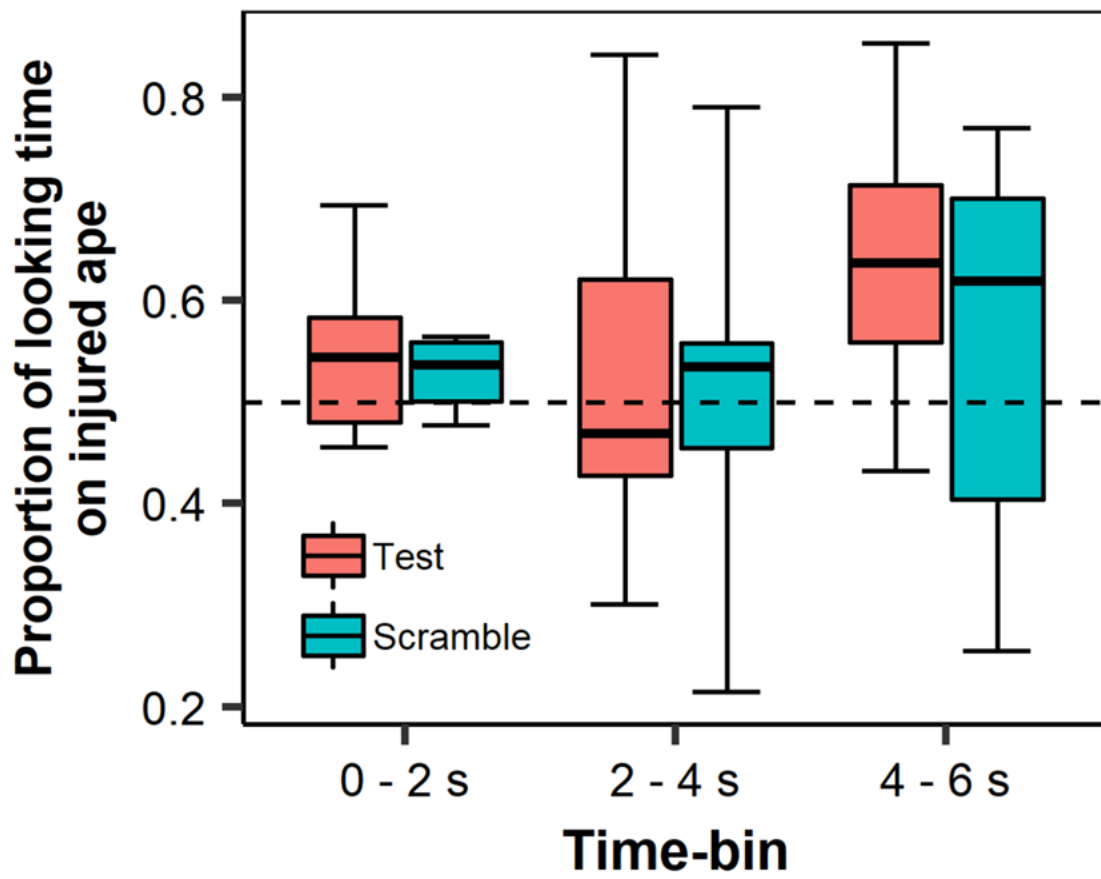
Fig. 3 Apparatus in preceding experiments (Supplementary Materials), Study 2 and Study 3. **a** Setup for the thermal imaging experiment. **b** An example of a thermal image. The AOI is indicated as a black circle on the nasal tip. The color bar on the right hand indicates the temperature (°C).
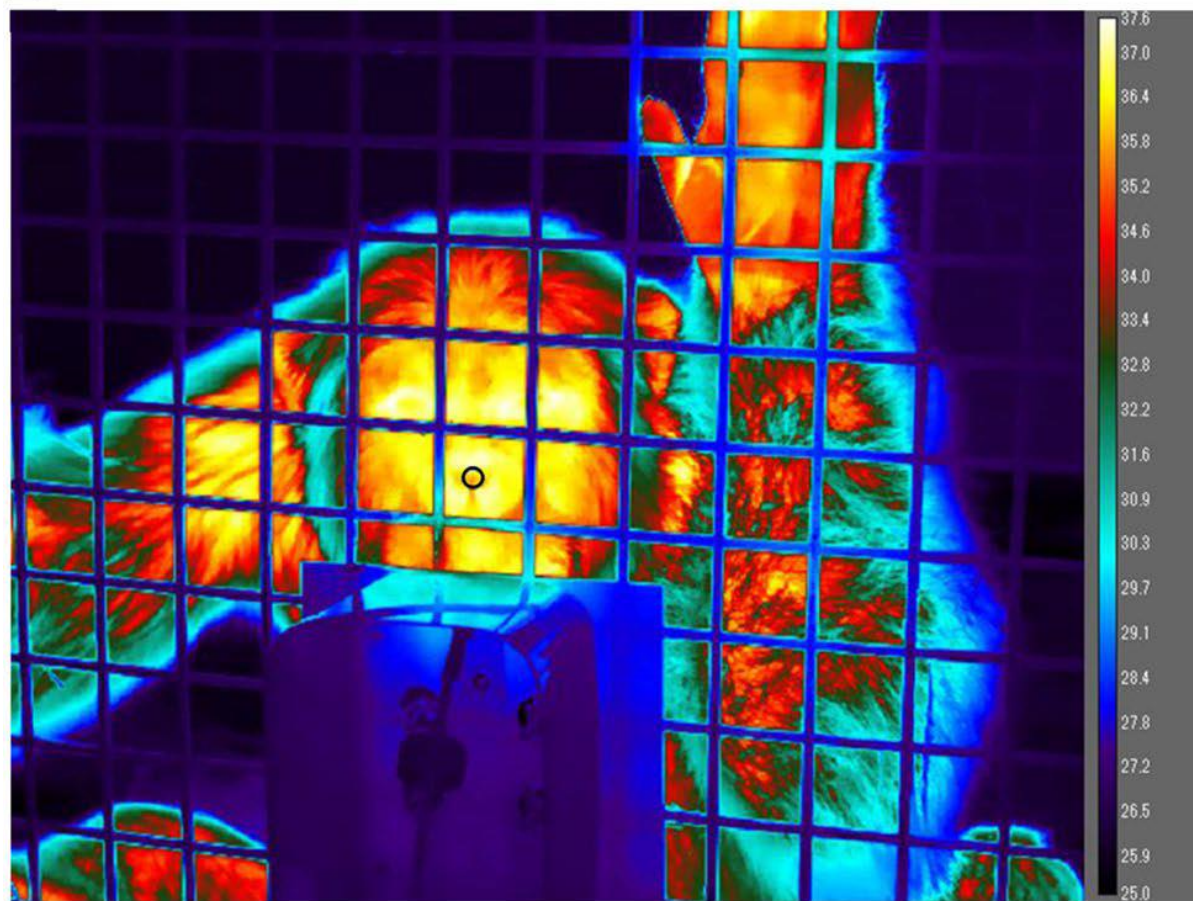
A

B

Fig. 4 Study 2 and Study 3 stimuli. **a** Injury make-up. Blood emerged from a tube hidden under the sleeve (the sleeve was slightly rolled up for visualization purposes in this photo). **b** Fake thumb stabbed with   a needle

A

B

Fig. 5 Mean temperature change (°C) as a function of time from stimulus onset (s) in Study 2 (*n* = 6). Dots represent individual data
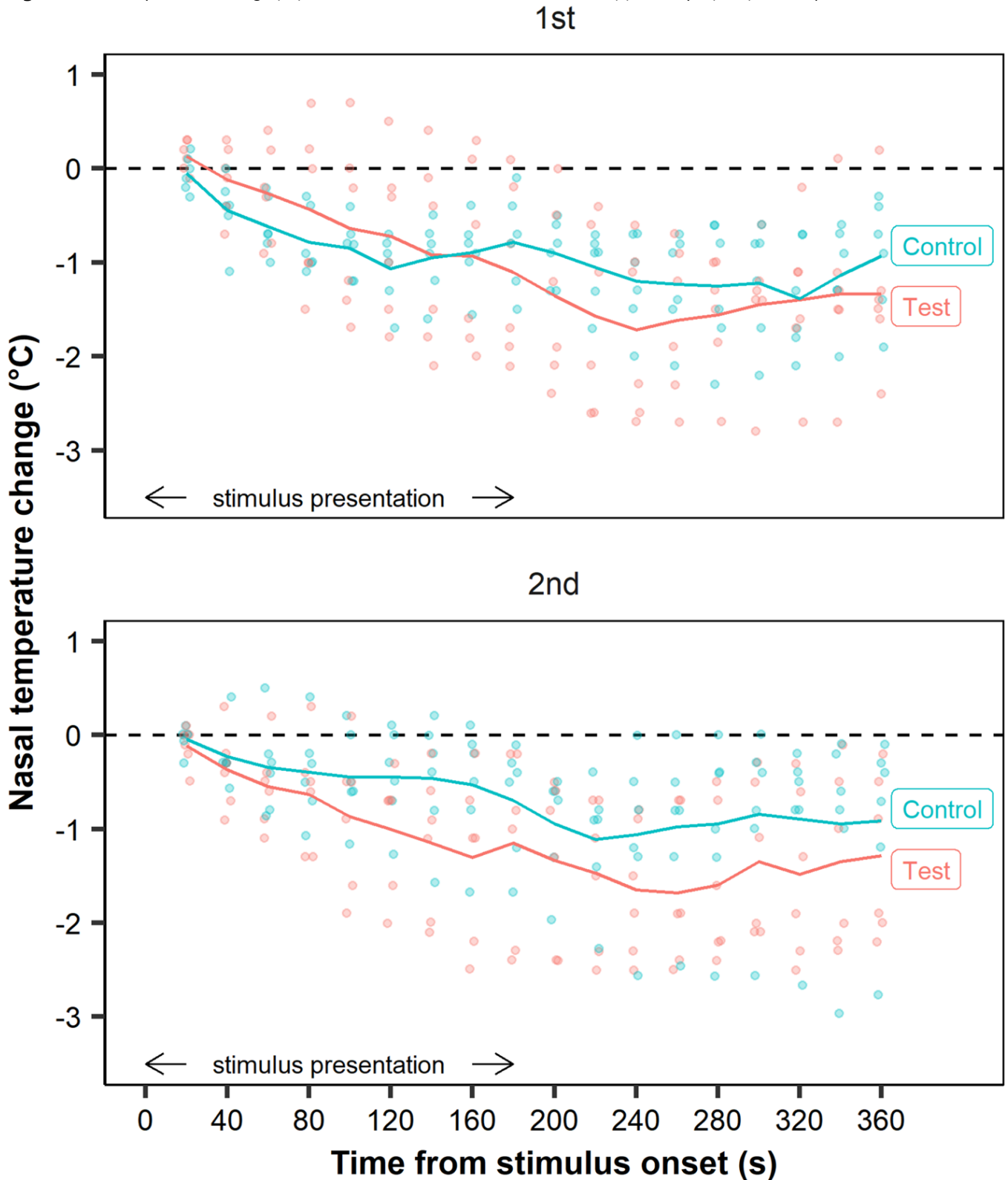

Fig. 6 Nasal temperature change (°C) of each chimpanzee participant in Study 2. Dots rep- resent observed data and lines represent predicted values by the model. The top three panels show data of adolescent females (Hatsuka and Iroha: 9 years old) and an adult male (Zamba: 22 years old); and the bottom three panels show data of adult females (Natsuki: 12 years old; Misaki: 19 years old; Mizuki: 21 years old)
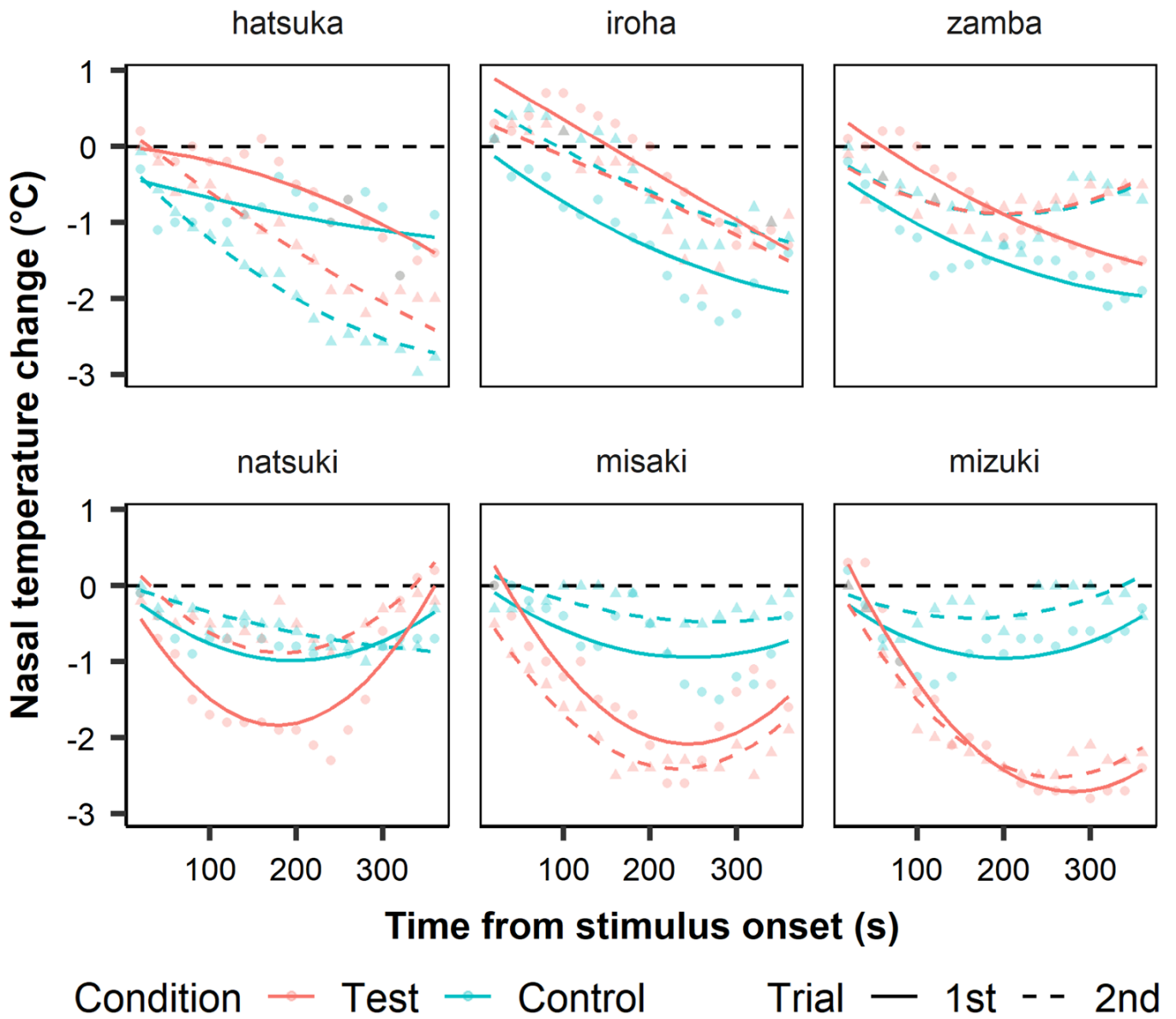
Fig. 7 Mean temperature change (°C) as a function of time from the stimulus onset (s) in Study 3 ($n = 6$). Dots represent individual data
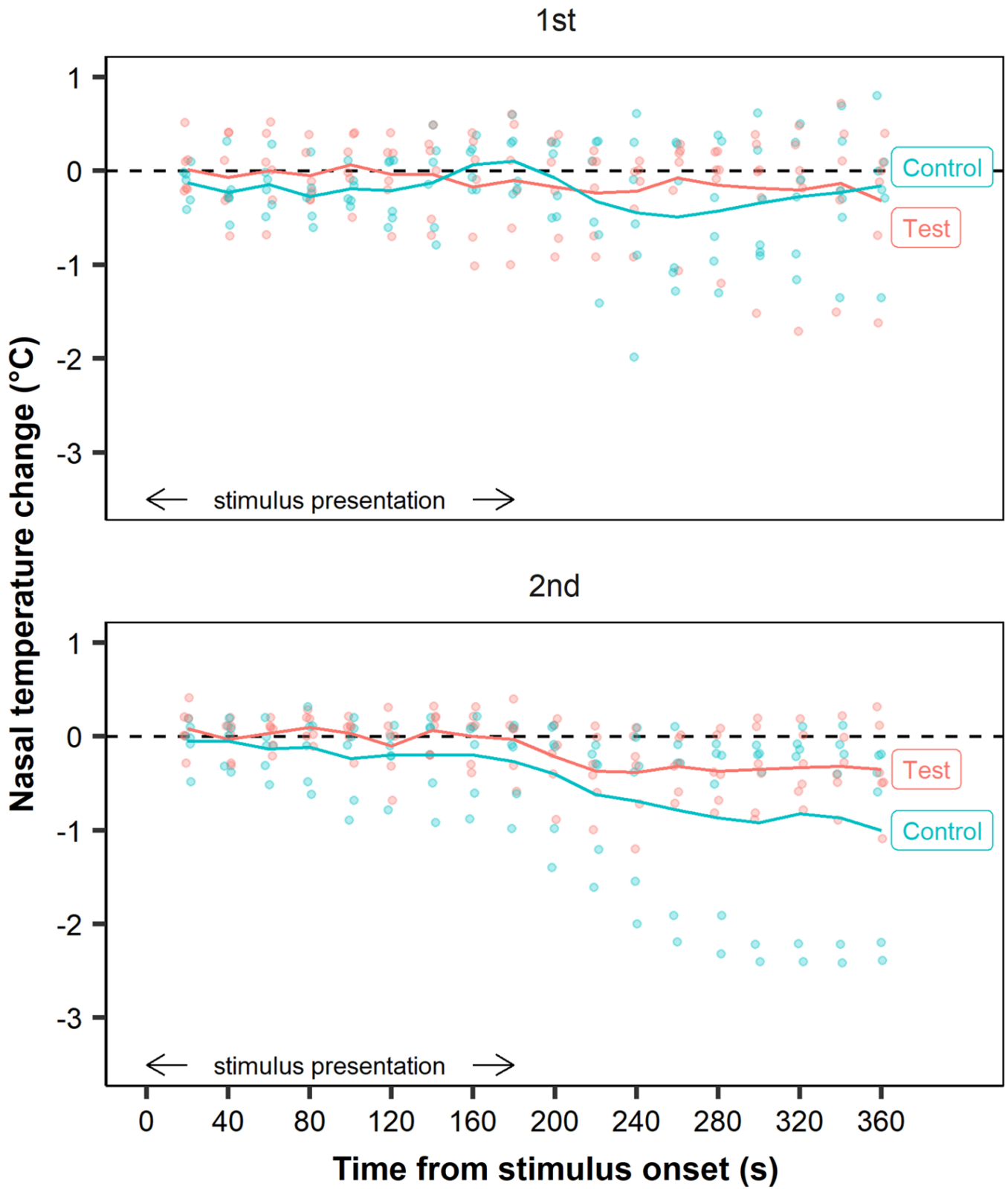
Fig. 8 Nasal temperature change (°C) of each chimpanzee participant in Study 3. Dots rep- resent observed data, and lines represent predicted values by the model. The top three panels show data of adolescent females (Hatsuka and Iroha: 9 years old) and an adult male (Zamba: 22 years old); and the bottom three panels show data of adult females (Natsuki: 12 years old; Misaki: 19 years old; Mizuki: 21 years old)