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Are Bonobos Anxious When Others Are Ignorant of a Threat? Using an Affect Measure to Assess Theory-of-Mind Abilities in Bonobos

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Abstract

Previous studies have shown that bonobos, along with other great apes, possess certain theory-of-mind (ToM) abilities, such as the ability to attribute states of knowledge and belief to others. Our study is the first to assess ToM abilities in bonobos using scratching behavior, a widely used affective measure in great apes. Subjects watched two videos; one video showed a group member ignorant of a snake threat while the other video showed a group member knowledgeable of a snake threat. The ToM hypothesis predicted greater frequency of scratching in subjects watching the ignorance video compared to subjects watching the knowledge video. Results were consistent with this prediction. All but one subject scratched more while watching the ignorance video, and subjects scratched nearly 4 times more often on average while watching the ignorance video. Small sample size prevents any strong conclusions to be reached; however, the experimental design has the potential to be used to assess the relation between affective states and ToM abilities in great apes and other species of nonhuman animals with ToM abilities in which there are reliable behavioral indexes of affective states.

Keywords: theory-of-mind, affect measure, bonobos, snake-model, scratching, alarm call

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Introduction

Theory of mind (ToM) is the ability to attribute mental states to other agents. Previous studies support the view that bonobos, along with other great apes, are capable of attributing mental states, such as states of knowledge and belief, to other agents (Buttelmann et al., 2017; Krupenye et al., 2016; Maclean & Hare, 2012). Historically, ToM has been studied in humans and great apes with an interest in discovering its relation to socio-cognitive and communicative abilities (Baron-Cohen et al., 1985; de Villiers, 2007; Tomasello & Call, 1999; Whiten & Byrne, 1988). A recent ToM study in children (Moll et al., 2016) used - for the first time - an affective measure to assess the relation between belief attribution and the affective state of surprise in 3-year-olds. Interestingly, there are no ToM studies in great apes that have directly investigated the relation between ToM and affective states. Previous ToM studies in great apes have used behavioral indexes of cognitive states, such as states of prediction and inference, rather than affective states, as dependent measures. For example, Krupenye et al. (2016) and McClean and Hare (2012) used looking behavior and Buttelman et al. (2017) and Hare et al. (2000) used object-choice behavior as behavioral indexes of apes' ability to predict or infer things about other agents' behaviors and mental states. While some ToM studies in great apes (e.g., Hare et al., 2000; Kaminski et al., 2008) involve competitive contexts, which could potentially cause stress in the participating subjects, none of these competitive ToM studies used an affective measure to assess the relation between ToM and affective states in subjects. One recent ToM study in great apes (Girard-Buttoz et al., 2020) recorded startling behavior as a measure of negative arousal in chimpanzees. However, in that study, startling behavior was not used as a dependent measure to test for ToM abilities in the chimpanzees. Our study is the first to use a widely recognized affective measure in great apes, scratching, to investigate the relation between ToM (specifically, the ability to attribute knowledge and ignorance to others) and the negative affective state of anxiety in a species of great ape, the bonobo.

Scratching in anxiety-inducing situations (e.g., agonistic encounters or demanding cognitive tasks) is a well-documented and widely used behavioral index of the negative affective state, anxiety, in great apes (chimpanzees [Aureli & de Waal, 1997; Baker & Aureli, 1997; Hopkins et al., 2006; Itakura, 1993; Koski & Sterck, 2007; Kutsukake, 2003; Leavens et al., 1997, 2001, 2004; van Lawick-Goodall, 1968; Yamanashi & Matsuzawa, 2010]; bonobos [Clay & de Waal, 2013; Rosati & Hare, 2013]; orangutans [Elder & Menzel, 2001]; gorillas [Carder & Semple, 2008]). Although great apes scratch in a wide range of situations from various external skin irritations, these studies show that in stressful situations, great apes increase scratching in the absence of any external skin irritation compared to non-stressful situations. Consistent with studies on scratching in great apes, several studies on scratching in monkeys show that a number of different monkey species increase scratching in anxiety-inducing situations (Castles & Whiten, 1998;

Diezinger & Anderson, 1986; Easley et al., 1987; Kaburu et al., 2012; Maestripieri, Schino, et al., 1991; Palagi & Norscia, 2011; Pavani et al., 1991; Peignot et al., 2004; Polizzi di Sorrentino et al., 2012; Schino et al., 1990; Schlafani et al., 2012; Scucchi et al., 1991; Troisi et al., 1991). Pharmaceutical studies in monkeys report an increase in scratching with anxiogenic drugs and a decrease in scratching with anxiolytic drugs (Maestripieri, Martel, et al., 1991; Schino et al., 1991, 1996), providing additional support for the view that increase starching in the absence of external skin irritation is a behavioral index of the negative affective state of anxiety in monkeys. There are, however, a few studies on scratching in monkeys that report no increase in scratching in an anxiety-induced situation compared to a control situation (Duboscq et al., 2014; Judge et al., 2006; Pearson et al., 2015; Semple et al., 2013), and two studies in marmosets (Adriaense et al., 2021; Neal & Caine, 2016) that report an increase in scratching in "positive" situations. Neal and Caine (2016) suggest that increase in scratching in positive situations (e.g., playing with conspecifics) may be an indicator of the positive affective state of excitement in marmosets; Adriaense et al. (2021), on the other hand, interpret the increase in scratching in positive situations (e.g., hearing food calls from a conspecific) as a possible indicator of the negative affective state of frustration in marmosets. The results of these monkey studies may raise questions about the reliability of scratching as an index of anxiety in anxiety-induced situations in some species of monkey, and whether scratching in positive situations may be an index of affective states, such as excitement or frustration, that differ in valence from the negative affective state of anxiety. However, we do not see that these monkey studies provide strong grounds to question the well-documented reliability of scratching in anxiety-induced situations as a behavioral index of anxiety in great apes. A recent study on emotional contagion in orangutans (Laméris et al., 2020) used scratching in 'tense' situations as a behavioral index for general emotional arousal rather than anxiety because the researchers took 'tense' situations in their study not to include typical anxiety-inducing situations, such as agnostic interactions. While the study by Laméris et al. (2020) may recommend interpreting scratching in tense situations in great apes more neutrally as a behavioral index for emotional arousal, their study does not provide any strong grounds for questioning the reliability of scratching in anxiety-induced situations as a behavioral index of anxiety in great apes. Below we provide grounds for taking the situation in which our bonobos are placed (i.e., seeing a video of a snake) as an anxiety-inducing situation rather than just a tense situation. We would like to add that nothing of substance hangs on whether scratching in our study is interpreted as a behavioral index for the negative affective state of anxiety rather than for a more neutral affective state, such as emotional arousal, as both anxiety and emotional arousal are affective states that lie on a continuum of valences from negative to positive, and the main objective of our study is to initiate an investigation into the relation between ToM and affective states in great apes.

In our study, we use a video-based, knowledge-ignorance ToM test modeled on the experimental design of experiment 2 in Crockford et al. (2017). Crockford and colleagues ran an innovative knowledge-ignorance ToM test in the field using a snake model and audio recordings of chimpanzee alarm calls (“alert hoos”) and non-alarm calls (“rest hoos”) played from speakers hidden in the bushes along a path traveled by a group of chimpanzees. When a chimpanzee in the group came upon the snake model on the path, researchers played either an alarm call (indicating that the other group members now knew [informed] of a threat) or a non-alarm call (indicating that the other group members were ignorant [uninformed] of a threat). We modeled our study on experiment 2 in Crockford et al. (2017) for two reasons. First, the sight of snakes (real or virtual) has been shown to be an anxiety-inducing situation for chimpanzees and bonobos (Crockford et al., 2017; Girard-Buttoz et al., 2020; Hopper et al., 2021). Second, in the experimental design of the videos, the observable (onscreen) behaviors of the knowledgeable member and the ignorant member are the same. Having the observable (onscreen) behaviors of the knowledgeable and ignorant member be the same is important for controlling for possible behavior-reading explanation of potentially positive results. Because previous ToM studies show that bonobos are capable of attributing mental states of knowledge and belief to others (Buttelmann et al., 2017; Krupenye et al., 2016; Maclean & Hare, 2012), we predict a greater frequency of scratching, taken as an index for anxiety, in the ignorant condition (when a group member is ignorant/uninformed of a threat) than in the knowledge condition (when a group member knows/is informed of a threat).

We also use our experiment to test the affect hypothesis in primate alarm call research. A recent snake-model study (Girard-Buttoz et al., 2020), similar to Crockford et al. (2017), showed that bonobos and chimpanzees are three times more likely to emit alarm calls upon sight of the snake model, when their fellow group members were ignorant of the threat than when their fellow group members knew of the threat. This type of finding has been interpreted as supporting the view that bonobos and chimpanzees emit alarm calls with the intention to inform ignorant members of potential danger (Crockford et al., 2017; Hessen et al., 2022). Contrary to this view, the affect hypothesis holds that bonobos and chimpanzees emit alarm calls in the presence of ignorant group members not to inform members of danger but merely to express their anxiety over group members’ safety (similar to screaming “Oh, no!” at the sight of someone who is unknowingly about to step on a snake). The affect hypothesis thus predicts that in our experiment, bonobos should emit the greatest number of alarm calls in the experimental condition in which they produce the greatest frequency of scratching (index for anxiety).

Methods

Participants

Participants were 7 bonobos (*Pan paniscus*), 3 males, 4 females (age range: 13–43; mean age: 23) from the Ape Initiative, Des Moines, IA. All procedures were in accordance with the ASAB/ABS Guidelines for the Use of Animals in Research. The research was approved by the Ape Initiative Institutional Animal Care and Use Committee (IACUC # 180711-02). All subjects were experienced with and trained to participate in video-based testing. None of the subjects had participated in a video-based knowledge-ignorance test before our study.

Subjects live in a group setting at the Ape Initiative and have daily access, weather permitting, to indoor/outdoor enclosures. Subjects have occasionally seen fox snakes (*Pantherophis vulpinus*) in the outdoor area and have been observed emitting alarm calls upon seeing the snakes. One year prior to the current study, subjects were shown a video of a fox snake slithering through grass with audio of the snake's characteristic rattle sound. All subjects showed interest in the snake video, and 5 of the 7 subjects emitted alarm calls upon seeing the snake in the video. Recordings of the alarm calls were made and used in the knowledge video (described below). Subjects were separated from their group and tested individually.

Procedure

Two experimental videos – knowledge video and ignorance video – were created using PowerPoint and converted into mp4 videos. Each video used an enhanced photo of the subjects' outdoor area as background scenery, and each video had the same embedded video and audio of a fox snake slithering through grass. Videos were viewed by subjects in their home cages on a flatscreen video monitor with speakers (see Figure 1). Subjects were seated directly in front of the monitor at the start of each trial. Once subjects were seated in front of the monitor, videos were played, and subjects were, when needed, verbally encouraged by the research assistant to remain in front of the monitor but were allowed to leave and return to the monitor at will during the testing trial.

Figure 1

Bonobo Watching Experimental Video

Knowledge video: The video opens with a view of the outdoor area. An audio recording of a bonobo alarm call (an alarm call recorded one year prior) plays while an enhanced photo image of a bonobo (a group member) walks into the outdoor area and sits down in the grass with its back to the viewing subject. After the group member sits down, an area in front of the member's back lights up with a flash icon (to direct the viewing subject's attention to the area), and then in that area, an embedded fox snake video and rattle audio play on a loop. In the embedded snake video, a fox snake slithers through grass toward the seated group member. The critical period of the video starts from the video's opening to the end of the first loop of the snake video (25 sec). For the remaining 155 s of the knowledge video, the embedded snake video loops several times. Total duration of the knowledge video is 180 sec.

Ignorance video: The ignorance video is the same as the knowledge video, except that in place of the alarm call, a non-alarm call (food peep) is played. We used an audio recording of a bonobo food peep as the non-alarm call. Food peeps are acoustically different from high pitched alarm calls and are typically given when bonobos have discovered preferred food items (Clay & Zuberbühler, 2009; de Waal, 1988).

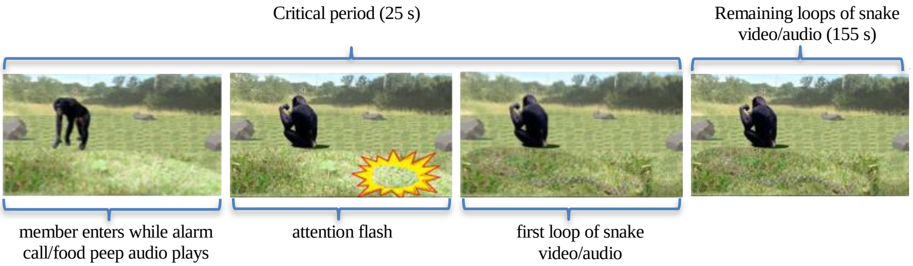
The narrative structure of both experimental videos, as well as the strategy for distinguishing knowledgeable (informed) and ignorant (uninformed) group members, are modeled on the experimental design used in experiment 2 of Crockford et al. (2017). In both videos, the onscreen member's behavior is the same. This is done to ensure that any difference in the frequency of scratching or alarm calling by the viewing subjects is not due to a difference in the onscreen members' behavior. Equally important is that the onscreen member in both videos has its back to the snake and never sees the snake approaching. However, the onscreen member in the knowledge video is informed of a threat by the alarm call that is being played. The onscreen member in the ignorance video, on the other hand, is not informed of a threat by the food peep being played (see Figure 2). This is analogous to the strategy Crockford et al. (2017) used in experiment 2 for distinguishing knowledgeable and ignorant group members.

There are antecedent reasons to expect the bonobos in our study to understand the alarm call being played in the knowledge video, but not the food peep being played in the ignorant video, to be informative of a threat. The bonobos in our study have either emitted alarm calls or have heard other group members emit alarm calls in the presence of snakes (real or video recorded), indicating that they have experienced a threat-alarm call association in the past. Girard-Buttoz et al. (2020) found that bonobos are three times more likely to emit an alarm call in the presence of group members who have not seen a snake treat than in the presence of group members who have seen the snake, suggesting that bonobos understand alarm calls as informing group members of a threat. Girard-Buttoz and colleagues also report data that suggest that bonobos are less likely to be startled by the sight of a snake if they have heard an alarm call prior to encountering the snake, suggesting that bonobos understand alarm calls as providing information of a potential threat. Previous studies on food peeps in bonobos (de Waal, 1988; Clay & Zuberbühler, 2009, 2011), however, report that food peeps are produced by bonobos most often in the presence of preferred food and likely function to inform group members of a preferred food source, not of a potential threat.

In our study, subjects were presented with each experimental video once, with the order of presentation counterbalanced across subjects. Four subjects received the knowledge video first and the ignorance video; three subjects received the ignorance video first and the knowledge video second. Intertrial interval was on average 9 days (range: 6–11 days). The total running time of each experimental video is 180 s. The first 25 s of each video presents the critical period of the video narrative: the alarm/non-alarm call, the group member's entrance, and the first loop of the embedded snake video. Subjects are encouraged by a research assistant to remain directly in front of and facing the video monitor during the critical period, and all but one subject (Clara) remained directly in front of and facing the monitor during the critical period. In the remaining 155 s of each experimental video, the embedded snake video runs on a continuous loop (see Figure 2). During the 155 s after the critical period while the snake-video continued to loop, some subjects moved away from the monitor for brief periods of time but remained in their home cage until the end of the video. Subject behavior was recorded during the total 180 s running time of each video by a cell phone or video camera. Alarm call and scratching behaviors of subjects were coded from the video recordings.

Figure 2

Narrative Structure of Experimental Video



Behaviors and Coding

Individual scratching events and alarm calls are coded and counted from the video recordings. A scratching event involves a subject's finger(s), hand, or wrist contacting and/or swiping across its body or face without any apparent external reason for contact/swipe (e.g., swatting an insect, grooming, picking food/scab on body). A scratching event ends when the subject's finger(s), hand, or wrist are no longer contacting and/or swiping across the subject's body. A high-pitched screech emitted from the subject's mouth followed by 1 s silence was counted as an individual alarm call. All trials were coded by R. L. A second rater, naïve to the experimental conditions, coded 7 (50%) randomly selected trials (3 knowledge trials; 4 ignorance trials). Interrater reliability was assessed with a Spearman's correlation test. Results show that interrater reliability was high (r[5] = .964, *p* < .001).

Results

A Shapiro-Wilks test for normality on the scratching data showed non-significance (*p* = .67), suggesting normally distributed scratching data. However, because small sample size (*N* = 7) generally mandates conservatism, we opted to run a non-parametric test. With alpha set at .05, results of a one-tailed, Wilcoxon signed-rank test indicated no evidence of greater scratching in the ignorance condition than in the knowledge condition (*W* = 4, *p* = .054). Effect size was large (*r* = .64) using the Wilcoxon *r* effect size code ($r = \frac{Z}{\sqrt{N}}$). We also ran a Bayes factor analysis as a way of providing another method of statistical analysis of our data given the small sample size. We used JASP 0.19.1 software with default Cauchy prior of 0.707. To extract a Cohen's *d* effect size and Bayes factors we ran a one-tailed, paired-t test, which indicated a significant difference between frequency of scratching in the ignorance condition (*M* = 28.7, *SD* = 29.8) and frequency of scratching in the knowledge condition (*M* = 7.6, *SD* = 8.3), t(6) = 2.3, *p* = .032[1], with a large effect size *d* = 0.86. Results of the Bayes factor analysis showed that data were three times more likely under the alternative hypothesis that there would be more scratching in the ignorance condition than knowledge condition (BF_{10} = 3.15). This is considered moderate evidence in support of the alternative hypothesis (van Doorn et al., 2021).

Given the small sample size, we focus primarily on descriptives and ratio data to evaluate our hypothesis and consider the results preliminary rather than confirmatory. The average number of scratches subjects made in the ignorance condition (*M* = 28.7, *SD* = 29.8) was 3.8 times greater than the average number of scratches subject made in the knowledge condition (*M* = 7.6, *SD* = 8.3). All but one subject (6/7, 86%) scratched more in the ignorance condition than the knowledge condition, with the single exception (Clara) being the only (and potentially anomalous) case of zero scratches in any condition. On average, subjects scratched twice as frequently in the first condition (*M* = 23.8, *SD* = 31.6) than in the second condition (*M* = 12.7, *SD* = 11.2) and 8.7 times more frequently in the first ignorance condition (*M* = 47.7, *SD* = 38.1) than in the first knowledge condition (*M* = 5.5, *SD* = 4.12) (see Table 1).

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[1] Note that the *t*-test, one-tailed, was statistically significant, but we prefer the non-parametric test for the reasons given in the main text.

Table 1

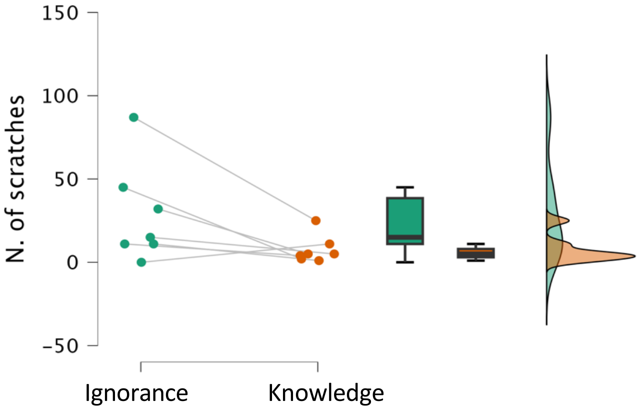
Number of Scratches and Alarm Calls Produced in Ignorance and Knowledge Conditions

		Scratching		Alarm calls	
Subject	Condition order	Ignorance	Knowledge	Ignorance	Knowledge
Clara	K, I	0	11	0	0
Elikya	K, I	11	1	0	0
Kanzi	K, I	32	5	0	0
Maisha	K, I	15	5	0	0
Mali	I, K	11	4	0	0
Nyota	I, K	87	25	0	0
Teco	I, K	45	2	0	0
Total		201	53	0	0
M		28.71	7.57	0	0
SD		29.75	8.32	0	0

There was a greater spread of scratching in the ignorance condition (IQR = 27.5) than in the knowledge condition (IQR = 5.0) (see Figure 3).

Figure 3

Raincloud Plots and Boxplots of Scratching in Ignorance and Knowledge Conditions



Subjects did not emit any alarm calls in either experimental condition (see Table 1), preventing us from running any statistical test on the data.

Discussion

Using a video-based, knowledge-ignorance ToM test modeled on Crockford et al.'s (2017) experiment 2, we tested the ToM hypothesis that bonobos scratch more, interpreted as an increase in anxiety, when in the presence of a group member who is ignorant of a threat compared to when in the presence of a group member who knows about a threat. Due to constraints on the availability of subjects with sufficient experience and training with video testing procedures, as well as the novelty of our experiment, we were able to run our test on $N = 7$ bonobos. It is relevant to note that there are only seven bonobos at the Ape Initiative center where the experiment was conducted. Our experiment has the potential, however, to be used on a larger population of subjects who have sufficient experience and training with video testing procedures. Scratching data were consistent with and in the direction of the ToM hypothesis; although, a formal test did not rule out the null hypothesis. All but one subject (6/7, 86%) scratched more frequently in the ignorance condition than in the knowledge condition. The one exception was Clara who did not scratch in the ignorance condition, which may have been due to her failure to view the entire 25 s of the critical period of the ignorance video. On average, subjects scratched nearly four times more often in the ignorance condition than in the knowledge condition. It is unlikely that these results are due to an order effect. Although subjects produced twice as much scratching on average in first condition than in second condition, they produced 8.7 times more scratching in first ignorance condition than in first knowledge condition, suggesting that type, not order, of condition accounts for the nonsignificant difference in scratching frequencies across the two experimental conditions.

There have been deflationary explanations of ToM-like behaviors in great apes (Heyes, 2015; Povinelli & Vonk, 2004). Povinelli and Vonk (2004) have argued that the designs of the experiments used to test ToM hypotheses in great apes are constitutively unable to control for deflationary explanations, such as behavior-reading or stimulus-specific explanations, of positive results. Subject to the caveats around statistical power, the design of our experiment rules out some possible deflationary explanations. A significant increase in scratching in the ignorance condition compared to the knowledge condition, for example, would be difficult to predict or explain in terms of a behavior-reading hypothesis that subjects are simply responding to different observable behavioral cues presented in the two conditions, as the ignorant member and the knowledgeable member behave in the same way in both conditions. Neither could a significant increase in scratching in the ignorance condition compared to the knowledge condition be plausibly predicted in terms of a stimulus-specific hypothesis that food peeps (or some other non-alarm call) cause more anxiety or scratching than alarm calls, as there are no studies that we know showing that food peeps (or some other non-alarm call) produce more anxiety or scratching in bonobos than alarm calls. While our results were not statistically significant, the point here is that the design of our experiment can rule out some possible deflationary explanations of significant positive results if such results are achieved.

We also used our experiment to test the affect hypothesis that alarm calls in bonobos are simply expressions of anxiety and not intended to inform group members of a threat. This hypothesis predicts that in our study, alarm calls should occur most often in the condition in which scratching (index for anxiety) occurs most often. Interestingly, the bonobos in our study did not emit any alarm calls in either condition, preventing us from making any claims about the truth or falsity of the affect hypothesis. We cannot rule out that the level of anxiety the bonobos experienced while watching the videos in our study was insufficient to produce alarm calls. As noted in Procedure, all subjects were shown a snake video one year prior to our study. It is possible the absence of alarm calls in our study is due to subjects' habituating to a snake video. To avoid the possibility of habituation, future research should be run with subjects who have not been exposed to snake videos prior to testing together with a control group of subjects who are presented with a snake video but not administered the test videos.

ToM has been investigated in great apes for over 40 years with the exclusive interest in discovering its relation to socio-cognitive and communicative abilities in great apes. There have been no direct investigations of the relation between ToM and affective states in great apes. Our study is the first to attempt to investigate the relation between ToM abilities (specifically, the ability to attribute knowledge and ignorance to others) and affective states (specifically, the negative affective state of anxiety) in a great ape species, the bonobo. The design of our study has the potential to be used to investigate the relation between ToM and affective states in other nonhuman species that have also shown to possess ToM abilities (e.g., chimpanzees [Hare et al., 2000; Krupenye et al., 2016], corvids [Bugnyar et al., 2016], monkeys [Hayashi et al., 2020], and dogs [Schünemann et al., 2021]). While scratching during anxiety-induced situations is an appropriate behavioral index for anxiety in great apes, other affect measures (e.g., piloerection, cortisol levels, skin or tympanic membrane temperature, self-directed behaviors) can be used that may be more appropriate for the animal species being tested.

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