

Applying an eye tracking technique to gibbons: First study using scanpath
measurements for visual stimuli

Makiko Uchikoshi¹, Lira Yu^{2,3}, and Yuko Hattori¹

1: Center for the Evolutionary Origins of Human Behavior, Kyoto University

2: Graduate School of Arts and Sciences, The University of Tokyo

3: Japan Society for the Promotion of Science

Declarations of interest: none

Corresponding authors: Makiko Uchikoshi and Yuko Hattori

Postal address: Center for the Evolutionary Origins of Human Behavior, Kyoto
University, Inuyama Campus, Kanrin, Inuyama, Aichi 484-8506, Japan

e-mail: uchikoshi.makiko.2e@kyoto-u.ac.jp; hattori.yuko.8w@kyoto-u.ac.jp

Tel:(+81) 568-63-0587

Abstract

Compared to the abundance of research on cognition in various nonhuman primate species, studies of gibbons -- often called “the small apes” -- remain limited, despite the importance of gibbons for understanding evolutionary processes in humans and other apes. Over the past decade, eye tracking techniques have been established in chimpanzees and other nonhuman primates using the free-participation method, which requires no physical restraint of the subjects. We investigated the feasibility of using the same method to record visual scanpaths in gibbons. We attempted to measure the eye movements of three adult gibbons while they spontaneously viewed images, with no prior fixation training. Calibration was successful in all three individuals, with errors of less than one degree. In total, 24 stimuli were used, with landscape and nonhuman primate face photographs presented on one-quarter of the screen, to test the prediction that gibbons would change their viewing time depending on image category. All three gibbons viewed the images for longer than the background, and primate face images for longer than landscapes. These results are consistent with previous findings in other primate species that faces attract more attention than non-face stimuli, suggesting that this effect is common across primates. This study demonstrates the feasibility of using eye tracking with gibbons. Further studies on gibbon visual exploration and cognition may enhance our understanding of the phylogenetic origins of hominid intelligence as well as the unique evolution of gibbons.

Keywords: Gibbons, Eye-tracking, Methodology, Visual attention, Comparative cognition

1 **Introduction**

2 Comparative studies of gibbons (*Hylobatidae*) are important for understanding the
3 evolutionary origins of human behavior and mind, considering their phylogenetic
4 position and uniqueness. Gibbons are apes, having evolved in their particular ecological
5 niche after diverging from the common ancestor of humans and great apes
6 (chimpanzees, bonobos, gorillas, and orangutans) around 17 million years ago. Gibbons
7 are a diverse group, with 20 species in four genera currently recognized. Gibbons have a
8 unique constellation of characteristics, including relatively small body size, specialized
9 anatomical adaptations for arboreality, small group size, monogamy with long-term
10 pairing, territorial behavior, and elaborate vocal behaviors called songs (Brockelman,
11 2009; Geissmann, 2000).

12 However, despite gibbons' scientific importance, our understanding of their cognitive
13 characteristics remains limited. Relatively few studies have been done on gibbons
14 compared to great apes (Fan & Bartlett, 2017), especially in the area of cognition (e.g.,
15 Casper et al., 2018; Cunningham et al., 2006; Munir & Nealen, 2023). Among them, a
16 few have employed a looking-time paradigm, with manually coded gaze direction used
17 as an indicator of gibbon visual attention when presented with schematic facial figures,
18 printed pictures showing gaze directions, or live acts by a human, such as "looking up"
19 (Horton & Caldwell, 2006; Liebel & Kaminski, 2012; Myowa-Yamakoshi & Tomonaga,
20 2001a, b). Against this background, there is a need to refine and expand research
21 methods for studying gibbons.

22 Because eye-tracking can be used to measure perceptual and cognitive processes based
23 on spontaneous looking behavior, without requiring any specific motor response from
24 participants, its introduction as a tool for research on gibbons would be highly

1 advantageous. Over the past decade, noninvasive eye-tracking techniques developed for
2 use with humans have been adapted for nonhuman primates in restraint-free conditions
3 (Hopper et al., 2021; Lewis & Krupenye, 2022), with successful use reported in at least
4 seven species of platyrrhine and catarrhine monkeys and great apes, in studies of
5 responses to various types of stimuli. Eye tracking has also been used in studies of a few
6 nonprimate mammal species, notably dogs (Huber et al., 2023) and recently, giant
7 pandas (Huang et al., 2023).

8 In this study, we conducted free-participation eye tracking in gibbons. To our
9 knowledge, this is the first report of successful scanpath measures in gibbons. We
10 describe the specific methods used for gibbons as the primary purpose. Gibbons are
11 diurnal and have trichromatic color vision (Hiwatashi, et al., 2011), and visual
12 processing is crucial in their adaptation to arboreal life. We assume that images capture
13 their visual attention. Previous studies of humans, great apes and macaque monkeys
14 have demonstrated that biologically relevant stimuli, such as animals, attract more
15 attention than non-animal stimuli (Hanazuka et al., 2012; New et al., 2007).
16 Furthermore, faces are more attention-eliciting than non-face stimuli, as evidenced from
17 visual search tasks (Nakata et al., 2018; Tomonaga & Imura, 2015) and eye-tracking
18 studies (Di Giorgio et al., 2012; Kano & Tomonaga., 2009; Kano et al., 2012). We can
19 assume that in primates there has been strong evolutionary pressure to pay attention to
20 faces to obtain social information, including whether the individual is a threat or not
21 (Gonçalves, et al., 2022). Thus, like humans (Jakobsen et al., 2021), nonhuman primates
22 may share a general face bias, beyond just own-species face bias. Considering gibbons'
23 phylogenetic position between monkeys and great apes, along with their sociality, we
24 predicted that face stimuli would capture more attention than a plain background, and

more than non-face stimuli.

Method

Participants

Three adult male gibbons (*Hylobates spp.*) participated. At the start of data collection, *Tsuyoshi* was 24, *Raja* was 23 and *Mamy* was estimated to be 52 years old, respectively. They were housed at the Center for the Evolutionary Origins of Human Behavior, Kyoto University. They were never deprived of food or water, but every day received food consisting of mainly fresh fruits and vegetables, and seasonally available plants. Portions of their food were presented in puzzle feeders and other enrichment devices; water was available ad libitum. All research procedures followed institutional guidelines (Primate Research Institute 2010 version of ‘The Guidelines for the Care and Use of Laboratory Primates’) and the experimental protocol was approved by the Animal Welfare and Animal Care Committee of the Center for the Evolutionary Origins of Human Behavior, and the Animal Research Committee of Kyoto University. All procedures adhered to the Japanese “Act on Welfare and Management of Animals”.

Tsuyoshi and *Raja* were brothers, born from the same parents in 1998 and 1999, and raised by humans from the age of 2 weeks because their mother’s caretaking behaviors were inadequate. Human caregivers scheduled daily visits by the infants to the parents (*Hylobates agilis* and *Hylobates albibarbis*) and another adult male-female pair (*Hylobates lar*) to promote the young apes’ normal social development. *Raja* lived with his elder brother, *Tsuyoshi*, from infancy, and both were returned to their mother when *Tsuyoshi* was 2 years old. After the mother died 4 years later, the two brothers lived together for another 4 years. Since then, they have been housed individually, albeit with

1 constantly available opportunities for visual, auditory, and limited tactile contact with
2 each other and their biological father, *Mamy*. *Mamy* arrived at the Primate Research
3 Institute (PRI), Kyoto University in 1973 when he was estimated to be 2 years old. Now
4 elderly and showing symptoms of heart failure, in 2018 he developed paralysis in his
5 right foot. *Mamy* has shown no signs of cataracts, nor have the other two gibbons shown
6 any sign of eye disease.

7 The gibbon facility consists of four indoor cages, connected in circular fashion via aerial
8 pathways and sliding doors. Each gibbon uses one or two cages and connected
9 pathways on a rotational basis by day or time of day. *Tsuyoshi* and *Raja* previously
10 participated in a cognitive experiment using touch-screen monitors (Tanaka &
11 Uchikoshi, 2010). In that study, reliable data were obtained only from *Tsuyoshi*. *Mamy*
12 has had no experience with cognitive experiments involving a viewing monitor.

14 Apparatus

15 The experiment was conducted in an indoor home cage, about 3 m wide, 2.5 m deep,
16 and 2.5 m high. Using lumber and a 3 mm thick clear acrylic panel as the main material,
17 an experimental viewing window was constructed (Fig.1). This removable window was
18 attached to the sliding door of the home cage for each experimental session. A Tobii
19 TX300 eye-tracking device was used to record the movement of both eyes (300 Hz;
20 Tobii Technology AB, Stockholm, Sweden). The eye tracker was connected to a 23-
21 inch TFT monitor (ca 43° × 24°), on which photos were presented with Tobii Pro Lab
22 software (ver. 1.194). The device was mounted on a wooden table with casters, and the
23 distance between the monitor and the participant was adjusted to approximately 65 cm.
24 To encourage the gibbons to sit still in front of the acrylic panel and face the eye tracker,

a licking tube was attached to the panel, which produced regular drops of isotonic water --a favorite drink-- during the experiment (Fig. 1). The height and depth of the licking tube was adjusted for each gibbon by constructing acrylic panels and wooden frames to match their sitting heights and postural preferences. White curtains with high light-blocking properties were used to control the brightness of the room, but were fully closed only at the window nearest the participant for about 10 min during the preparation and running of the experiment. LED lights in the ceiling near the participant were turned off to avoid interference in gaze measurements. Illuminance was measured using a multitest-meter (Laserliner®) and maintained at optimum (i.e., 2 lux in front of the monitor) for collecting scanpath data. Most areas of the room remained moderately bright, and the gibbons chose freely where to be within the test cage.

Fig. 1

Stimuli

Twenty-four stimuli of 1920 x 1080 pixels (ca 43° × 24°) were prepared, each combining a plain background and a color photographic image (Fig. 2). The images consisted of 12 facial photos of nonhuman primates and 12 landscapes. All individuals and landscapes in the photos were unfamiliar to the gibbons. Each face image showed a different monkey or lemur species. The landscape photos showed 12 different locations; none contained any animals. The screen was divided into four quadrants: upper left,

lower right, etc., and the presented photo image (ca $22^{\circ} \times 12^{\circ}$) appeared in one of them. The remaining three quadrants of the screen presented a blank grey background. The positions of photos were counterbalanced.

Fig. 2

Procedure

Experimental sessions were conducted once per day, in the morning. Each gibbon's participation was voluntary. Drops of isotonic water dripped from the tube attached to the panel, and the session began with calibration when the gibbon placed his mouth on the tip of the tube and sat steadily in front of the eye tracker. Manual calibration was done by showing a short video clip in each opposing corner of the screen (2-point). Duck or blue puppy movies with accompanying sound that were included with Tobii Pro Lab software were often presented to get the gibbon's attention during calibration, but we also used short home-made movies of gibbons, cats, frogs, humans, pigeons, etc. We used two types of calibration target: video, and resizing video. In the former, the size and position of the movie remain constant; in the latter, the movie begins in full screen and is scaled down to a specific calibration target position. Between calibration points, the video is again expanded to full screen. If the gibbon did not look, a small paper sticker or small toy was used to attract his attention. We set the calibration accuracy to less than 1° . If accuracy did not reach this criterion after several attempts, we reused successful calibrations for that individual from previous sessions. Lighting

conditions remained the same throughout the experiment. The position of the monitor and eye tracker was kept as constant as possible for each participant by placing marker tape on the floor. The angle of the device was also fixed.

For each gibbon the daily session usually lasted about 5 minutes, and no longer than 10 minutes. Each session included several trials, the first trial consisting of calibration, followed by alternating presentations of two stimuli, one face and one landscape photo in alternating order. From the second trial, calibration was skipped and the two stimuli were presented. Each photo was presented only once, each time for 2 sec. In total, 12 primate faces and 12 landscape photos were presented. The order of stimulus presentation was the same for all three gibbons. If the gibbon never fixated the stimulus, whether background or image, an additional trial with the same stimulus was conducted after completion of all normal sessions. The number of stimuli retested was 6 each for *Tsuyoshi* and *Raja*, and 12 for *Mamy*. We finished data collection for *Tsuyoshi* and *Raja* in 5 days (5 sessions), and for *Mamy* in 8 days (8 sessions). Track loss percentages were calculated for each trial; [(number of "eyes not found"/number of samplings during stimulus presentation) $\times$ 100]. The average track loss values were as follows; *Tsuyoshi* :32.7% $\pm$ 20.4 (SD), *Raja* :31.5% $\pm$ 20.5 (SD), *Mamy* :66.5% $\pm$ 18.4 (SD). The major reason for track loss was the participant looking away from the screen. The criterion was at least one fixation on each stimulus, as mentioned above. Therefore, if the track loss during stimulus presentation was 96% or less, the data were retained and no retest was conducted.

Data Analysis

Data from the first 200 msec of each presentation were discarded, thereby eliminating

fixations that might have begun before the stimulus onset (Kano et al., 2012). Before analyzing the eye-tracking data, we applied Tobii Pro Lab's I-VT fixation filter in the default setting (e.g., using binocular averages, discarding fixations shorter than 60 msec) to retain "true" fixations in the raw data. The following two settings were changed with reference to previous studies (e.g., Tsitsi et al., 2021): (1) 5-point median was used to reduce the level of noise (default: 3-point median); and (2) gap fill-in interpolation was used to compensate for short periods of missing data (default: gap fill-in interpolation disabled).

Each stimulus was divided into two areas of interest (AOI): image and background. Each region was 20 pixels larger than the precise outline to compensate for error in fixation point estimation. We used total fixation duration for each stimulus as a dependent variable indicating attention. Our data of total fixation duration for each AOI in each stimulus were continuous, with skewed distribution. The data contained many zeros, as participants did not look at the background for most stimuli. First, to test the difference between AOIs (image vs. background), a non-parametric Wilcoxon signed-rank test was used. Then, we focused on the total fixation durations while looking at images. To test the effect of image category (primate face vs. landscape) on total fixation duration, a linear mixed-effects model (LMM) was used. We assessed data normality using QQ-plots and histograms and by visual inspection. In the model, we considered image category as fixed effects and participants as random effects. We used R. 4.3.2 and GAMLj package (Galluci, 2019) in Jamovi 2.3.16 (The jamovi project, 2022) for statistical analysis. Jamovi is a free, open source, stand-alone software that uses R syntax, R. 4.1(R Core Team, 2021).

Results

We obtained successful eye movement recordings from all three gibbons based on their spontaneous looking behaviors. The data had a calibration accuracy standard of less than 1 degree, comparable to studies on great apes (Kano et al., 2012). Examples of eye tracking records are shown in Fig. 3. The overall mean total fixation duration per stimulus (presentation: 1,800 msec) was 609 ± 390 (SD) msec, and the mean total number of fixations was 4.25 ± 2.41 (SD). The mean duration of single fixations was 152 ± 74.6 (SD) msec.

Consistent with our prediction, all three gibbons viewed the images longer than background (means in msec: images=560.8, SEM=43.45, 95% CI= [474, 647]; background=47.2, SEM=9.37, 95% CI = [28.5, 65.9]). The analysis revealed significant effects of AOI (Wilcoxon signed-rank test, $Z=7.33$, $p<.001$). The gibbons looked at the image region, which covered 25% of the monitor, on average 91.3% of the time (SD=17.7, 95% CI= [87.2, 95.5]). The LMM revealed a significant effect of image category, $F(1, 68) = 6.56$, $p=.013$, Est = -198, SEM=77.2, 95% CI= [-349, -46.3] (Fig. 4). The gibbons viewed photos of nonhuman primate faces longer than landscapes (means in msec: face=660, SEM = 69.4, 95% CI = [519, 800]; landscape=462, SEM =47.9, 95% CI = [365, 559]).

Fig. 3, 4

Discussion

This study shows, for the first time, the feasibility of automated eye-tracking with gibbons. Even though the gibbons were studied in their familiar environment, with other gibbons living nearby, there was little extraneous interference with data collection. We took care to minimize potentially anxiogenic objects and events, and neither the studied gibbons nor the other gibbons showed any negative emotional reactions (e.g., alarm calls) during testing. All three participants sat still in front of the monitor, but measuring eye movements for the elderly (*Mamy*) was more difficult than for the two younger males, resulting in more retests and higher track loss occurrence for the former. Possible reasons for this include low interest in the stimuli used in this study, lack of monitor-viewing experience, and some type of age-related vision change. We aim to find a more suitable testing arrangement for this individual.

As predicted, the gibbons viewed the image area longer than the plain grey background. Both landscape and face photos contained more information than the background, and carried potentially interesting ecological and social information, respectively. Furthermore, the gibbons' looking behavior varied with image category (see similar findings in rhesus macaques, Machado et al., 2011 and in dogs, Somppi et al., 2012; Törnqvist et al., 2020). Specifically, face photos were viewed for longer, suggesting that, as in chimpanzees (Gonçalves, et al., 2022; Tomonaga & Imura, 2009; Tomonaga & Imura, 2015), humans (Di Giorgio et al., 2012), and dogs (Somppi et al., 2012), faces are especially effective at attracting and maintaining visual attention in gibbons. The effect occurred even though the presented face photos were of monkeys and lemurs, not gibbons. These results support proposals that primates experienced strong evolutionary pressure to pay attention to faces and that this attentional bias is not only restricted to

1 their own species' face but extends to a broader face category.

2 This study describes a new method for investigating looking behaviors of gibbons. The
3 feasibility of eye-tracking research in gibbons opens up new avenues for understanding
4 evolutionary pathways in the ape lineage, including hylobatids, particularly in the
5 cognitive domain, which has long been under-represented in the comparative
6 psychological literature. Topics that we aim to examine with the help of eye-tracking
7 include episodic memory, social cognition based on own-species face perception,
8 temporal characteristics of attention shifts, and auditory perception.

10 **Acknowledgements**

11 We express our sincere appreciation to Mr. Norihiko Maeda, Mr. Akihisa Kaneko, Ms.
12 Akemi Hirakuri, Ms. Etsuko Ichino, Ms. Tomoko Takashima, and everyone involved in
13 the care of the gibbons. We thank Dr. Ikuma Adachi and other members of his research
14 group for their assistance and comments during the experiments. Special thanks to Dr.
15 André Gonçalves for the technical advice on use of the eye-tracker and for his valuable
16 suggestions on earlier drafts of the manuscript. Our sincere appreciations to Dr. James
17 Anderson for all his advice and help in developing the manuscript. Finally, we sincerely
18 thank the editor and the anonymous reviewers for their constructive comments that led
19 to significant improvements of this paper.

21 **Funding**

22 This work was supported by the Grant-in-Aid for Scientific Research (B) to Yuko
23 Hattori (#20H04490) and the Grant-in-Aid for Scientific Research (C) to Makiko
24 Uchikoshi (#21K02949).

1

2 Author Contributions

3 Makiko Uchikoshi (MU), Lira Yu (LY), and Yuko Hattori (YH) conceived and
4 designed the experiment. MU prepared the stimulus photographs. MU and YH set up
5 the experimental environment. MU performed the experiment, created figures, and
6 prepared the manuscript. MU, LY, and YH analyzed the data, and authored or reviewed
7 drafts of the paper and approved the final draft.

References

- Brockelman, W.Y. 2009. Ecology and the social system of gibbons, in: Lappan, S., Whittaker D.J. (Eds.), The gibbons, new perspectives on small ape socioecology and population biology. Springer, New York, pp. 211-239.
https://doi.org/10.1007/978-0-387-88604-6_11
- Casper, K.R., Mader, L. Pallasdies, F., Lindenmeier M., Begall, S. 2018. Captive gibbons (*Hylobatidae*) use different referential cues in an object choice task: insights into lesser ape cognition and manual laterality. Peer J, 6 (4).
<https://doi.org/10.7717/peerj.5348>
- Cunningham, C.L., Anderson, J.R., Mootnick, A.R., 2006. Object manipulation to obtain a food reward in hoolock gibbons, *Bunopithecus hoolock*. Anim. Behav. 71, 621-629. <https://doi.org/10.1016/j.anbehav.2005.05.013>
- Di Giorgio, E., Turati, C., Altoè, G., Simion, F. 2012. Face detection in complex visual displays: an eye-tracking study with 3- and 6-month-old infants and adults. J. Exp. Child Psychol. 113, 66–77. <https://doi.org/10.1016/j.jecp.2012.04.012>
- Fan, P., Bartlett, T.Q. 2017. Overlooked small apes need more attention! Am. J. Primatol. 79, e22658. <https://onlinelibrary.wiley.com/doi/10.1002/ajp.22658>
- Galluci, M. 2019. GAMLj: General analyses for linear models. jamovi module.
- Geissmann, T. 2000. Gibbon songs and human music from an evolutionary perspective. in: Wallin, N., Merker, B., Brown, S. (Eds.), The origins of music. MIT Press, Cambridge, Massachusetts, pp. 103-123.
- Gonçalves, A., Hattori, Y., Adachi, I. 2022. Staring death in the face: chimpanzees' attention towards conspecific skulls and the implications of a face module guiding their behaviour. R. Soc. Open Sci.9210349210349

<http://doi.org/10.1098/rsos.210349>

Hanazuka, Y., Shimizu, M., Kurotori, H., Midorikawa, A. 2012. Visual discrimination in an orangutan (*Pongo Pygmaeus*): measuring visual preference. Percept. Mot. Skills. 114, 429-432. <https://doi.org/10.2466/22.24.PMS.114.2.429-432>

Hiwatashi, T., Mikami, A., Katsumura, T., Suryobroto, B., Perwitasari-Farajallah, D., Malaivijitnond, S., Siriaronrat, B., Oota, H., Goto, S., Kawamura, S. 2011. Gene conversion and purifying selection shape nucleotide variation in gibbon L/M opsin genes. BMC Evol. Biol. 11, 312. <https://doi.org/10.1186/1471-2148-11-312>

Huang, X., Guo, L., Zhang, G., 2023. Friend or foe? Using eye-tracking technology to investigate the visual discrimination ability of giant pandas. Curr. Zool. 20, 1-10. <https://doi.org/10.1093/cz/zoad020>

Huber, L., Lonardo, L., Völter, C. 2023. Eye tracking in dogs: achievements and challenges. Comp. Cogn. Behav. Rev.18, 33-58.

Hopper, L., Gulli, R., Howard, L., Kano, F., Krupenye, C., Ryan, A., Paukner, A. 2021. The application of noninvasive, restraint-free eye-tracking methods for use with nonhuman primates. Behav. Res. Methods. 53, 1003–1030. <https://doi.org/10.3758/s13428-020-01465-6>

Horton, K.E., Caldwell, C.A. 2006. Visual co-orientation and expectations about attentional orientation in pileated gibbons (*Hylobates pileatus*). Behav. Processes 72, 65-73. <https://doi.org/10.1016/j.beproc.2005.12.004>

Jakobsen, K.V., White, C., Simpson, E. A. 2021. General and own-species attentional face biases. Atten. Percept. Psychophys. 83, 187–198. <https://doi.org/10.3758/s13414-020-02132-w>

- 1 Kano, F., Tomonaga, M. 2009. How chimpanzees look at pictures: a comparative eye-
2 tracking study. *Proc. R. Soc. B.* 276, 1949–1955.
3 <http://doi.org/10.1098/rspb.2008.1811>
- 4 Kano, F., Call, J., Tomonaga, M. 2012. Face and eye scanning in gorillas (*Gorilla*
5 *gorilla*), orangutans (*Pongo abelii*), and humans (*Homo sapiens*): unique eye-
6 viewing patterns in humans among hominids. *J. Comp. Psychol.* 126, 388–398.
7 <https://doi.org/10.1037/a0029615>
- 8 Lewis, L.S., Krupenye, C.K. 2022. Eye-tracking as a window into primate social
9 cognition. *Am. J. Primatol.* 84. <https://doi.org/10.1002/ajp.23393>
- 10 Liebal, K., Kaminski, J. 2012. Gibbons (*Hylobates pileatus*, *H. moloch*, *H. lar*,
11 *Symphalangus syndactylus*) follow human gaze, but do not take the visual
12 perspective of others. *Anim. Cogn.* 15, 1211–1216.
13 <https://doi.org/10.1007/s10071-012-0543-5>
- 14 Machado, C.J., Bliss-Moreau, E., Platt, M.L., Amaral, D.G. 2011. Social and nonsocial
15 content differentially modulates visual attention and autonomic arousal in rhesus
16 macaques. *PLoS ONE*, 6: e26598. <https://doi.org/10.1371/journal.pone.0026598>
- 17 Munir, G. M., Nealen, P. M. 2023. Preliminary assessment of siamang (*Symphalangus*
18 *syndactylus*) cognition using digital cognition testing software and touchscreen
19 technology. *Anim. Behav. Cogn.* 10,14-39.
20 <https://doi.org/10.26451/abc.10.01.02.2023>
- 21 Myowa-Yamakoshi, M., Tomonaga, M. 2001a. Perceiving eye gaze in an infant gibbon
22 (*Hylobates agilis*). *Psychologia* 44, 24–30.
- 23 Myowa-Yamakoshi, M., Tomonaga, M. 2001b. Development of face recognition in an
24 infant gibbon (*Hylobates agilis*). *Infant Behav. Dev.* 24, 215–227.

1 [https://doi.org/10.1016/S0163-6383\(01\)00076-5](https://doi.org/10.1016/S0163-6383(01)00076-5)

2 Nakata, R., Eifuku, S. Tamura, R. 2018. Crucial information for efficient face searching
3 by humans and Japanese macaques. *Anim Cogn.* 21, 155–164.

4 <https://doi.org/10.1007/s10071-017-1148-9>

5 New, J., Cosmides, L., Tooby, J. 2007. Category-specific attention for animals reflects
6 ancestral priorities, not expertise. *PNAS.* 104, 16598-16603.

7 <https://doi.org/10.1073/pnas.0703913104>

8 R Core Team. 2021. R: A language and environment for statistical computing. (Version
9 4.1)

10 Somppi, S., Törnqvist, H., Hänninen, L., Krause, C., Vainio, O. 2012. Dogs do look at
11 images: eye tracking in canine cognition research. *Anim. Cogn.* 15, 163-74.

12 <https://doi.org/10.1007/s10071-011-0442-1>

13 Tanaka, M., Uchikoshi, M. 2010. Visual preference in a human-reared agile gibbon
14 (*Hylobates agilis*). *Primates* 51, 63-67. [https://doi.org/10.1007/s10329-009-](https://doi.org/10.1007/s10329-009-0175-9)

15 [0175-9](https://doi.org/10.1007/s10329-009-0175-9)

16 The jamovi project. 2022. Jamovi. Computer Software (Version 2.3).

17 Tomonaga, M., Imura, T. 2009. Faces capture the visuospatial attention of chimpanzees
18 (*Pan troglodytes*): evidence from a cueing experiment. *Front. Zool.* 6, 14.

19 <https://doi.org/10.1186/1742-9994-6-14>

20 Tomonaga, M., Imura, T. 2015. Efficient search for a face by chimpanzees (*Pan*
21 *troglodytes*). *Sci. Rep.* 5, 11437. <https://doi.org/10.1038/srep11437>

22 Törnqvist, H., Somppi, S., Kujala, M.V., Vainio, O. 2020. Observing animals and
23 humans: dogs target their gaze to the biological information in natural scenes.

24 *PeerJ.* 8: e10341. <https://doi.org/10.7717/peerj.10341>

- 1 Tsitsi, P., Benfatto, M.N., Seimyr, G.Ö., Larsson, O., Svenningsson, P., Markaki, I.
- 2 2021. Eye-tracking in Parkinson's disease diagnosis. J. Parkinsons Dis. 11, 865–
- 3 875.

Figure Captions

Fig. 1. Gibbon *Raja* looks through an acrylic window at a monitor. Isotonic water is continuously accessible from a tube attached to the window.

Fig. 2. Examples of presented photo stimuli. a) nonhuman primate face, b) landscape.

Fig. 3. Example of eye-tracking records: a & b) Gibbon scanpaths during stimulus presentation are drawn in a different color for each gibbon. Circles represent fixation points. The larger the point, the longer the fixation. c & d) Heatmaps of accumulated gaze records of three gibbons. Colors from green to yellow to red represent the absolute duration of fixations from low to high. Visualization was made using Tobii Pro Lab software (ver. 1.217).

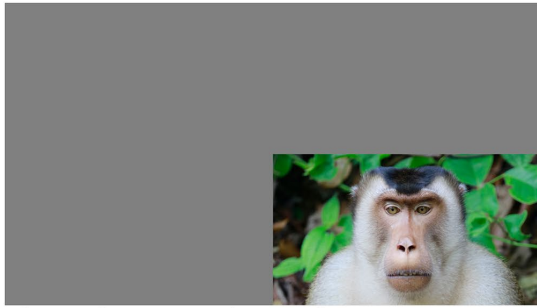
Fig. 4. Mean total fixation duration on the image for each image category. The error bar indicates SEM. The effect of image category is significant (LMM, $p=.013^*$).



1

2 Figure 1

3



a) nonhuman primate face

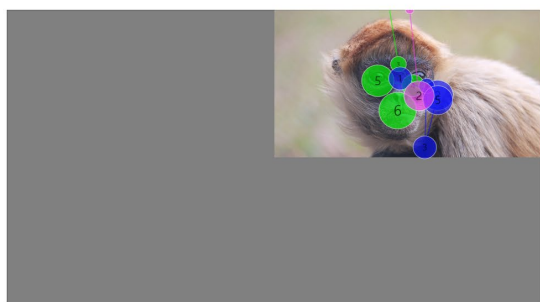


b) landscape

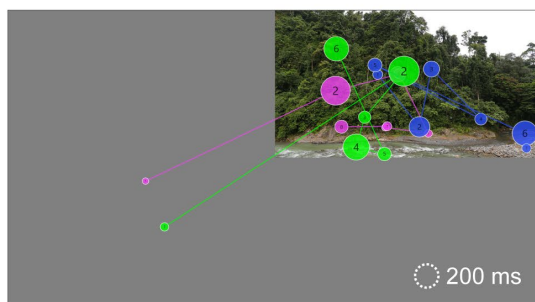
1

2 Figure 2

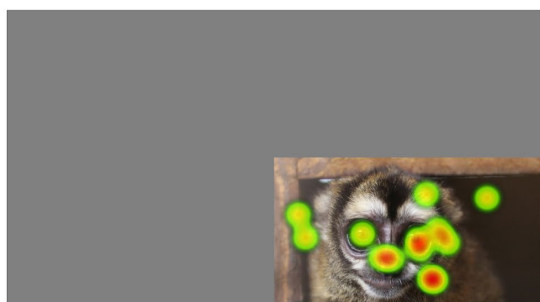
3



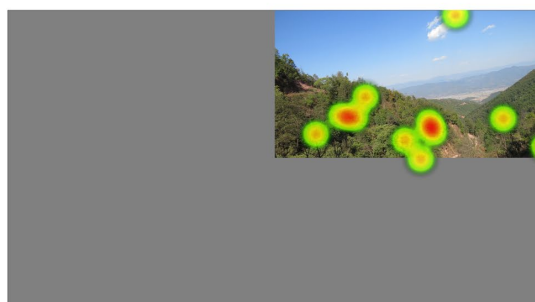
a)



b)



c)

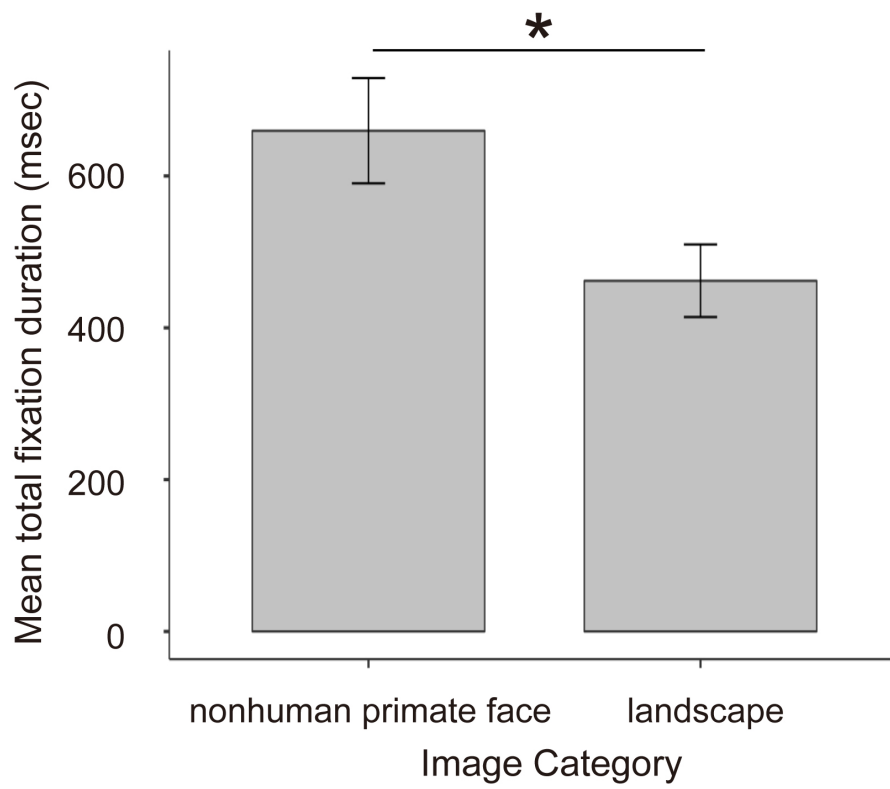


d)

1

2 Figure 3

3



1

2 Figure 4

3