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Gibbons (*Hylobates spp.*) Show Increased Attention to Eyes When Viewing Conspecific Faces: An Eye-Tracking Study

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Abstract – For humans, the face is a socially important visual stimulus, and the evolution of face perception has received considerable attention in research on non-human primates. However, little is known about face perception in gibbons, a key phylogenetic group among apes and humans. To address this gap, we used an eye-tracking device to examine how gibbons view face photographs, with the participation of three male adult gibbons. A total of 48 stimuli, consisting of gibbon and human faces showing neutral expressions were presented, and the gibbons were allowed to view them freely. Areas of interest (AOI) were defined for the eyes, nose, mouth, face periphery, and background in each image. We tested the effects of the AOIs and presented face species on viewing time. In analyses pooling data across individuals, gibbons spent significantly more time viewing the eyes than any other area and viewed gibbon eyes longer than human eyes. In separate analyses for each individual, two gibbons viewed the eyes significantly longer than the nose or mouth. Longer viewing times for gibbon eyes than human eyes were observed in all individuals. These results indicate that eyes are a highly salient facial feature for gibbons, albeit variably among individuals, and that gibbons' viewing patterns differ when looking at a conspecific or an allospecific face. These findings are consistent with face-scanning studies in macaques and great apes. Further studies are needed to confirm the generality of these results and to uncover other characteristics of gibbon face perception.

Keywords – Gibbons, Small apes, Eye-tracking, Face perception, Own-species bias

Investigating gibbon cognition could provide valuable insights into the phylogenetic origins of the human mind, considering these apes' phylogenetic position and uniqueness. However, gibbons are unrepresented in cognitive research (Munir & Nealen, 2023). Comprising four genera and 20 species, gibbons have evolved in their particular ecological niche after diverging from the common ancestor of humans and great apes (chimpanzees, bonobos, gorillas, and orangutans) around 17 million years ago (Carbone et al., 2014). Notably, they have a relatively small body size, specialized anatomical adaptations for arboreality, small group sizes based on monogamy with long-term pairing, and auditory communication called songs (Brockelman, 2009; Geissmann, 2000; Terleph et al., 2025).

Because social cognition is thought to be shaped by social structure (Maclean et al., 2013), comparisons of species that differ markedly in group size and social organization are informative. In this context, gibbons, the only apes with a predominantly pair-bonded social system and typically living in very small social groups, are a particularly valuable model for examining how variation in social structure relates

to differences in social cognition, and for comparisons with humans aimed at understanding the evolution of social cognition (Sánchez-Amaro et al., 2020). We previously reported successful application of eye tracking technology to gibbons, with the aim of developing research on their social cognition through their eye movements (Uchikoshi et al., 2024). In that study, gibbons looked at a screen quadrant containing a photographic image rather than the uniform gray background, and showed greater attention to faces than to landscapes. This suggests that in gibbons, as in humans and well-studied species such as rhesus macaques and great apes, eye movements can be used to measure cognitive and emotional processes, including visual-spatial attention, social information processing, and motivational states (Kano & Tomonaga, 2009).

Human adults are experts at recognizing faces, reflecting the central role of faces as social visual stimuli in everyday life (Maurer et al., 2002). Notably, the eye region attracts particular attention, containing a high density of information relevant to social perception and interaction (Itier & Batty, 2009). Face perception is a fundamental aspect of social cognition in monkeys and apes as well. Nonhuman primates have often been used as a model of human face perception (Leopold & Rhodes, 2010; Pascalis et al., 2021). Macaque monkeys, great apes, and humans show many similarities in eye movements when freely viewing photographs of faces, for example attending to the inner features of faces, especially the eyes, for longer durations and with earlier onset compared to other facial parts (Guo et al., 2003; Gothard et al., 2004; Kano et al., 2012). Some studies have reported differential sensitivity to conspecific and allospecific social stimuli (e.g., chimpanzees: Hattori et al., 2010; macaques and humans: Dahl et al., 2009; orangutans, gorillas, and humans: Kano et al., 2012), a phenomenon known as Own-Species Bias (Simpson et al., 2017). For example, Dahl et al. (2009) showed that both humans and rhesus macaques looked longer at the eyes of upright conspecific faces than allospecific faces.

Compared with the extensive body of research on humans, great apes, and macaques, relatively little is known about face processing in gibbons. Based on experiments conducted with a single infant, Myowa-Yamakoshi and Tomonaga (2001a, 2001b) suggested that gibbons may share similarities with humans in early face recognition, including a preference for face-like configurations and heightened sensitivity to the eye region. Although these findings imply a possible evolutionary continuity between humans and gibbons, knowledge about face perception in gibbons remains extremely limited, and no studies have yet examined face-viewing behavior in adult gibbons.

Our aim here was to examine how adult gibbons view faces. Considering evolutionary continuity, we hypothesized that gibbons would pay particular attention to the eyes when viewing photos of faces. We also asked if gibbons would express any bias toward conspecific faces.

Methods

Ethics Statement

All research procedures followed institutional guidelines (Primate Research Institute, 'The Guidelines for the Care and Use of Laboratory Primates' 3rd edition), 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 (#2022-051; #2023-157). All procedures adhered to the Japanese 'Act on Welfare and Management of Animals'.

Participants

Three adult male gibbons (*Hylobates spp.*), *Tsuyoshi*, *Raja*, and *Mamy*, participated in this study. At the start of data collection, *Tsuyoshi* and *Raja* (*Hylobates agilis* x *albibarbis*) were 23 years old, and *Mamy* (*Hylobates albibarbis*) was estimated to be 52 years old. *Tsuyoshi* and *Raja* were brothers, and *Mamy* was their biological father. All three individuals were reared by humans during their early life and interacted extensively with both humans and conspecifics, experiencing abundant daily exposure to the faces of both. They were housed at the Center for the Evolutionary Origins of Human Behavior, Kyoto University. Their daily diet consisted mainly of fresh fruits, vegetables, and seasonally available plants, and they were never

deprived of food or water. Although housed individually, they had constant opportunities for visual and auditory contact with each other, as well as limited tactile contact. The gibbon facility consists of four indoor cages, connected in circular fashion via aerial pathways and sliding doors, including the cage used for the experiment; however, access to the other cages was restricted during the experimental sessions.

Apparatus

The experiment was conducted in one indoor home cage, about 3 m wide, 2.5 m long, and 2.5 m high, which is used as part of the gibbons' regular housing. A Tobii TX300 eye-tracking device was used to record the gibbons' eye movements (300 Hz; Tobii Technology AB, Stockholm, Sweden). The eye tracker was connected to a 23-inch TFT monitor (ca 43° × 24°), on which photos were presented with Tobii Pro Lab software (ver. 1.181). The device was mounted on a wooden table with casters, and the distance between the monitor and the participant's face was approximately 65 cm. To encourage the gibbon to sit still and face the monitor, a licking tube was attached to an acrylic panel that separated the gibbon from the monitor; this tube regularly produced drops of isotonic water during the experiment (Figure 1).

Figure 1

A Gibbon, Tsuyoshi, Looking at the Monitor Through an Acrylic Window

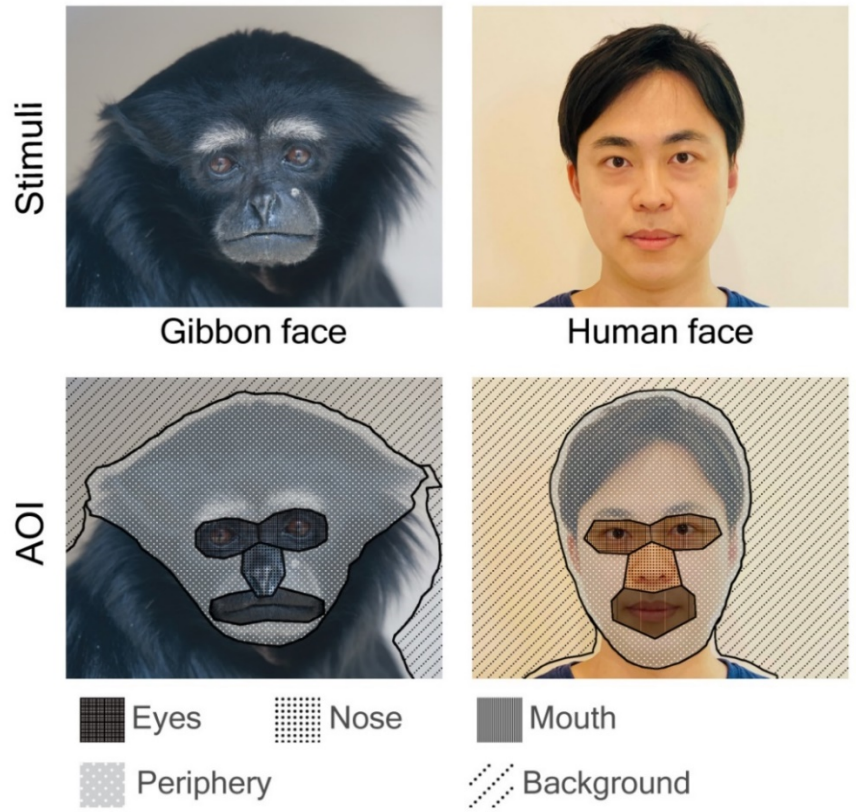
Note. Isotonic water is continuously accessible from a tube attached to the window.

Stimuli

Forty-eight color photos of faces were prepared, including 24 photos each of humans and gibbons (Figure 2). All photos showed a different adult individual, unfamiliar to the participants. Half of the photos showed male individuals of each species. Gibbon photos all showed the same genus as the participants (*Hylobates agilis*, *Hylobates muelleri*, *Hylobates lar*, *Hylobates pileatus*, *Hylobates moloch*). Photos were ca 31° x 24°, with no hair cropping or background manipulation. All photos were face-on portraits, showing neutral facial expressions, with eyes open and mouth closed.

Figure 2

Examples of *Stimulus* Face Photographs and Areas of Interest (AOI)



Note. The neck, shoulder, and other body parts were excluded from the analysis because this study focused on facial areas.

Procedure

The experiment relied on the gibbons' voluntary participation. 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. If the gibbon left the test position, the experimenter waited for several minutes and attempted to re-engage him through verbal cues. If he returned, the session continued; if not, the session was ended and no additional data were collected that day. Manual calibration was done at the start of each session by showing a short video clip in each opposing corner of the screen (two diagonal points). We set the calibration accuracy to less than 1°. If this accuracy was not obtained after several attempts, we reused the results of successful calibrations from previous sessions. Calibration results were reused in approximately one of every four sessions (For detailed methods, see Uchikoshi et al., 2024).

We conducted one session per day for each participant. Each session consisted of calibration and one to three trials. In each trial, one gibbon and one human face were presented in alternating order. Each photo was presented only once, each time for 3 s. Each session lasted between one and five minutes. The duration was kept brief to maintain interest in the images. If the participant showed insufficient attention to a photo (i.e., viewed it for less than 1 s), an additional trial with that photo was conducted after completion of all normal sessions. *Tsuyoshi* and *Raja* viewed all 48 photos over 25 and 27 days, respectively. *Mamy* participated for 13 days and completed half of the stimuli before data collection was terminated for health reasons. In total, we collected eye movement data from the three gibbons for 120 stimuli.

Data Analysis

Data collected during the first 200 ms of each presentation were excluded from the analysis, 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 ms) to retain only "true" fixations. The following two settings were changed: (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 photo was divided into five Areas of Interest (AOI), each 20 pixels larger than the precise outline of the relevant features to compensate for error in fixation point estimation. Each photo was divided into eyes, nose, mouth, face periphery, and background (Figure 2).

The proportion of viewing time for each AOI was calculated with respect to viewing time for the entire scene. Out-of-scene fixations were excluded from the analyses (6.7% of all fixations). To compensate for differences in AOI area sizes, viewing time was normalized by subtracting the proportion of area size from the proportion of viewing time, using the same computational methods as in previous studies (Dahl et al., 2009; Hirata et al., 2010; Kano et al., 2012), so that chance level was at zero. Any significant difference in viewing time from zero indicates that the AOI was looked at more or less than predicted by a uniform looking distribution.

Viewing time was not normally distributed (Shapiro–Wilk test), and its distribution around zero with both positive and negative values complicated the specification of appropriate GLMM distributions. Therefore, nonparametric statistical tests were used. The effect of AOIs on viewing times was analyzed using the Friedman test. When a significant main effect was found, pairwise comparisons between AOIs were performed using the Wilcoxon signed-rank test with Bonferroni correction. To examine whether the gibbons viewed inner facial features of gibbons and humans differently, we conducted Wilcoxon signed-rank tests comparing viewing times for the eyes, nose, and mouth regions within each trial. For these tests, we reported the exact statistic (W) when $N < 30$ and the standardized z-value when $N \geq 30$. Primary analyses were conducted on pooled data across three individuals and followed by separate analyses for each individual. AOI effects for male and female faces were examined separately using pooled data only. Unless otherwise specified, all tests were two-tailed, and statistical significance was set at $p < .05$. Jamovi 2.6.44 and R 4.4.1 software were used for statistical analysis.

Results

As basic information, total fixation duration per photo was $M = 1.51$ s ($SD = 0.49$), 95% CI [1.41, 1.61]. Single fixation duration was $M = 169.28$ ms (SD = 78.60), 95% CI [163.95, 174.62], and saccade size was $M = 6.60$ ° (SD = 4.71), 95% CI [6.31, 6.90].

Effect of AOIs on Viewing Times

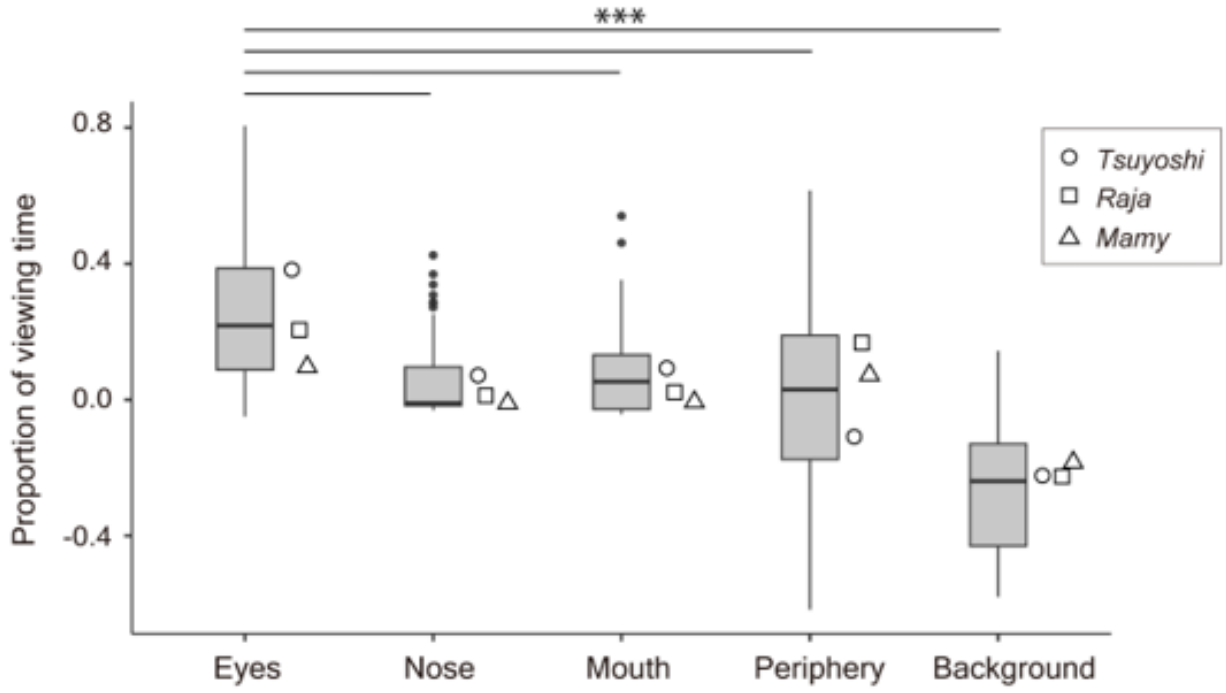
Analysis revealed significant differences in viewing times among the AOIs (χ^2 (4) = 228.21, N = 120, $p < .001$, $r = .69$). Post-hoc tests indicated that the gibbons spent significantly more time viewing the eyes than any other AOI ($N = 120$). Viewing time for the eyes was longer than the nose ($z = 7.32$, $r = .67$), mouth ($z = 7.14$, $r = .65$), face periphery ($z = 5.37$, $r = .49$), and background ($z = 9.50$, $r = .87$; all ps < .001) (Figure 3). Figure 4 shows examples of heat maps depicting which parts of the face gibbons looked at.

When the analyses were conducted separately for each individual, significant effects of AOI on viewing time were found for all three gibbons (χ^2 (4) = 130.38, 114.48, and 33.60; Ns = 48, 48, and 24; rs = .82, .77, and .59 for *Tsuyoshi*, *Raja*, and *Mamy*, respectively; all ps < .001). For *Tsuyoshi*, all pairwise comparisons involving the eyes were significant ($N = 48$): viewing time for the eyes was longer than the nose ($z = 5.80$, $r = .84$), mouth ($z = 5.86$, $r = .85$), face periphery ($z = 5.92$, $r = .85$), and background (z = 6.03, $r = .87$; all ps < .001). For *Raja*, viewing time for the eyes was significantly longer than for the nose

(z = 5.22, r = .75), mouth (z = 4.66, r = .67), and background (z = 6.03, r = .87; all ps < .001), but not face periphery (z = .52, p = .60; N = 48). For *Mamy*, post-hoc tests indicated a significant difference only between the eyes and the background (N = 24, W = 2, p < .001). Comparisons between the eyes and the nose (W = 147), mouth (W = 135), and face periphery (W = 115) were not significant (ps = 1.00). The median viewing times for each AOI, calculated separately for each individual, are shown in Figure 3.

Figure 3

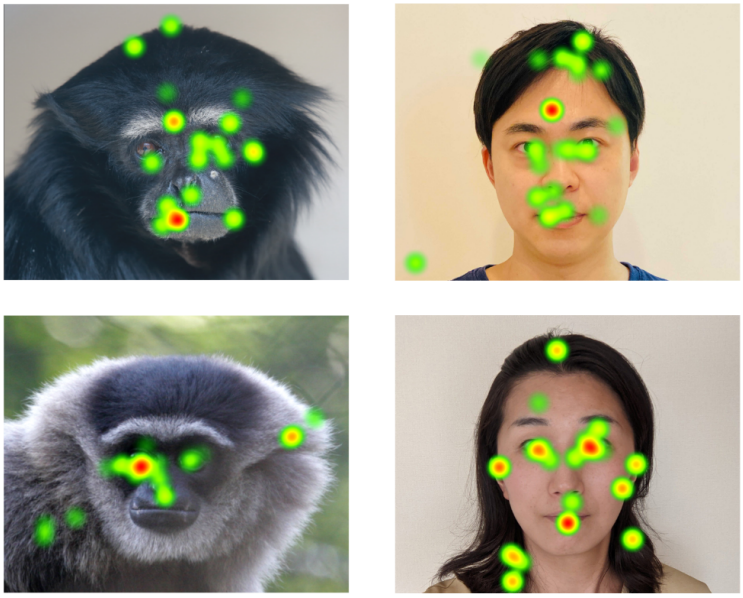
Viewing Times for each AOI for Gibbon and Human Photos



Note. A difference greater than 0 in viewing time indicates that the area was looked at more than or less than predicted by a uniform viewing distribution. Box-plots show data pooled across individuals; symbols to the right of each box plot indicate individual medians (○ *Tsuyoshi*, □ *Raja*, △ *Mamy*). Asterisks indicate statistically significant differences based on the pooled data from the three individuals.

Figure 4

Examples of Heatmaps Visualizing where the Gibbons looked at the Face Stimuli



Note. Cumulative data for three individuals. The colors green to yellow to red represent relative fixation duration from shorter to longer. In grayscale, longer durations correspond to darker shades, whereas shorter durations correspond to lighter shades.

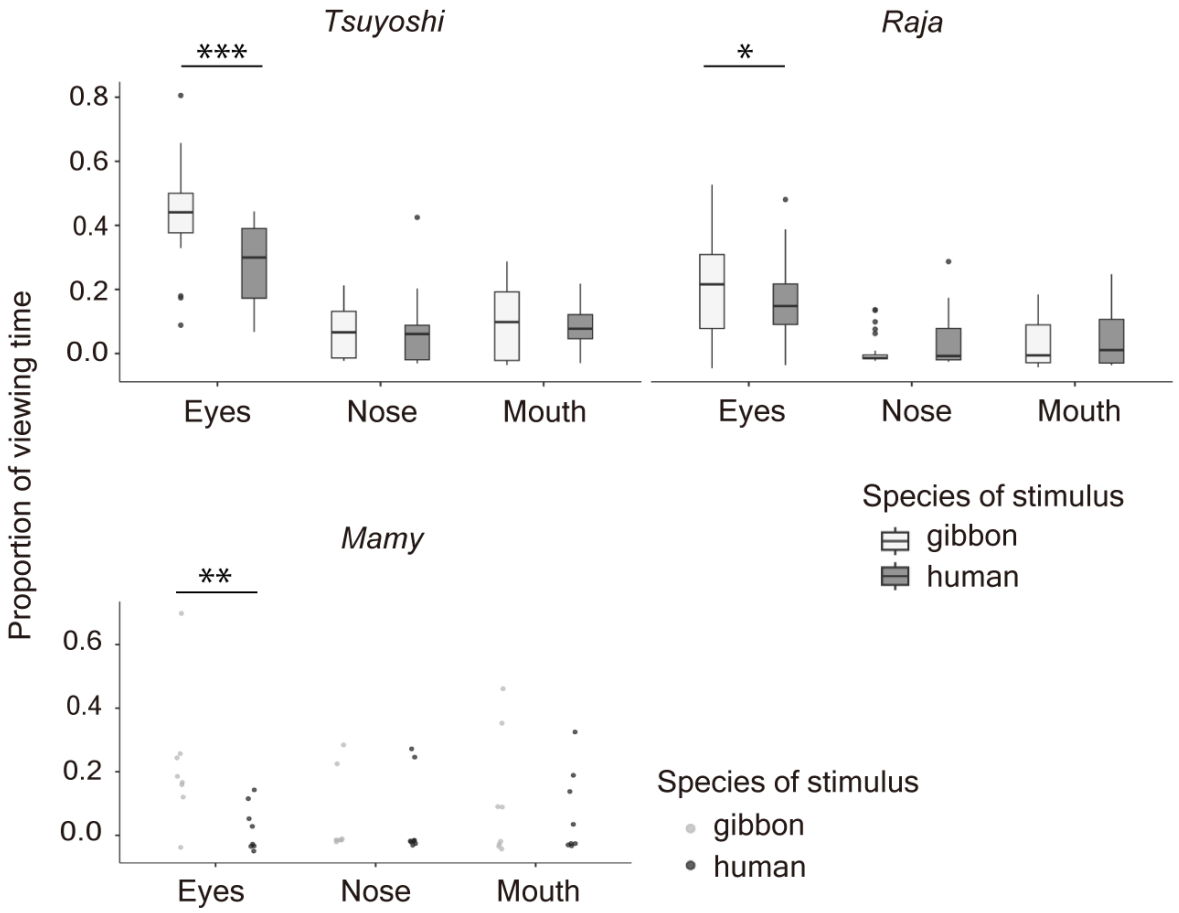
To examine whether the effect of AOIs on viewing time differed with the sex of the face stimuli, we conducted separate analyses for male and female faces. The overall pattern of results was consistent across stimulus sex. Significant effects of AOI on viewing time were found for both male (χ^2 (4) = 103.05, N = 59, p < .001) and female faces (χ^2 (4) = 125.84, N = 61, p < .001). Post-hoc comparisons indicated that, in both analyses, gibbons spent significantly more time viewing the eyes than the nose, mouth, face periphery, and background (all ps < .001). Specifically, for male face stimuli, viewing time was longer for the eyes than the nose (z = 5.08, r = .66), mouth (z = 4.89, r = .64), face periphery (z = 3.54, r = .46), and background (z = 6.67, r = .87). Similarly, for female face stimuli, viewing time was longer for the eyes than the nose (z = 5.23, r = .68), mouth (z = 5.20, r = .67), face periphery (z = 4.01, r = .51), and background (z = 6.79, r = .87).

The Effect of Species on Viewing Time

Gibbons viewed the eyes of gibbons longer than the eyes of humans (N = 56, z = 4.32, p < .001; r =.58). No significant differences were found for the nose (z =.21, p = .84) or mouth (z = .22, p = .82). When the analyses were conducted separately for individual animals, all three showed a pattern consistent with the pooled-data analysis: they viewed the eyes of gibbons significantly longer than the eyes of humans (*Tsuyoshi*: N = 24, W = 30, p <.001, r =.75; *Raja*: N = 24, W = 91, p = .048, r = .34; *Mamy*: N = 8, W = 1, p =.008, r = .85). For these individual-level tests on eye viewing time, one-tailed tests were used, reflecting the a priori directional hypothesis. No species-related differences were found for the nose or mouth in any individual (*Tsuyoshi*: nose, N = 24, W = 142, p = .83; mouth, N = 24, W = 130, p = .58; *Raja*: nose, N = 24, W = 125, p = .51; mouth, N = 24, W = 126, p = .51; *Mamy*: nose, N = 8, W = 13, p = .55; mouth, N = 8, W = 12, p = .46) (Figure 5).

Figure 5

Comparison of Viewing Times for Inner Facial Features of Gibbon and Human Faces in Three Individuals



Note. For *Mamy*, individual data points are shown instead of box plots because the sample size was small ($N = 8$).

Discussion

Our results from a pooled-data analysis based on three gibbons indicate that the eyes are the most salient feature for gibbons when viewing face photos, consistent with previous reports of strong visual attraction toward eyes in macaque monkeys, great apes, and humans (Emery, 2000; Guo et al., 2003; Kano et al., 2012). This finding suggests that gibbons share a common visual attention pattern with these species in this respect. However, individual-level analyses revealed variation in eye saliency across individuals. *Tsuyoshi* showed the clearest eye saliency, with significantly longer viewing times for the eyes than for all other facial regions. In contrast, *Raja* exhibited a more differentiated pattern: viewing times for the eyes were longer than those for the nose and mouth, but did not differ significantly from those for the face periphery. The color patterns of the gibbons' head and facial fur, along with humans' hairstyles, indicate species, sex, and individual characteristics. Unlike *Tsuyoshi*, *Raja* may have looked preferentially at these peripheral facial features of individuals encountered for the first time. *Mamy* showed no clear bias for the eyes relative to other facial regions, but notably completed only half as many trials as the other two individuals, which may have reduced statistical power. Together, our findings suggest that eye saliency may not be uniformly expressed across all individual gibbons.

What benefits might be gained from focusing on other individuals' eyes? Although eye movement and orientation are referred to in gibbons' behavioral repertoire (Baldwin & Teleki, 1976), the role of eye contact in their communication remains largely unstudied. Several reports describe eye contact during sexual behavior (Barelli et al., 2008; Mootnick & Baker, 1994), and it therefore seems likely that it is also used in other social contexts. Primates in face-to-face situations may convey information about some mental states such as interest, desire, rejection, or acceptance through eye signals (Emery, 2000; Whitham et al., 2024). Although the effect of AOI on viewing time appeared consistent across male and female face stimuli, we did not directly test for preferences for male versus female faces. Further eye tracking research involving presentation of various types of social stimuli and cues will help deepen our understanding of gibbons' visual attention and perception.

We also found that gibbons express different looking patterns for different social stimuli, namely conspecific and allospecific faces, as has also been reported in macaques, great apes, and humans (Dahl et al., 2009; Gothard et al, 2009; Hattori et al., 2010; Kano et al., 2012). The gibbon participants viewed conspecific eyes for longer than human eyes, despite their extensive experience with humans during early rearing. This finding suggests that gibbons may also have an Own-Species Bias when viewing faces. Further research should investigate how early rearing conditions and social experiences shape visual attention in gibbons and other primates.

This study provides new evidence on face scanning in gibbons and demonstrates the practicality of eye-tracking technology for studying these apes. It is a stepping stone toward progress in the study of social cognition in gibbons. However, only three male gibbons were tested. A more complete picture of facial processing in hylobatids requires further data, in particular from individuals raised naturally in social groups, both sexes, more species, and all four genera. Direct comparisons with other primate species are also needed.

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

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Conflict of Interest: The authors declare no competing interests.

Data Availability: Data are available from the corresponding author upon reasonable request.

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