Emotion

Monkeys Preferentially Process Body Information While Viewing Affective Displays

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BRIEF REPORT

Monkeys Preferentially Process Body Information While Viewing Affective Displays

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Despite evolutionary claims about the function of facial behaviors across phylogeny, rarely are those hypotheses tested in a comparative context—that is, by evaluating how nonhuman animals process such behaviors. Further, while increasing evidence indicates that humans make meaning of faces by integrating contextual information, including that from the body, the extent to which nonhuman animals process contextual information during affective displays is unknown. In the present study, we evaluated the extent to which rhesus macaques (*Macaca mulatta*) process dynamic affective displays of conspecifics that included both facial and body behaviors. Contrary to hypotheses that they would preferentially attend to faces during affective displays, monkeys looked for longest, most frequently, and first at conspecifics' bodies rather than their heads. These findings indicate that macaques, like humans, attend to available contextual information during the processing of affective displays, and that the body may also be providing unique information about affective states.

Keywords: Macaca mulatta, nonhuman primate, face perception, affect perception, naturalistic displays

It is widely believed that facial behaviors communicate veridical information about primate emotions (Chevalier-Skolnikoff, 1973; Ekman, 1972; Keltner & Ekman, 2000; Preuschoft, 1992; Shariff & Tracy, 2011; Visalberghi, Valenzano, & Preuschoft, 2006). Yet, a growing human literature suggests that the story is more complicated. For example, humans use contextual information to help understand facial behaviors. Providing perceivers with linguistic labels, conceptual information, or narrative or visual information about the context in which displays occur shifts how accurately they are able to categorize facial behaviors associated with emotions (Barrett & Gendron, 2016; Barrett, Lindquist, & Gendron, 2007; Hassin, Aviezer, & Bentin, 2013). Contextual information is so powerful that it even drives whether people accurately catego-

rize facial displays as being associated with positive or negative affective states (Kayyal, Widen, & Russell, 2015). Increasing evidence from humans indicates that contextual information—especially information about the body—influences how we understand facial behaviors (Hassin et al., 2013). The body also appears to communicate information about an individual's emotion (de Gelder, 2006; de Gelder, de Borst, & Watson, 2015; Klin, Jones, Schultz, Volkmar, & Cohen, 2002; Kret & de Gelder, 2010; Kret, Stekelenburg, de Gelder, & Roelofs, 2017; Riby & Hancock, 2008; Smilek, Birmingham, Cameron, Bischof, & Kingstone, 2006; for reviews see Hassin et al., 2013; Enea & Iancu, 2016). Given the strong evolutionary claims made about homologies of emotion-related facial behaviors (Ekman, 1972; Keltner & Ekman, 2000; Shariff & Tracy, 2011) and the importance of bodies for communicating social information (Holland, Wolf, Looser, & Cuddy, 2017) in the absence of comparative data, evaluating how nonhuman primates process information about bodies during affective displays is critically important for establishing strong evolutionary theory. Macaque monkeys, the most widely used species in research (Carlsson, Schapiro, Farah, & Hau, 2004), like humans, have a broad repertoire of stereotyped facial behaviors and body postures (Andrew, 1963; Bliss-Moreau & Moadab, 2017; Chevalier-Skolnikoff, 1973; Hinde & Rowell, 1962; Maestripieri, 1997; Redican, 1975; van Hooff, 1967) that are often assumed to be expressions of emotions (but see Bliss-Moreau & Moadab, 2017). The extent to which they use contextual information, including that related to the body, to make meaning of facial behaviors is unknown.

While the extent to which macaques' process body information during affective displays in unknown, information about the body modulates human emotion perception (Aviezer et al., 2008;

Meeren, van Heijnsbergen, & de Gelder, 2005). For example, when human faces, isolated without context, are thought to convey "disgust" are placed on bodies that convey other emotions (e.g., "fear", "anger", "sadness"), accurate categorization of the face drops significantly (e.g., only 11% categorized correctly when presented with an "angry" body) (Aviezer et al., 2008; for a review, Hassin et al., 2013). Yet, visual attention to static human faces engaged in emotion-related behavior was greater than visual attention to static human bodies engaged in emotion-related behavior (Kret, Stekelenburg, Roelofs, & de Gelder, 2013; Shields, Engelhardt, & Ietswaart, 2012).

Despite the importance of understanding how body information, and contextual information more generally, influences emotion perception, and the strong evolutionary claims that are made about the importance of facial behaviors for communicating emotions, few studies have tested macaques with dynamic, content-rich stimuli that mimic naturalistic affective displays. Instead, macaques are typically tested with static and/or isolated facial behaviors lacking contextual information—including bodies (Dahl, Logothetis, Bulthoff, & Wallraven, 2010; Dal Monte, Noble, Costa, & Averbeck, 2014; Deaner, Khera, & Platt, 2005; Gibboni, Zimmerman, & Gothard, 2009; Guo, Robertson, Mahmoodi, Tadmor & Young, 2003; Gothard, Erickson, & Amaral, 2004; Hanley, McPhillips, Mulhern, & Riby, 2012; Hirata, Fuwa, Sugama, Kusunoki, & Fujita, 2010; Keating & Keating, 1982; Leonard, Blumenthal, Gothard, & Hoffman, 2012; Machado, Whitaker, Smith, Patterson, & Bauman, 2015; Paukner, Bower, Simpson, & Suomi, 2013; Wilson & Goldman-Rakic, 1994). Brain regions supporting perception of bodies generating affective displays appear to be homologous across macaques and humans (de Gelder & Partan, 2009), suggesting homology in perceptual processes. Yet, only a few studies include faces and bodies, and those that do used static images. For example, when rhesus macaques (*Macaca mulatta*) were shown static images of full bodied conspecifics with neutral faces (i.e., those with no affect-related display), they looked longest and most frequently at hands (Hu et al., 2013). When viewing static positive or negative affective content, rhesus monkeys spent more time looking at faces relative to bodies (McFarland et al., 2013). Whether this effect is driven by affective content is not clear because there was no neutral condition.

Methodological choices, like testing macaques only with isolated faces or static conspecific images, leaves open questions about whether macaques integrate other information (such as body posture, context, social environment, etc.) with the face to understand intentions and actions. Evidence from the human literature indicates that dynamic facial behaviors are perceived as more intense, arousing, and realistic than static facial behaviors (Krumhuber, Kappas, & Manstead, 2013). In daily life, both humans and macaques must understand the intentions and actions of conspecifics whose behavior is dynamic, not static. Thus, evaluating how macaques process dynamic, naturalistic affective displays should provide ethologically relevant insights about the nature of emotion-related communication.

As a first step toward understanding how macaques use contextual information to make meaning of facial behaviors, we tested the hypothesis that rhesus macaques attend to information other than the face—specifically the body—during realistic, dynamic affective displays. We hypothesized that subjects would look longest, most frequently, and first at the face/heads of conspecifics

engaged in affective displays, but would also pay significant attention to their bodies (that is, fixation durations and frequencies for bodies would be nonzero). Further, we hypothesized that attention to the whole conspecifics (faces plus bodies) would be greatest when conspecifics engaged in affective behaviors relative to neutral behaviors; this effect would also manifest in less time attending to information other than the conspecifics (e.g., the conspecific's caging, filming backdrop, etc.) for videos with affective content as compared to neutral content.

Method

Experimental procedures were carried out at the California National Primate Research Center (CNPRC) at University of California Davis (UC Davis) and were approved by the UC Davis Institutional Animal Care and Use Committee in accordance with the recommendations in the Guide for the Care and Use of Laboratory Animals of the National Institutes of Health.

Subjects and Living Conditions

Subjects were six adult male rhesus macaques ($M = 7.39$, $SD = 1.29$) that were born into large, seminaturalistic social groups (ranging from 60–150 monkeys/group living in 0.2 hA; 30.5 m × 61.0 m × 2.4 m) at the CNPRC. All subjects lived in these groups for at least 2 years before being relocated in to indoor housing. Due to compatibility issues, one animal had no access to a social partner during the duration of his participation in the experiment. The other animals were paired with a compatible male social partner and housed in standard caging (size based on animal weight). They had access to their social partner either 6 hours per day, 5 days a week, or 24 hours/day depending on pair compatibility. Pairs were allowed to interact either in full contact or restricted contact through a one-inch mesh grate. Animal rooms were maintained at 17.78–28.89 °C and on a 12-hr light–dark cycle (lights on at 0600). Subjects were fed twice daily (Lab Diet #5047, PMI Nutrition International INC, Brentwood, MO), provided with fresh produce biweekly, had access to water ad libitum and a variety of enrichment devices.

Experimental Protocol

Animal training, equipment, and experimental stimuli are fully detailed in previous publications (Bliss-Moreau, Machado, & Amaral, 2013; Machado, Bliss-Moreau, Platt, & Amaral, 2011). We analyzed attention associated with a subset of the social videos from Bliss-Moreau et al. 2013; Machado et al. 2011—the "subject-directed" videos (see Figure 1) in greater detail. Subject-directed videos were 30-s videos in which a single conspecific generated affective or nonaffective behaviors toward the camera. Videos included multiple "scenes" that featured different conspecifics, but each scene only had one conspecific. Conspecifics and subjects had never physically interacted but may have been housed in the same room and been in visual contact at periods of time prior to the experiment. Monkeys viewed 60 videos that belonged to one of three categories: aggressive (including threats, cage displays, etc.), submissive (including bared teeth displays, lipsmacks, submissive body postures, etc.) or neutral (including movement within the cage such as walking, hanging, foraging, etc., but no facial or body
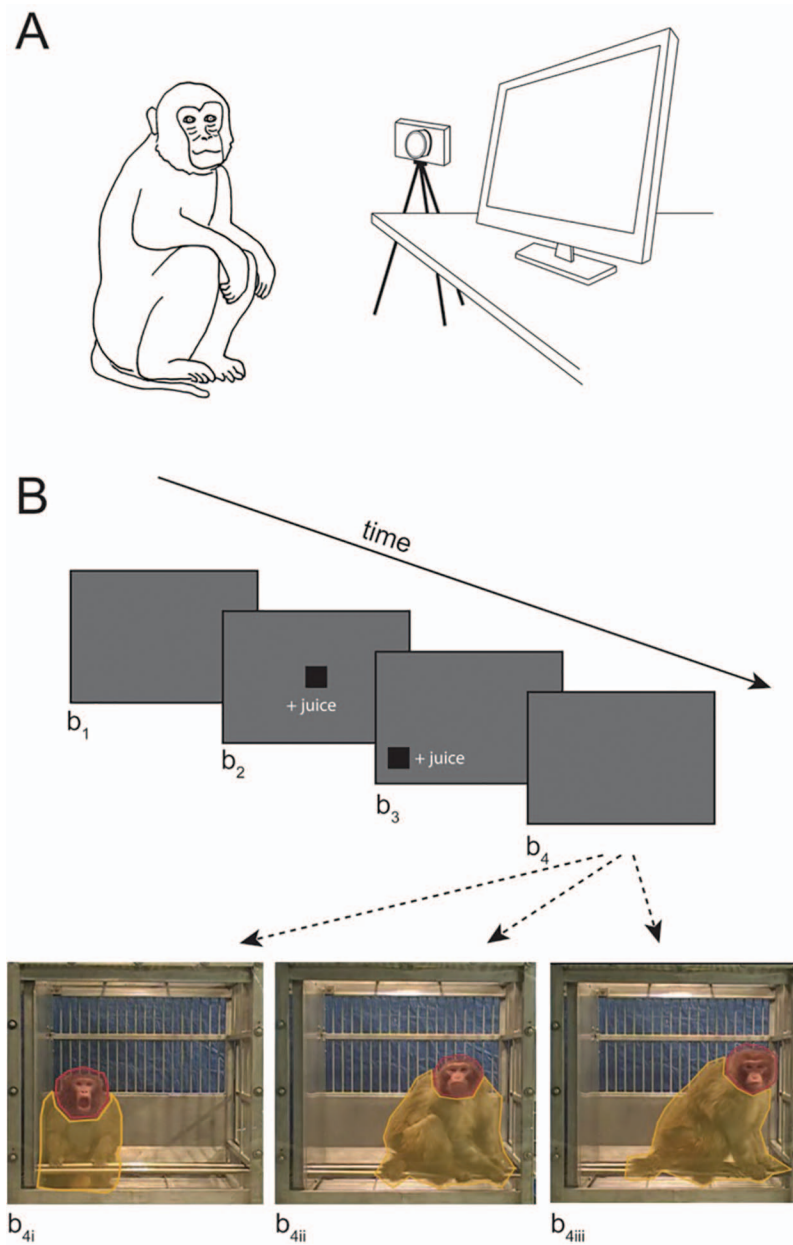
Figure 1. Experimental design. (A) Testing occurred with subjects seated in a box chair, with their heads secured using custom-fit thermoplastic helmets and their arms and feet were tethered and secured comfortably to the chair using leather straps (1.3 cm × 3 mm × 1 m). Subjects sat in front of an infrared eye tracker, depicted here as a camera (Applied Science Laboratories, Bedford, MA; Model R-HS-S6; positioned 53.34 cm from the animals' eyes) and a large computer monitor (60.96 cm diagonal; Gateway Inc., Irvine, CA; positioned 127 cm from the animal's eyes) in a darkened sound attenuated chamber (Acoustic Systems, Austin, TX; 2.1 m × 2.4 m × 1.1 m). Auditory distractions were masked with a white-noise generator (60 dB). (B) The experiment began with a gray screen for 10 s (b_1), followed by a fixation target in the center of the screen (b_2), and a fixation target at the periphery of the screen (b_3). Each fixation screen required that the subjects fixate on the target for at least 500 ms before advancing to the next screen. Successful fixation was rewarded with juice dispensed from an automatic juice dispenser (Crist Instrument Co., Inc.; model # 5-RLD-E3) with curved mouthpiece (Crist Instrument Co., Inc.; model # 5-RLD-00A) attached to the top-left of the chair. Thirty-second videos were presented after the second target fixation (b_4). For the present report, we analyzed data from videos in which a single conspecific engaged in aggressive (b_{4i}), submissive (b_{4ii}), and neutral (b_{4iii}) behaviors. ROIs were drawn around the conspecific's head (red; [dark gray]) and body (yellow; [light gray]). See the online article for the color version of this figure.

posture displays). Daily test sessions included three phases: (a) calibration—eye-tracker was calibrated for each monkey by having him fixate on small videos presented in nine positions on the monitor; (b) test-chamber acclimation—animals watched ten 30-s video screen-savers to acclimate them to the test area and (c) the experimental phase (see Figure 1 for details) which consisted of 50 videos per day. Testing occurred over 12 days.

Eye-Tracking Data Collection and Processing

Foveal gaze location and duration data were used to infer visual attention specific to two ROIs within each subject-directed video, rather than global attention to entire video (as previously analyzed in Machado et al., 2011). ROIs were hand drawn on each frame of the 30-s video using Applied Science Laboratory (ASL) software (Results Plus, Bedford, MA). Fixation and dwell data for each ROI were extracted using Results Plus with the default settings. Fixation onset occurred when gaze coordinates remained within a $1° \times 1°$ visual angle for 100 ms and terminated when gaze coordinates left that space for greater than 360 ms. Total fixation duration was calculated from the summation of each individual fixation within each ROI for each video (i.e., 30-s max). The number of unique fixations was totaled for each ROI for each video.

Data Analysis Strategy

Statistical analyses were completed using IBM SPSS Statistics version 23 (IBM Corp. Armonk, NY) Data were evaluated for non-normality and corrected when appropriate as indicated below. When Mauchly's Test of Sphercity was significant, we used Greenhouse-Geisser corrected degrees of freedom. We used a series of repeated measures ANOVAs with video type (submissive, aggressive, or neutral) and ROI (head, body) as the repeated factor. It is important to note that because the videos included a substantial amount of space outside the head and body, looking at the head or body was not necessarily a zero-sum trade off.

Results

Fixation Duration

A main effect of affective content indicated that fixation duration differed based on the meaning of the conspecifics' behaviors, $F(2, 20) = 5.98$, $p = .020$, $\eta_p^2 = 0.54$. Subjects fixated for significantly longer on videos with neutral content as compared to videos with affective content; neutral > aggressive: $t(5) = 2.74$, $p = .041$, $d = 1.16$; neutral > submissive, $t(5) = 2.79$, $p = .039$, $d = 0.93$. There was not a significant difference between the two conditions with affective content, $t(5) = 0.20$, $p = .846$, $d = 0.03$. This main effect of affective content was influenced by an interaction with ROI, $F(2, 10) = 79.40$, $p < .0001$, $\eta_p^2 = 0.94$. Contrary to our hypotheses, while viewing both videos of aggressive or submissive conspecifics, subjects fixated for longer durations on bodies than heads. In contrast, while watching the neutral conspecifics, subjects fixated longer on their heads than their bodies. There was no significant main effect of ROI, indicating that across all videos, subjects fixated for equal durations on heads and bodies, $F(1, 5) = 0.35$, $p = .58$, $\eta_p^2 = 0.07$. See Figure 2A.

Fixation Frequency

Patterns of fixation frequency mirrored that of fixation duration, revealing a significant Affective Content × ROI interaction, $F(2, 10) = 50.73$, $p < .001$, $\eta_p^2 = 0.91$ that was not consistent with our hypotheses. While viewing aggressive or submissive conspecifics, subjects fixated more frequently on their bodies than heads. In contrast, while viewing neutral conspecifics, subjects fixated more frequently on their heads than bodies. Neither the main effect of video type nor ROI were significant, indicating that across all trials subjects fixated equally often on aggressive, submissive, and neutral videos, $F(2, 10) = 0.40$, $p = .68$, $\eta_p^2 = 0.07$ and at comparable frequencies on both heads and bodies, $F(1, 5) = 2.75$, $p = .16$, $\eta_p^2 = 0.35$. See Figure 2B.

First Fixation Latency

We next evaluated whether affective content might influence whether subjects looked at heads or bodies first, by evaluating the latency to first fixation. Subjects fixated first on conspecifics' bodies on average, as indicated by a main effect of ROI, $F(1, 5) = 8.36$, $p = .034$, $\eta_p^2 = 0.63$. Importantly, this was only true for videos depicting aggressive and submissive affective behaviors as indicated by a significant affective content × ROI interaction, $F(2, 10) = 13.71$, $p = .001$, $\eta_p^2 = 0.73$. For videos in which conspecifics generated affectively neutral behaviors, the latency to fixate first on heads and bodies were statistically equivalent. Affective content did not significantly influence how quickly subjects made their first fixations, $F(2, 10) = 1.08$, $p = .38$, $\eta_p^2 = 0.18$—that is, the presence of affective behavior did not capture attention more rapidly (Figure 2C).
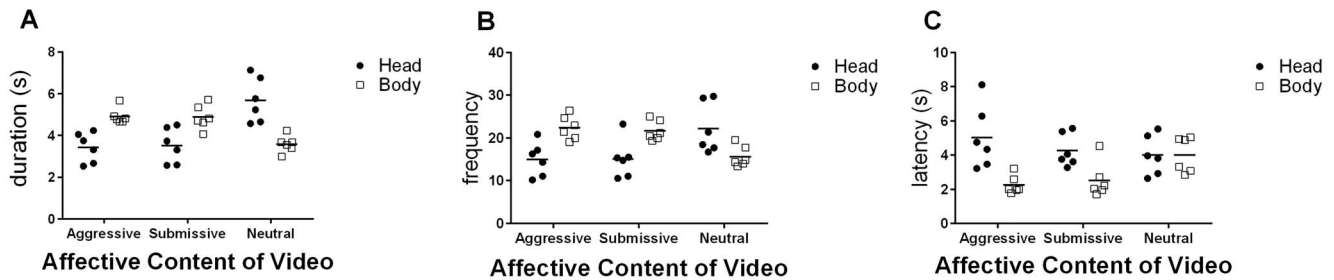
Nonconspecific Fixations

Finally, we evaluated whether attention to regions other than the conspecifics (i.e., all areas of the video outside of the head + body; e.g., caging) varied by affective content. Affective content did not significantly influence either the duration or frequency of fixations on areas other than the conspecifics' heads and bodies, $F(2, 10) = 0.243$, $p = .789$, $\eta_p^2 = 0.046$, and $F(2, 10) = 1.75$, $p = .224$, $\eta_p^2 = 0.26$, respectively. See Figures 2D and 2E. Taken together, these analyses suggest that attention allocation to regions other than the conspecifics was similar for both affective and neutral information.

Discussion

Across several metrics of attention, our data demonstrate that not only do rhesus macaques attend to the bodies of conspecifics during dynamic affective displays, but they attend to bodies for the longest period of time, most frequently, and first. In addition, we observed no significant differences in either fixation duration or frequency between the two affective content types—aggressive behaviors and submissive behaviors—indicating that both classes of behavior were prioritized similarly in attention. These findings suggest that monkeys encode information about the bodies of conspecifics while processing affective displays providing support for the hypothesis that, like humans (e.g., Aviezer et al., 2008; Kayyal et al., 2015; Meeren et al., 2005; Wenzler, Levine, van Dick, Oertel-Knochel, & Aviezer, 2016; for a review Hassin et al., 2013), monkey facial displays have multiple meanings that are

Attention to conspecifics
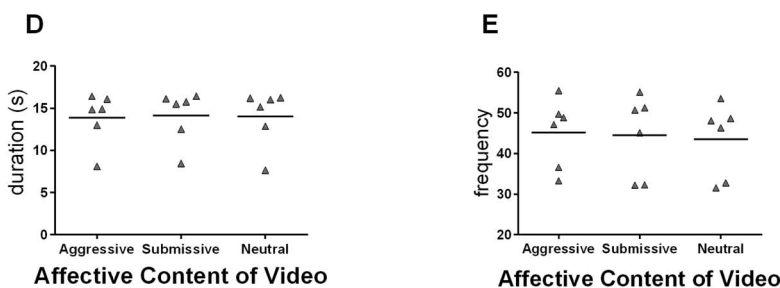
Attention to regions other than conspecifics

Figure 2. Visual attention during dynamic affective displays. Horizontal lines represent mean values. Individual points represent individual monkeys. (A) Each monkey's average total fixation duration for conspecifics' heads and bodies, by affective content of video. (B) Each monkey's average total fixation frequency for conspecifics' heads and bodies, by affective content of video. (C) Each monkey's latency to first fixation for conspecifics' heads and bodies, by affective content of video. (D) Each monkey's average total fixation duration for areas outside the head and body ROIs. (E) Each monkey's average total fixation frequency for areas outside the head and body ROIs.

context dependent. In this view, the position, movement, and shape (e.g., crook of the tail) of the body are all important sources of that contextual information. In all likelihood, monkeys, like humans, require additional contextual information in addition to information about the body, to fully understand facial behaviors. Accumulating evidence from biological anthropology indicates that the same facial behavior, the silent bared teeth display, has multiple meanings depending on the context in which it occurs (social peace vs. social conflict) (Beisner & McCowan, 2014). Together, these findings suggest facial behaviors are not evolved "expressions" of emotion that can be "read" alone. This idea stands in stark contrast the predominant evolutionary views about the meaning of facial behaviors (e.g., Ekman, 1972; Keltner & Ekman, 2000; Shariff & Tracy, 2011).

One surprising finding from this experiment was that subjects fixated more frequently on heads than bodies of conspecifics who were not generating affective displays. The lack of clear affective information in these displays may signal the perceiver to continue processing the available visual scene, increasing the extent to which the face is scanned. Another possibility is that the effect was driven by visual properties of the videos themselves. Compared to videos with affective content, videos with neutral content included more frames in which the camera zoomed in on the face, rendering it larger. This possibility should be explored in future testing using

a new set of neutral videos. However, had this been the case, we expected to see shorter fixation durations and fewer fixations on areas outside the conspecific (because there would be less area outside)—which was not the case. Taken together, these data indicate that neutral and affective social information are prioritized similarly in attention. This is consistent with other findings from our laboratory that demonstrated that rhesus macaques were more behaviorally reactive to neutral social information than to neutral nonsocial information (Bliss-Moreau, Bauman, & Amaral, 2011).

In conclusion, our findings clearly indicate that rhesus macaques, like humans, attend to contextual information—in this case, bodies—during dynamic affective displays. Understanding the extent to which and the process by which that information shapes an understanding of faces in humans and nonhuman animals is an important avenue for future research since it forms the core of our social decision-making processes and is impaired in many psychiatric disorders.

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