How Macaques View Familiarity and Gaze in Conspecific Faces

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The pattern of visual fixations on an image depends not only on the image content but also on the viewer’s disposition and on the function (or pathology) of underlying neural circuitry. For example, human viewers display changes in viewing patterns toward face images that differ in gaze direction or in the viewer’s familiarity with the face. Macaques share many face processing abilities with humans, and their neural circuitry is used to understand perception across species, yet their viewing responses to gaze and familiarity of faces is poorly understood. In this study, rhesus macaques passively viewed faces of familiar and unfamiliar conspecifics whose head-and-eye gaze was directed either toward or away from the viewing monkey. The eyes of faces were viewed more than any other feature; furthermore, familiar eyes were viewed more than unfamiliar eyes. In contrast, ears, though not as salient as eyes, were viewed about twice as often for unfamiliar faces as familiar faces. Directed-gaze eyes were fixated earlier, and for a greater proportion of saccades than were the eyes of averted-gaze faces, suggesting that mutual gaze attracts a more immediate and sustained scanning of the eyes. Ears and external features were more salient for averted, as compared with directed gaze. In general, effects were more robust (within and across subjects) for the gaze contrast than for familiarity, perhaps as a consequence of the greater image-based differences for the gaze than the familiarity stimuli used in this study.

Keywords: scan path, mutual gaze, gaze following, face processing, visual search

Facial expressions, gaze, and identity (whether or not they are familiar and what is their social status) can be used to predict social exchanges and their likely outcomes. The succession of visual fixations (scan paths) to facial features measures attention to those features, thereby indicating which aspects of the image are important for specific perceptual and cognitive processes (Noton & Stark, 1971a; Noton & Stark, 1971b; Just & Carpenter, 1976; Walker-Smith, Gale, & Findlay, 1977; Daffner, Mesulam, Cohen, & Scinto, 1999; Yarbus, 1967).

In humans, scan paths vary with facial expressions and identity. The eye region has been considered most informative—diagnostic—for identity, whereas the mouth region is considered to be diagnostic for discriminating expressions (Schyns, Bonnar, & Gosselin, 2002; Malcolm, Lanyon, Fugard, & Barton, 2008; Smith, Cottrell, Gosselin, & Schyns, 2005); but see (Baron-Cohen, Wheelwright, & Jolliffe, 1997). Averted-gaze faces (eyes but not head) elicit more fixations and a higher amount of initial fixations to the eyes in humans (Iter, Villate, & Ryan, 2007) and identity is not as well encoded with averted as with direct gaze (Mason, Hood, & Macrae, 2004). Gaze direction not only provides information such as the locus of an individual’s attention (Nummenmaa & Calder, 2009; Calder et al., 2002); directed gaze provides an opportunity to engage in mutual gaze, an important communicative device (Symons, Hains & Muir, 1998; Hains & Muir, 1996; Kleinke, 1986). Human neuroimaging and neuropsychological testing has revealed a network of brain regions sensitive to gaze in face processing and in predicting the intentions of the seen individual, including key structures such as the superior temporal sulcus/superior temporal gyrus (STS/STG) and the amygdala, as well as occipitotemporal areas such as the fusiform gyrus (FG) and inferotemporal cortex (IT), intraparietal sulcus (IPS), orbitofrontal cortex, anterior cingulate cortex, and the fronto-parietal circuit associated with voluntary or goal-directed shifts in gaze (for recent reviews, see Itier & Batty, 2009; Nummenmaa & Calder, 2009). Changes in scanning behavior can be diagnostic of social affective disorders or disruption of function in these structures (Vecera & Rizzo, 2004; Akiyama et al., 2007; Adolphs, Tranel, & Damasio, 1998; Pelphrey, Morris, & McCarthy, 2005).
Face scanning can also differ for face categories of a more conceptual nature such as familiarity with the face of a known individual (“personal familiarity”). In humans, personally familiar faces (e.g., friends and family), as compared with famous or familiarized faces, show a distinction in how they are processed (Bobes, Quiñonez, Perez, Leon, & Valdés–Sosa, 2007; Carbon, 2008). Humans tend to use the internal features of personally familiar or famous faces more than those of unfamiliar faces (Ellis, Shepherd, & Davies, 1979; Young, Hay, McWeeny, Flude, & Ellis, 1985) at least during pair-wise comparisons of faces (Stacey, Walker, & Underwood, 2005; but see Althoff & Cohen, 1999). In addition, one study suggested that the viewing of unfamiliar faces was more distributed and stereotyped (Althoff & Cohen, 1999). In contrast, a recent study found that for images with external contours removed, after the initial few fixations, familiar face features tend to be sampled more, whereas for unfamiliar faces, a common central location between the eyes is preferred (van Belle, Ramon, Lefèvre, & Rosston, 2010). The type of familiarity with an individual is also associated with different patterns of activation in the brain, including anterior IT, fusiform gyrus, medial temporal lobe structures, the amygdala and insula, and pST/temparoparietal junction and precuneus (Gobbini & Haxby, 2007). Many of these structures were also implicated in gaze processing, and, indeed, any one structure has been associated with a variety of functions. To understand the neural coding mechanisms that differentiate various aspects of face processing within a structure, and thereby the relative contributions of these structures as part of a network, direct recordings of neural activity may be employed, typically in macaques. These types of studies often presume equivalent behavior between face processing in macaques and humans, though the supporting literature is far more scarce for macaques than for humans, as we will describe.

Macaques are sensitive to some of the same facial characteristics that humans perceive. Rhesus macaques discriminate gaze (Campbell, Heywood, Cowey, Regard, & Landis, 1990), show arousal differences with directed/averted gaze (Hoffman, Gothard, Schmid, & Logothetis, 2007), and, along with stumptail and pigtail macaques, follow the direction of gaze of a seen individual (Emary, Lorincz, Perrett, Oram, & Baker, 1997; Ferrari, Kohler, Fogassi, & Gallese, 2000; Tomasetello, Call, & Hare, 1998). Despite this, little is known about how gaze direction per se affects face scanning in macaques. Of the limited studies with macaques in which gaze has been treated as an independent variable, averted-gaze faces elicit fewer fixations as compared with direct gaze (Keating & Keating, 1982, two of two subjects; Gibboni, Zimmerman, & Gothard, 2009, two of three subjects; Mosher, Zimmerman, & Gothard, 2011), although this effect is opposite to what is seen in infant macaques, where direct gaze is scanned less (Mendelson, Haith, & Goldman–Rakic, 1982). Additionally, there is evidence of neural specializations that serve these functions, which appear to be homologous to the specializations in humans (Campbell, Heywood, Cowey, Regard, & Landis, 1990). Whether or not these specializations are associated with similar processing strategies, however, is unknown.

Rhesus macaques are also sensitive to identity (Rosenfeld & Van Hoesen, 1979; Gothard, Erickson, & Amaral, 2004; Gothard, Brooks, & Peterson, 2009), but it remains unclear if they share with humans strategies for discriminating individuals from facial identity. Guo and colleagues (2003) investigated face scanning for familiar versus unfamiliar individuals, but identified no difference in internal feature viewing between the unfamiliar and familiar conditions. Instead, they found a greater probability of refixation of the eye region of unfamiliar faces during the first few seconds of the trial (Guo, Robertson, Mahmoodi, Tadmor, & Young, 2003). From this study, however, it is unclear if other aspects of the stimuli may have confounded the results (e.g., sex, age, gaze or low-level image features).

Here we sought to determine if macaques alter their viewing preference and scan paths as a function of the gaze and familiarity of a conspecific face. Using a set of face images that vary in gaze direction and familiarity, we analyzed the free viewing patterns from a nondifferentially reinforced (“passive viewing”) task. We predicted that macaques would fixate internal features more frequently for familiar, as compared with unfamiliar individuals, and that the eyes of directed-gaze faces would be fixated more (i.e., mutual gaze) than the eyes of gaze-averted faces. Understanding whether and how behaviors differ across these attributes of faces can provide behavioral diagnostics of underlying neural function (or dysfunction). Furthermore, they may reveal important face-viewing controls for the experimental design of studies on the neural basis of face/social stimulus perception.

**Method**

**Subjects**

Four adult female rhesus macaques (Macaca mulatta) were tested (LU, AN, RI & LE, ages 5, 5, 5, and 11 years, respectively). Procedures were approved by the York University Animal Care Committee and were performed in accordance with the Canadian Council on Animal Care.

**Stimuli**

A stimulus set of 24 face images was constructed for each monkey (see Figure 1). Of the 24 images, half were familiar faces and the other half unfamiliar faces. The familiar images included three male and three female macaques who were housed in the same colony. The housing arrangement is such that all monkeys share visual contact, and some same-sex individuals had full social contact. The unfamiliar images were selected from a macaque face database (Gothard et al. 2004). The unfamiliar and familiar individuals each contributed one averted (head and eyes away from the viewer) and one direct (head and eyes toward the viewer) face image, and were matched for sex and head size (as head size varies with age) in addition to the degree of deviation of gaze angle for the different head orientation images. None of the unfamiliar macaques in the unfamiliar images had been seen by the subjects prior to the experimental sessions. The macaques that were tested never viewed their own face as a stimulus.

Images were prepared with Adobe Photoshop CS3 (San Jose, CA). Each face was cut from its original background leaving as much as possible of the original contour and hairline and placed on a gray background, with feathering at the transition to diminish artificially introduced edges. Images were scaled and rotated to roughly match attributes across images. Images were also mean luminance normalized. Skin coloration can also play a role in face preference (Waitt et al., 2003). To control for this, the facial
coloring between images was compared using the method described by Dubuc and colleagues (2009). Unmatched images were adjusted to ensure that skin coloration was balanced across the familiarity condition (in total, three images from the unfamiliar category were adjusted).

**Behavioral Procedure**

**Apparatus.** During the experiment, the subjects were seated in a primate chair in a closed cubicle and were permitted to freely move their head. The stimuli were presented on a Dell LCD monitor (40 × 32 cm at 60 Hz, 32 bit color) via NBS Presentation software. The monitor was positioned 57 cm from the head, subtending an area of visual angle of 39° by 31°. Eye movements were recorded using an iViewX Hi-Speed Primate remote infrared eye tracker (SensoMotoric Instruments, SMI, Berlin, Germany). Viewing was binocular with monocular tracking (left eye). This monocular signal was sampled at 1,250 Hz and stored for offline analysis. Calibration of the eye tracker required that monkeys fixated 13 separate points equally distributed on the screen, during which they received manually controlled juice rewards.

**Training sessions.** There were five daily training sessions for each animal prior to experimental sessions. During these sessions, a random set of 24 objects was shown. The animal had to fixate inside of a 22° by 15° window around the object for a cumulative total of 3 s to receive a reward. If gaze exited this region, the cumulative time was paused, only to resume upon reentry. At the end of the 3 s, the image disappeared after which the monkey received a preferred food/fluid reward through a spout, marking the end of that trial. After 1 s, a new image appeared. This continued until all 24 images had been presented once. All macaques performed the task readily; in no case were more than five training sessions required.

**Experimental sessions.** The experimental task was the same as the training, although instead of object images each monkey viewed the stimulus set of 24 face images. On average the faces occupied an area of 9° by 9° inside the 22° by 15° window. Due to the freedom of viewing within the larger image bounds, and the various start locations of initial fixations, scan paths here are likely to be more naturalistic and less constrained than the scan paths reported when central fixation is required for image onset (Arizpe, Kravitz, Yovel, Baker, & Barton, 2012). The experimental sessions lasted a total of 10 days, one session per day, divided into blocks of five sessions (i.e., 5 days) each. The 24 images were shown in pseudorandom order; the same identity was never shown consecutively.

**Data Analysis**

Typically, each animal completed 240 trials (24 trials over 10 days). Due to poor eye tracking data on 6 days, 144 trials were omitted from analysis. Five of those omitted came from one subject (Sessions 6–10 from TI), the remainder were from a second subject (Session 8 from RI). Fixations and saccades events were identified offline with iViewX iTools IDF Event Detector, using a dispersion-based algorithm (I-VT) with a minimum fixation duration of 80 ms and maximum dispersion of 100 pixels.
Further analysis was performed in MATLAB (Natick, MA) using in-lab purpose-built code. Differences in viewing based on image familiarity and gaze direction were evaluated using Welch’s t-test (Welch, 1947) and corrected for false discovery rate with the Benjamini & Hochberg procedure (Benjamini & Hochberg, 1995). All significant results based on data pooled across individuals for a measure type (i.e., number of fixations) were followed up by comparing the individual data making up the grand pool. Here again, all tests were done using Welch’s t-test and corrected for false discovery rate. A traditional omnibus measure of significance was not suitable due to the variance of the eye movement data.

Area of interest (AOI) measures for facial features required that AOIs be drawn around the location of the eyes, ears, nose, mouth, and the nonidentifying features (NIF; Figure 1B), the area on the face which was not included in eye, nose, mouth or ear AOIs. These AOIs were hand drawn for each image prior to analysis (Figure 1C). For all measurements of fixations within a given AOI, values are normalized for the size of their respective areas (1/AOI size) to ensure that differences in fixation counts were not a trivial consequence of differences between the sizes of the AOIs in question. In two cases the AOIs were grouped. Internal features were defined as the eye, nose, and mouth AOIs, whereas external features were defined as the ears and the NIF.

Trial duration was measured as the elapsed time required to reach the cumulative on-image looking time of 3 s. An elapsed time similar to the cumulative time requirement indicates that gaze was focused within the image bounds for the duration of the trial, whereas the elapsed time would be longer than the 3 s cumulative time requirement if the subject’s gaze left the image bounds during the trial.

Visual scan paths include the distance and duration of the sequence of shifts in gaze on an image. We calculated the distance of gaze shifts (“gaze shift length”) in degrees of visual angle on the image: low values indicate the tendency for fixations to remain on a feature or location, whereas high values are indicative of sampling new features or distant locations on the image. The length of gaze shift is similar to saccade amplitude, except that, strictly speaking, it is calculated using the contributions of both head and eye position, however, when gaze shift lengths are short (<10°) head movement is negligible (e.g., Martinez–Trujillo, Klier, Wang & Crawford, 2003). Our face stimuli were 9° × 9°, with typical gaze shifts under 3°, suggesting that the contribution of head movements in this experiment would be minimal, thus gaze shifts would be equivalent to saccade amplitude.

As a final group of measures, we calculated timing of gaze in areas of interest, including the latency to fixate an AOI, expressed as the ordinal fixation number, the duration of that first fixation in an AOI after the image is presented, the total duration in the AOI, expressed as fixation count, and the proportion of fixations in the AOI.

Results

Three classes of behaviors were considered for each image category: trial duration, gaze shift characteristics, and the temporal pattern of looking in feature-based areas of interest (AOIs), see Figure 2. Unless otherwise specified, p values are based on grand pool data. Tables 1-3 show the full results.

**Gaze**

**Trial duration.** The grand pool median revealed a difference in trial duration between direct and averted gaze. The trials with

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**Figure 2.** (a) Probability of fixation is plotted for a single trial of a gaze directed image (top) and of a gaze-verted image (bottom) for subject L.E. (b) Behavioral rasterplot showing when each feature was fixated for all trials for subject L.E (top). Each color represents fixations in a feature, listed at the bottom. All trials for a given condition are sorted by the amount of eye looking over the entire trial. Trials longer than 4 s are cropped. The sum of all fixations across trials is shown below the respective raster plot (middle).
Averted gaze were longer than trials with directed gaze (p < .05, directed (mean [standard deviation]): 3,058 ms (722), averted: 3,134 ms (3,121), see Figure 2b for an example of one subject’s trial durations). Individually, the effect was evident for one subject (RI: p < .05) with another showing a similar trend (LE: p < .1). Longer averted gaze trials may have been indicative of a propensity to shift focus away from the image and toward the direction of the averted gaze stimulus; alternatively, directed gaze images may have led to mutual “held” gaze, reducing the probability of fixating away from the directed-gaze image, yielding shorter trial durations.

**Gaze shift length.** The length of gaze shifts were longer for averted faces when comparing both the medians, (p < .001), directed: 2.45° (1.19°), averted: 2.63° (1.66°) and the sum of all gaze shift lengths, p < .001. If directed-gaze faces elicit mutual gaze, one might expect more fixations within the relatively restricted eye region, thereby leading to the shorter gaze shifts with directed-gaze faces than that seen for averted-gaze faces, though other possibilities remain.

**Latency to first fixation in AOI.** The elapsed number of fixations from start of trial to the first fixation in an area was compared. For directed gaze, the eyes were fixated sooner than for averted-gaze (Figure 3a; p < .001). Similarly, the elapsed time from start of the trial to the first eye fixation was about 300 ms faster for directed than for averted faces (p < .01, three of four subjects). In contrast, the nonidentifying features were fixated over...
two fixations later for directed than for averted gaze ($p < .001$, four of four subjects). These effects are consistent with a drive to engage in mutual gaze.

**Duration of the first fixation.** Of all the AOIs tested, only the nonidentifying features evoked different first fixation durations across gaze categories. Averted gaze faces received longer first fixations to the NIF after image onset than directed gaze faces, $p < .01$, directed: 142 ms (93.24), averted: 157 ms (131.08). The generally similar fixation durations across categories means that duration is not compensating for fixation count (where many short fixations could equal fewer short fixations). Thus, as an alternative to fixation durations, fixation count and proportion of fixations are used to approximate time spent fixating.

**AOI fixation count.** When the number of fixations in each AOI was compared for direct as opposed to averted gaze, the ears showed about 0.5 more fixations for averted gaze faces (Figure 3b; $p < .001$). Nonidentifying features were also fixated more for averted than directed gaze faces, though on average only by 1/10th of a fixation ($p < .001$, three of four subjects). The number of fixations was also higher for the external features of faces with averted gaze ($p < .001$, four of four subjects).

**Proportion of fixations.** In line with previous literature, subjects frequently fixated the eyes. Of all the fixations on the face, there was a higher proportion of fixations to the direct-gaze eyes (Figure 3c; $p < .01$), possibly supporting the opportunity for mutual gaze. Additionally, there was a threefold increase in the proportion of fixations to the ears of averted-gaze, as compared with directed-gaze faces ($p < .001$). The proportion of internal to external fixations was greater for directed gaze faces (Figure 3d; $p < .001$). In both cases, the difference in proportion of fixations to the ears and external features for gaze type were consistent for all subjects.

**Summary of gaze results.** External features were more salient for averted, as compared with directed faces. Many of the effects across the gaze contrast were robust across subjects. All subjects showed larger gaze shifts for averted faces. All looked more at the ears and external features of averted faces, as compared with directed gaze faces. For directed faces the first fixation...
to the eye was faster, and a greater proportion of fixations were directed to the eyes. This was true not only for eyes but also internal features, more generally: the proportion of fixations to internal, as compared with external features was higher for directed gaze, whereas the proportion of fixations to ears was higher for averted gaze.

Familiarity

**Trial duration.** When pooled across individuals, unfamiliar trials took longer than familiar trials, \( p < .05 \), familiar: 3,062 ms (2,452), unfamiliar: 3,108 ms (2,071), one of four subjects. The shorter trial durations to familiar faces may be indicative of greater interest in viewing the image of a known individual.

**Gaze shift length.** The median length of gaze shifts were greater for unfamiliar faces, \( p < .001 \), familiar: 2.45° (1.19°), unfamiliar: 2.63° (1.66°), one of four subjects. The sum of gaze shift lengths across the trial was also greater for unfamiliar faces than familiar faces (\( p < .001 \), one of four subjects). This difference may be the consequence of the size and distributions of the preferred facial features across categories, as described below.

**Latency to first fixation in AOI.** The first fixation in the eye area occurred earlier for familiar than unfamiliar faces (Figure 3e; \( p < .01 \)). In contrast, the first fixation to ears occurred earlier for unfamiliar than familiar faces, by about one fixation (\( p < .05 \), two of four subjects) or when measured in elapsed time, by about 450 ms (\( p < .01 \), three of four subjects).

**Duration of the first fixation.** The duration of the first fixation to the eyes after image onset was longer for familiar faces, \( p < .5 \), familiar: 162 (120.17), unfamiliar: 155.5 (82.03), but otherwise fixations durations were constant across conditions.

**AOI fixation count.** When the number of fixations in each AOI was compared across familiarity condition, the ears of unfamiliar faces received on average 0.7 fixations more per trial than those of familiar faces (Figure 3f; \( p < .001 \)). In addition, external features of unfamiliar faces received on average 1.1 more fixations per trial than those of familiar faces (\( p < .001 \), three of four subjects). These two measures showed the most consistent effects of face familiarity on face viewing, revealing more fixations to the external regions (including ears) of unfamiliar faces.

**Proportion of fixations.** Of all the fixations on the face, a higher proportion of fixations were made to the eyes of familiar, as compared with unfamiliar faces (Figure 3g; \( p < .01 \)). In contrast, ears were less frequently fixated than eyes; and when compared across conditions, ears of unfamiliar faces received a higher proportion of fixations than those of familiar faces, \( p < .01 \), familiar: 0.05 (0.11), unfamiliar: 0.08 (0.14). Finally, the proportion of internal to external fixations was high, and familiarity increased the preference to view internal features (Figure 3h; \( p < .01 \)).

**Summary of familiarity results.** Among the most robust effects were the emphasis of looking at the ears and external features of unfamiliar faces. Specifically, when viewing unfamiliar, as compared with familiar faces, fixations to the ears happened earlier in the trial and there were more fixations to the ears and external features throughout the trial.

**Sex Differences**

Two measures revealed a difference in the pattern of fixations to male, as compared with the female faces (see Table 2). The first fixation to female ears (but not other areas), occurred earlier in the trial than it did for male ears, in both elapsed time, \( p < .01 \), male: 776.5 ms (765.79), female: 1419.85 ms (797.98), two of four subjects), and fixation number, \( p < .001 \), male: 7.66 (3.97), female: 6.04 (3.84), two of four subjects). Additionally, overall, male eyes received more fixations than female eyes (\( p < .001 \), two of four subjects). Finally, there were a higher number of fixations to nonidentifying features of male faces (\( p < .01 \)), but only in one of four subjects (AN: \( p < .001 \)).

**Discussion**

This study builds on previous work by using personally familiar or unfamiliar stimuli that vary in head-and-eye direction while being balanced for contrast, hue, luminance, expression, and sex. The pattern of fixations differed for both familiarity and gaze

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Table 2

<table>
<thead>
<tr>
<th>Sex (male/female)</th>
<th>pool (408)</th>
<th>LE (120)</th>
<th>LU (120)</th>
<th>RI (108)</th>
<th>AN (60)</th>
</tr>
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<tr>
<td><strong>Trial duration</strong></td>
<td>( ns )</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Fixation count by feature</td>
<td>( n_{df} )</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>NIF eye</td>
<td>3.39**</td>
<td>0.1</td>
<td>0.09</td>
<td>0.54</td>
<td>3.76***</td>
</tr>
<tr>
<td>First fixation to area (time)</td>
<td>( n_{df} )</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ear (fixation number)</td>
<td>3.48**</td>
<td>2.97**</td>
<td>1.34</td>
<td>1.66</td>
<td>4.00***</td>
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<tr>
<td>ear</td>
<td>3.79***</td>
<td>3.42**</td>
<td>1.34</td>
<td>1.66</td>
<td>3.34**</td>
</tr>
</tbody>
</table>

*Note.* Values in parenthesis are the \( n_{df} \) size. Cell values reflect \( t \) scores. n.s. represent nonsignificant values, in these cases individual tests were not calculated. NIF = nonidentifying features, the portion of the face not occupied by eyes, ears, nose or mouth. n.s. results (not shown in table) are as follows: first fixation to area (time & fixation number)—eye, mouth, nose; NIF = duration of first fixation in area: eye, ear, mouth, nose; NIF—proportion of fixations: eyes vs. rest, ears vs. rest; fixation duration (median and sum)—all, ear, ear; gaze shift length (median & sum).

All \( p \) values corrected for FWE. * \( p < .5 \). ** \( p < .01 \). *** \( p < .001 \).
conditions on a number of measures. Most notably, in both conditions there are differences in how ears are fixated, and in the proportion of fixations to internal versus external features.

**Trial Durations and Overall Interest**

Shorter elapsed trial durations signify more consistent looking at the image, thus gaze duration has been interpreted as a measure of general interest in the image (Wilson & Goldman–Rakic, 1994; Gothard et al., 2009). Both gaze and familiarity categories showed differences in trial duration by stimulus condition. See Figure 2b for an example of elapsed trial durations for one of the subjects. Typically, the subjects looked at the image without gazng away during the trial, therefore most trials were completed within an elapsed time that was the same as the required cumulative on-image looking time of 3 s, that is, without break. Nevertheless, trials with familiar faces were completed faster than those with unfamiliar faces and trials with direct gaze were completed faster than those with averted gaze, suggesting familiarity and direct gaze are more interesting or engaging types of stimuli than their counterparts. In future studies, longer trials, or operant measures of viewing (Colombo, Mitchell, & Horowitz, 1988), may be more robust in determining interest.

Because the on-image viewing time was fixed (at 3 s), one might expect a tradeoff between some of the fixation measures we report. For example, a higher number of fixations would require shorter fixation durations, to sum to 3 s of viewing. Although this is true of total fixations on the image, where we report differences in fixation count or proportion of fixations, we examine only parts of the image, thus, fixation duration could, in principle, remain similar across the same conditions. In practice, this was generally the case: fixation durations remained similar whereas fixation counts and/or proportions of fixations varied across condition for a given region of interest (see Table 1). We therefore focus the discussion on the size of gaze shifts, fixation counts, and proportion of fixations rather than fixation duration.

**The Many Faces of Familiarity**

The term “familiarity” appears in numerous studies of face perception, however, the definition of familiarity differs. Famous faces have often been treated as familiar stimuli in human studies (Ellis, Shepherd, & Davies, 1979; Young et al., 1985; Stacey et al., 2005; Barton, Radcliffe, Cherkasova, Edelman, & Intriligator, 2006). Even more common, but less germane to the present experiments, are studies that use novel faces that are “familiarized” over a number of trials and contrasted to the novel presentation of other faces (Parr, Winslow, Hopkins, & de Waa, 2000; O’Donnell & Bruce, 2001; Bonner, Burton, & Bruce, 2003; Gothard et al., 2004). Familiarity with an individual (“personally familiar”), although used with humans (van Belle et al., 2010) and monkeys (Guo et al., 2003; Pokorny & de Waa, 2009), are the least commonly used of the three types. The distinction is critical, though, because in humans different types of familiarity are not equivalently perceived; personally familiar faces are processed differently than famous faces (Carbon, 2008) and familiarized faces (Bobes et al., 2007). Moreover, distinct neural activation patterns are seen for faces of family members, of other personally familiar individuals, of individuals made familiar through the media, and of faces made familiar only in the context of exposure during the experiment (Gobbini & Haxby, 2007). Macaques lack the “famous faces” category for conspecifics, making it important to know whether their behavioral responses to cohabiting conspecifics resemble those of humans. This is especially relevant for studies addressing the neural substrates of face processing, when the activity in key structures such as the amygdala, perirhinal cortex, IT, STS, and fusiform gyrus is thought to differ according to face familiarity.

Here, we compared viewing of faces of individuals who were either known by the subjects through cohousing (“personally familiar”) or who had never been seen outside of the context of the experiment. Although the possibility exists that the unfamiliar faces were familiarized over the course of the experiment, it is unlikely since each subject was exposed to each unfamiliar identity only twice per day for 3 s (once for each gaze direction), and subjects were not required to learn the faces (this was a nondifferentially reinforced task). Thus, it is improbable that any subject would have been overtrained on the unfamiliar identities. Critically, any such familiarization of these “unfamiliar” faces would work against seeing the category-level differences we report.

Familiar face trials had shorter elapsed trial times, shorter gaze shifts, and fewer fixations to the mouth or external features. In addition, they showed a shift toward internal features with familiarity. In humans, external features are associated with recognition memory, yet as faces become increasingly familiar, internal features become more important (Bruce & Young, 2000). Here we see agreement with human data in that external features were fixated more for unfamiliar faces (Bruce et al., 1999). Furthermore, the proportion of fixations to internal features, as compared with external features was higher for familiar faces—that is to say, internal fixations are more likely during familiar than unfamiliar face viewing. In general, the different viewing pattern for familiar faces resembles the viewing shown by humans.

**Gaze Following and Mutual Gaze**

Along with longer trial times, gaze-avoided faces also received longer gaze shifts than direct faces. Macaques, like humans, show gaze following (or joint attention) (Emery et al., 1997; Tomasello, Call, & Hare, 1998; Mosher et al., 2011), and static images of conspecifics looking away from the viewer have been used to orient attention to the area of gaze (Deaner & Platt, 2003; Shephard, Deaner, & Platt, 2006). In the present experiment, the gaze-avoided faces might have increased the probability for the viewing subjects to break fixation in the direction of the averted gaze stimuli.

A non, mutually exclusive alternative is that direct-gaze faces encouraged mutual gaze, reducing the motivation to break fixation and gaze away from the image in this condition relative to the gaze-avoided condition. Mutual (direct) gaze signals communication between two individuals (Emery, 2000). We found that engaging in mutual gaze when the option exists seems to be of importance. First, there was a higher proportion of time spent looking at face when gaze was direct (shorter trials lengths). Second, direct-gaze eyes are fixated sooner. Third, macaques fixated the eye proportionally more, as compared with the rest of features for direct-gaze faces. The importance of direct gaze and
the eyes during direct gaze suggests that mutual gaze constrains face viewing of direct-gaze faces.

Ears

Based on the relative difference in the number of fixations, the ear was the best feature for discriminating across category for both gaze and familiarity conditions. These results may represent a potential difference in how humans, as compared with macaques look at ears. For example, human infants rarely fixate ears (Maurer & Salapatek, 1976) and adults are unable to detect their vertical displacement (Brooks & Kemp, 2007). Human pinnae have roughly the same visual complexity as the face and are unaffected by facial expressions (Hurley, Arbab-Zavar, & Nixon, 2008). In macaques, pinnae are of similar general shape to humans’, but are proportionately larger in macaque infants than in human infants, and macaques move the ears as a component of their facial expressions. Unfortunately, because most human studies don’t report ear fixations, and many crop images around the hairline, it is unclear if humans would show similar scan paths to those described here, or if instead, macaques use and perceive the ears differently from humans.

The Effects of Gaze as Compared With the Effects of Familiarity

There was a trend for all subjects to show greater scan path differences between gaze conditions than familiarity conditions. For gaze, there were more measures that were significant for the majority of the group (three or more) than there were measures significant for a minority of the group. Although there were similarities among individuals in how familiar and unfamiliar images were fixated, they were far more likely to be significant for a minority of the group.

For familiarity, the two measures with the most consistent differences between individuals were fixation count to the ear and fixation count to external features, seen in three of four subjects. There was no difference in how nonidentifying features were fixated in the grand pool comparison. Because there is no difference in how nonidentifying features were fixated in the familiarity condition it is possible that fixations to the ear AOI were driving the overall effect of increased fixations to external regions; however, for the gaze condition there were distinct effects for both fixations to the ear (four of four subjects) and to nonidentifying features (three of four subjects). In this case the increase in fixations to external regions for averted faces cannot be solely attributed to a difference in ear fixations.

Sex

It was important that our stimuli were balanced for sex as macaques have been shown to discriminate sex from faces (Koba & Izumi, 2008; Paukner, Huntsberry, & Suomi, 2010). A small cluster of measures did indeed reveal that a difference in the pattern of fixations for male, as compared with female faces occurred. Of these differences, the most consistent effects were in the elapsed time prior to the first fixation to the ears. Here, measured in both elapsed fixations and elapsed time, the first fixation to male ears occurred on average two fixations (or 500 ms) later in the trial than female ears. This effect was apparent in two of the subjects, with the other two showing a similar trend. With female macaques as viewers, there are more fixations to the eyes, and a delayed first fixation to the ears of male faces.

A possible confound in this study arises in that permitted contact between familiar males and females was dissimilar. No males in the colony were permitted contact with the female subjects, whereas all females had at least some history of contact with each other.

Comparison With Previous Studies

Our work contrasts with the findings of Guo and colleagues (2003). Although both studies show a greater probability of refixation of the eye region of unfamiliar faces, Guo and colleagues found no other differences in how normal unfamiliar and familiar faces were scanned. The differences in findings could be due to two methodological differences between studies. First, we balanced images across category for low-level visual cues and sex, and all featured neutral expressions. Second, we customized AOIs (fitted polygons) for each image, providing greater accuracy of boundaries between facial areas than fixed rectangles. Customized AOIs can be considered especially important in depicting the group of nonidentifying features, which can be underrepresented with less flexible rectangular or ellipsoid AOIs.

Like the results reported in humans, we see a shift toward internal features for familiar faces (Bruce et al., 1999). Responses to shifts in gaze, however, are ostensibly different across species. Like previous findings in macaques (Keating & Keating, 1982; Gibboni et al., 2009), we see that direct-gaze faces are fixated earlier and more, exactly opposite to that which was reported in humans (Itier et al., 2007). There, only eyes were averted, therefore humans should be tested with head-and-eye averted gaze and macaques with eye-only gaze to determine the root of the discrepancy. The role of ears in the present study suggests another feature that may be important to include in future studies, across species. Overall, the present results are consistent with the importance of eye contact in social interactions, and help build a more comprehensive picture of viewing patterns to relevant facial characteristics in macaques.

References


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