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Facial expression recognition in rhesus monkeys, *Macaca mulatta*

Lisa A. Parr^{a,*} and Matthew Heintz^{b,1}

^aDivision of Psychiatry and Behavioral Sciences, and Yerkes National Primate Research Center, Emory University

^bDepartment of Biology, University of Chicago

Abstract

The ability to recognize and accurately interpret facial expressions is critically important for nonhuman primates that rely on these nonverbal signals for social communication. Despite this, little is known about how nonhuman primates, particularly monkeys, discriminate between facial expressions. In the present study, seven rhesus monkeys were required to discriminate four categories of conspecific facial expressions using a matching-to-sample task. In experiment 1, the matching pair showed identical photographs of facial expressions, paired with every other expression type as the nonmatch. The identity of the nonmatching stimulus monkey differed from the one in the sample. Subjects performed above chance on session 1, with no difference in performance across the four expression types. In experiment 2, the identity of all three monkeys differed in each trial, and a neutral portrait was also included as the nonmatching stimulus. Monkeys discriminated expressions across individual identity when the non-match was a neutral stimulus, but they had difficulty when the nonmatch was another expression type. We analysed the degree to which specific feature redundancy could account for these error patterns using a multidimensional scaling analysis which plotted the perceived dissimilarity between expression dyads along a two-dimensional axis. One axis appeared to represent mouth shape, stretched open versus funnelled, while the other appeared to represent a combination of lip retraction and mouth opening. These features alone, however, could not account for overall performance and suggest that monkeys do not rely solely on distinctive features to discriminate among different expressions.

Keywords

facial expression; facial features; FACS; *Macaca mulatta*; matching-to-sample; rhesus monkey

The ability to recognize and accurately interpret facial expressions is critically important for nonhuman primates that rely on these nonverbal signals for social communication. Detailed ethograms describing the facial expressions of a number of species have been published, including the rhesus monkey (Hinde & Rowell 1962; van Hooff 1967), a standard animal model for human behaviour, and the chimpanzee, our closest living relative (Goodall 1968; van Hooff 1973; Parr et al. 2005). Among these species, several facial expressions are proposed to be homologous with human expressions. These include the silent bared-teeth display, the human smile, the relaxed open-mouth face (or play face) and human laughter (van Hooff 1972; Preuschoft & van Hooff 1995). This evidence suggests that the production of some facial expressions shares a common phylogenetic history. The perception of facial expressions,

however, has received little attention in experimental research, despite its importance in primate social communication. The same facial expression, for example, can be used in multiple contexts, appear graded in intensity, be faked, or can become blended with other expression types, making both recognition and interpretation challenging perceptual problems (Marler 1976; Parr et al. 2005).

One of the few studies on facial expression perception in monkeys is by Kanazawa (1996), who studied two Japanese macaques, *Macaca fuscata*. Subjects were given 30 training sessions where they were required to match identical pictures of 20 different facial expressions that varied by category and intensity. Only one monkey performed above chance after the 30 sessions. A confusion matrix was then constructed with the single subject's data and analysed using multidimensional scaling procedures. This procedure generates a two-dimensional spatial plot, where clusters of expression represent low perceived dissimilarity, or perceptual confusion among the exemplars. Two main clusters of expressions were found. One, labelled the subordinate–dominant axis, involved bared-teeth displays and threat faces, where the correlated features included the position of the brow, eye width, and the degree of mouth curvature and thrust. The second was labelled a neutral–tense axis and included a cluster of neutral and tense-mouth faces. These expressions were correlated according to their brow position. When the same procedure was repeated with human expressions, many confusion clusters resulted except for the smile, which was an interesting result because of its proposed homology with the macaque bared-teeth display. Thus, the morphological similarities between these two expressions may have facilitated accurate interspecific discriminations by the macaques.

Gothard et al. (2004) used an eye-tracking procedure to compare the scan patterns of four rhesus monkeys when viewing conspecifics' facial expressions: lipsmack, bared-teeth display, open-mouth threat and yawn. These facial expressions were presented using a visual paired comparison task where subjects first habituated to an identical pair of neutral face portraits. Subjects were then presented with the same neutral portrait and one of the four facial expressions performed by the same monkey. Subjects dishabituated to each facial expression, spending more time scanning it than the previously seen neutral face. Moreover, they attended to different facial features for each expression, fixating more on the eyes and mouth during open-mouth threat and yawn trials, on the mouth (teeth) during bared-teeth display trials, and on the eyes during lipsmack face trials. This finding is somewhat contradictory to the results found by Nahm et al. (1997) several years earlier. They showed rhesus monkeys the same four facial expression categories along with a neutral face and found that after 1 s of viewing time, monkeys fixated more on the eyes of the open-mouth threat and bared-teeth displays, and about equally on the eyes and mouth of the lipsmack and yawn expressions. Subjects viewed the eyes most often in the neutral portraits, similar to the data presented by Gothard et al. (2004). Interestingly, these differences in scanning patterns disappeared when dynamic displays were presented.

Parr et al. (1998) were the first to examine facial expression discrimination in chimpanzees using a computerized, joystick-testing paradigm. Without any prior experience with facial expression stimuli, subjects discriminated photographs of two different individuals making the same facial expression from that of a neutral portrait of a third chimpanzee. Of the five expression categories presented, bared-teeth display, pant hoot, scream, relaxed-lip face and the play face, subjects learned to discriminate all but the relaxed-lip and the neutral face. This finding is interesting because these two faces are emotionally neutral, but the relaxed-lip expression contains a distinctive droopy lower lip. To understand the role of unique and distinctive facial features (e.g. mouth position, visibility of the teeth, staring eyes) in expression discrimination, Parr et al. (1998) conducted a second experiment in which each expression category was paired with every other, so that every dyadic combination of expression type was

represented. Performance discriminating these dyads was then correlated with the number of features shared between the two expression types. If performance was based on the detection of specific features, then expression dyads that shared these features would result in poorer performance than expression dyads that had no feature overlap. This hypothesis was supported only for some expression types, the bared-teeth display, pant hoot and relaxed-lip face, but not others, such as the play face or scream. It may be that the features of some expressions are more salient than others, or that something other than facial features was being used, such as overall configuration.

In the present study, rhesus monkeys were presented with two facial expression discrimination tasks. All subjects had prior experience matching conspecifics' faces, showing only neutral portraits and nonface stimuli, such as clip art and houses, but had never before seen photographs of species' typical facial expressions (Parr & Heintz 2006; Parr et al. 2008a). In both tasks, every dyadic combination of facial expressions was presented for discrimination, similar to the format described above for Parr et al. (1998). In experiment 1, the correct pair showed identical photographs of expressions, while the nonmatch showed a different monkey making a different expression type. We hypothesized that subjects would perform very well on this task, as the matching pair showed identical photographs, but we anticipated that some pairs would be more difficult than others based on the number of features shared between the matching expressions and the nonmatching one. In experiment 2, all individuals shown in a trial were different (e.g. the correct pair showed two different individuals making the same expression type, while the nonmatching photograph showed a third individual making a different expression). Based on previous studies in chimpanzees, we hypothesized that this task would be more difficult and that subjects' performance would be best for those trials where the two expressions had little or no redundancy in specific facial features, such as mouth open versus mouth closed. Performance was expected to be poorest for trials in which the two expressions shared several features in common. These results will provide important comparative data on the role of distinctive features in facial expression processing in monkeys using methods similar to previous studies in apes.

METHODS

Subjects

Data were collected from seven rhesus monkeys (5 females, 2 males), born into large social groups at the Yerkes Primate Center field station, Lawrenceville, GA, U.S.A. Two of the females were born in the spring of 2001, and the other monkeys were 1 year older. At 4 years of age, the subjects were pair housed and relocated to the Yerkes National Primate Center main station in Atlanta, and began participating in studies of face recognition using computerized touchscreen tasks (Parr & Heintz 2006; Parr et al. 2008a). At the onset of the present study, subjects were approximately 6 years old and had never before been presented with facial expressions as stimuli. All tasks presented before this study included only neutral portraits of unfamiliar conspecifics and other species' faces, and nonfacial images such as houses and clip art. All procedures were approved by the Institutional Animal Care and Use Committee of Emory University.

Matching-to-sample Format

Subjects performed tasks using a computerized touchscreen interface either in their home cage using a custom set-up, or in a dedicated testing room (see Parr et al. 2008a, b). Images were presented in a matching-to-sample (MTS) format in which subjects were first required to orient to a single image on the touchscreen, hereafter referred to as the sample, by touching it three times in rapid succession. This format ensured that subjects looked at the sample stimulus. The sample appeared randomly against any of the four walls of the touchscreen, in a central location

(top, left, bottom, or right side). After orienting to the sample, two comparison images were presented in each corner of the touchscreen on the wall opposite to the sample, forming a triangular configuration. The delay between the presentation of the sample and the two comparisons was approximately 500 ms. Subjects were then required to select the comparison image that matched the sample. For the experiments presented here, the sample image remained on the screen during the selection period (simultaneous MTS). If the response was correct, the subject would receive a food reward from an automatic feeder followed by an intertrial interval (ITI) of 2 s, while an incorrect response was followed by an ITI of 8 s and no food reinforcement. All procedures were approved by the Institutional Animal Care and Use Committee of Emory University.

Experiment 1: Facial Expression Matching with Identical Pictures

Stimuli and procedures—The stimuli used in experiment 1 consisted of four different species-typical facial expressions, the bared-teeth display (BT), open-mouth threat (OMT), scream (SC) and relaxed open-mouth face, or play face (PF). These occur with high frequency in ongoing behaviour and can easily be captured by still photography. Figure 1 shows an illustration of each of these expression types. These stimuli were combined so that the matching pair showed identical photographs and the nonmatching stimulus, or foil, was each of the remaining expression types, making three different trials possible for each expression type, 12 trials total. The BT, for example, was paired with the OMT, SC and PF. Note, however, that every individual photograph in this task was unique, so no stimulus was repeated across 12 trials. Figure 2 shows an example of a trial pairing BT with the OMT (shown on the left).

Prior to testing, the stimuli were converted to greyscale and cropped to a height of 300 dpi (dots per inch). The background information in each picture was homogenized using the paintbrush tool in Adobe Photoshop with an opacity of 75%, effectively blurring out details in the background. Each unique trial ($N = 12$) was presented four times in a daily testing session, totalling 48 trials per session. Subjects received these trials until their performance exceeded 75% correct. We analysed subjects' performance at two points: (1) when their overall performance exceeded chance in a single session (binomial z score: $P < 0.05$, two-tailed as 31/48, or $> 64.58\%$); and (2) when their performance exceeded the final criterion of more than 75% correct. We examined differences in performance across expression type ($N = 4$) at the two criteria (chance versus final) as within-subject factors using a repeated measures ANOVA. Of interest was whether performance differed across expression type and whether performance changed from the first to the final criterion.

Results—All subjects performed significantly above chance on their first testing session (mean $\pm$ SE = $70.24 \pm 2.07\%$). As expected, subjects' performance improved significantly by the final criterion (mean $\pm$ SE = $78.57 \pm 1.18\%$; $F_{1,6} = 16.8$, $P < 0.006$). There was no significant difference in performance across expression categories at the chance criterion (ANOVA: $F_{3,18} = 0.221$, $P = 0.88$), but the difference in performance approached significance by the final criterion ($F_{3,18} = 2.95$, $P = 0.06$). There was no significant interaction between expression type and performance at the two criteria (expression $\times$ criteria: $F_{3,18} = 1.04$, $P = 0.40$). Thus, the manner in which facial expressions were discriminated did not change with repeated exposure. Figure 3 illustrates the mean performance ($\pm$ SE) for each expression type at both criteria.

Experiment 2: Facial Expression Matching with Nonidentical Pictures

Stimuli and procedures—The stimuli used in experiment 2 consisted of the same facial expression categories as in experiment 1, although all new examples were used with no repetition of any individual photograph within this task. In addition to the four expressions, neutral portraits were also included as a nonmatching category only, and this always showed

a different individual monkey from those represented in the matching pair. Each image was edited as described above. In this experiment, all of the individual monkeys within a trial were unique, such that the correct pair showed two different individual monkeys making the same facial expression and the nonmatch showed a different monkey making a different expression (see Fig. 4). The expressions were paired in a dyadic format, similar to previous studies in chimpanzees (Parr et al. 1998, 2008b). According to this procedure, every expression was paired with every other expression type, so every dyadic combination of expressions (including the four neutral foil trials) was represented in each direction (e.g. BT versus SC, and SC versus BT).

The stimuli were presented in seven rounds in the following format: a, b, c, d, c, b. Every round included the four neutral trials, where each expression category was paired with a neutral foil (e.g. BT + N, PF + N, OMT + N, SC + N). Round 1 presented the four neutral trials plus the three dyadic trials for the play face (e.g. PF + TH, PF + BT, PF + SC). Each of these seven trials was repeated eight times in a single session, totalling 56 trials (32 neutral control trials + 24 PF dyads). In round 2, the BT dyadic trials were added, so this round contained the four neutral controls, the three dyadic PF and three dyadic BT trials (10 unique trials). Round 3 added the OMT trials (13 unique trials), and round 4 added the final category, SC (16 unique trials). So as not to present too many trials in a single session, in rounds 2–4, each trial was repeated only four times and subjects were tested twice per day. According to this format, round 2 had 40 trials per session, round 3 had 52 trials per session, and round 4 had 64 trials per session. After round 4, expression categories were removed, starting with the first one added, the PF. Round 5, therefore, presented neutral, BT, TH and SC trials (2×52 trial sessions). Round 6 presented neutral, TH and SC trials (2×40 trial sessions). In the final round 7, neutral and SC trials were presented and, as in round 1, these were presented eight times each totalling 56 trials in a single session. According to this procedure, each expression type was presented in four different rounds, where each trial was seen a total of 32 times.

Subjects' performance for each expression category was analysed separately using a repeated measures ANOVA where the dyad was the within-subject factor. A confusion matrix was then created for each expression category where the distribution of errors for each dyad within that category was calculated. This confusion matrix was analysed using a multidimensional scaling (MDS) analysis, which produces a geometrical map, or cluster plot, of expressions illustrating their perceived dissimilarity (Everitt & Dunn 2001; Parr et al. 2008b). In this case, perceived dissimilarity was inferred from the error performance, where a low percentage of errors resulted in expressions being widely dispersed in the cluster plot, indicating a high degree of perceived dissimilarity. Data from the trials containing a neutral foil were analysed separately so as to create a square, asymmetrical matrix for MDS analysis using a Euclidian distance scaling model.

Results—The mean performance across each expression dyad can be seen in Table 1. To perform above chance on 32 trials, subjects were required to exceed 67% correct, or 22/32 correct responses (binomial test: $P < 0.05$). Repeated measures ANOVAs for each expression category showed that performance differed depending on the identity of the nonmatching, or foil, expression, for the bared-teeth display ($F_{2,12} = 27.87$, $P < 0.001$) and the open-mouth threat ($F_{2,12} = 20.82$, $P < 0.001$). No differences were found for performance on the play face ($F_{2,12} = 1.77$, $P = 0.21$), or scream expressions ($F_{2,12} = 2.72$, $P = 0.11$). Follow-up comparisons were performed using paired t tests to determine how performance on these expression types differed depending on the foil category. These were adjusted for multiple comparisons using Bonferroni's correction procedure ($\alpha^1 = \alpha/\text{number of comparisons}$) where there were three possible comparisons per category ($\alpha = P < 0.017$). These analyses revealed significant differences for all possible dyads involving the bared-teeth display (BT–PF versus BT–TH: $t_6 = 4.22$, $P < 0.006$; BT–PF versus BT–SC: $t_6 = 3.84$, $P < 0.009$; BT–TH versus BT–SC: $t_6 =$

6.93, $P < 0.001$). For discriminations involving the open-mouth threat, significant differences were found between TH–PF and TH–BT ($t_6 = 4.97$, $P < 0.003$) and between TH–PF and TH–SC ($t_6 = 6.06$, $P < 0.001$).

Table 2 shows the confusion matrix, the percentage of errors made for each expression category based on the identity of the foil (number of errors for dyad A–B/total errors expA). Thus, the errors sum to 100% for each sample expression category. The matrix is asymmetrical, in that performance for dyad A–B was independent of performance for dyad B–A. These data were then subject to a multidimensional scaling analysis (MDS) using SPSS 15.0. The MDS model produces a stress value corresponding to how closely it fits the original dissimilarity matrix (Table 2), where lower values indicate less stress and therefore more stability. Young's S-Stress formula 1 produced five iterations that corresponded to an S-Stress value of 0.005, which is a good indicator that that model could not be improved further. Similar stress values were reported in previous studies (Kanazawa 1996). Overall, the Kruskal's stress formula 1 was less than 0.003, again indicating an excellent fit with the original data matrix (as a rule of thumb, 0.2 = poor fit, 0.1 = fair fit, 0.05 = good fit, 0.025 = excellent fit; Everitt & Dunn 2001). The model also indicated that over 99% of the variance in the matrix was accounted for ($R^2 = 0.999$) by the distances shown in the cluster plot (Fig. 5).

Performance on the neutral foil trials was very high for all expression categories except the scream (Table 3). A significant main effect of expression type was found ($F_{3,18} = 11.11$, $P < 0.001$). Performance on play face and bared-teeth displays differed significantly from scream (PF versus SC: $t_6 = 4.97$, $P < 0.003$; BT versus SC: $t_6 = 5.46$, $P < 0.002$), and the difference between open-mouth threat and scream approached significance ($t_6 = 2.36$, $P = 0.056$).

DISCUSSION

In the first experiment, subjects performed above chance matching identical pairs of four expression categories, scream, bared-teeth display, open-mouth threat and play face, when paired with every other category on the first testing session. Performance across expression type also remained stable as more trials were given, indicating that the manner in which the expressions were first discriminated did not change after repeated exposure, and the identity of the nonmatching expression did not interfere with the detection of the identical match. This was not an unexpected result as monkeys could simply use a pattern-matching strategy to perform the trials correctly. However, the neutral foil trials in experiment 2 presented two different monkeys making the same facial expression as the correct pair, and the nonmatch showed a third neutral monkey. In this case, subjects were easily able to match the same expression across individual identity, making a pattern-matching explanation unlikely. It remains possible, however, that subjects were aided by a strategy whereby they avoided the neutral face, as trials where the foil was another expression caused greater difficulty. Avoidance of the neutral face would require either gradual learning based on reinforcement history over repeated trials, or a strategy from day 1 that would predict uniformity across subjects and expression types. It is not clear whether subjects used this strategy in cases where the choice was not clear. Although the exact details of the stimuli differed, the performance of the seven subjects in our experiment appeared to be much better than that reported by Kanazawa (1996) for Japanese macaques, where only one of two monkeys learned to match an identical pair of facial expressions (similar to experiment 1) only after many trials. Whether this reflects species differences or differences in the experimental details is not clear.

To understand how rhesus monkeys discriminate facial expressions, we examined the pattern of errors for each expression dyad in experiment 2 using multidimensional scaling analyses (Fig. 4). Using this analysis, the perceived dissimilarity among facial expression pairs can be interpreted by considering the unique configuration of features present in each. To assess

unique features of facial expressions, we adapted the Facial Action Coding System, or FACS, used for humans (Ekman & Friesen 1978), in which facial movement is described according to the action of the underlying facial muscles. Each movement is referred to as an 'action unit', or AU, and given a numerical code (e.g. AU1 + 2: brow raiser, raises brow up; AU5: upper lid raiser, widens the eye; AU10: upper lip raiser, raises the upper lip). A similar system has been developed for chimpanzees (Vick et al. 2007) and macaques (L. A. Parr, B. M. Waller, Burrows, S. J. Vick & K. M. Gothard, unpublished data). The bared-teeth display, for example, is characterized by a raising of the upper lip (i.e. AU10) and a depression of the lower lip (AU16), completely exposing the teeth, and a slight lip-corner retraction (AU12), pulling the mouth corners back and up (Fig. 1). Like the bared-teeth display, the scream expression also exposes the upper and lower teeth by raising the upper lip and depressing the lower lip, respectively (AU12 + AU16), in addition to the lip corners being pulled backwards and up (AU12). However, unlike the bared-teeth display, the mouth of the scream is stretched wide open, AU27 (Fig. 1). In the open-mouth threat, the brow is notably raised, flattening the brow ridge (AU1 + 2) and causing the eyes to appear wide open and staring (AU5). There is also an open-mouth display with the lips funnelled forward (AU22 + AU26), but no exposure of the teeth (Fig. 1). Finally, the play face is characterized by the mouth stretched wide open (AU27), as in the scream, and a depression of the lower lip (AU16), exposing the bottom teeth. The upper teeth, however, are concealed, similar to the play face of the chimpanzee (Parr et al. 2008b). In contrast to humans and chimpanzees, the rhesus monkey play face does not necessarily contain a distinct lip-corner retraction, or AU12, caused by the contraction of the zygomatic major muscle (see Fig. 1). In summarizing these features with regard to the perceived dissimilarity shown in Fig. 4, dimension 1 can be characterized by the degree to which the mouth is stretched open, exposing the teeth (AU27), as in the play face and scream, or the degree to which the lips are funnelled forward with raised brow (AU1 + 2 + AU22), as in the open-mouth threat. Although it is difficult to code brow lowering from still photographs, the play face and scream expressions used in this study appeared to have less brow raising than did the open-mouth threats and bared-teeth displays. Thus, brow position may also be important in describing dimension 1 (Fig. 1).

Dimension 2 can be characterized by degree to which the bottom lip is depressed (AU16), as in the bared-teeth display and play face, or retracted (AU12), as in the scream. The open-mouth threat has no teeth exposure, so it falls near the midpoint of dimension 2. The distribution of these expressions with regard to FACS coded movements is similar to the results of principal components analysis covering a detailed ethogram of visual components associated with macaque visual and vocal signals (Partan 2002). The only real difference being that scream and 'grimace' (probably the bared-teeth display) were clustered in the same quadrant of the two-dimensional plot in Partan's (2002) study; however, this is not surprising given that Partan's (2002) study included many more behavioural elements, including vocalizations and body postures. Notably, Partan (2002) found no significant contribution of brow position. Our results are also consistent with previous eye-tracking studies in macaques that showed the greatest attention to the mouth and eye region for open-mouth threat and bared-teeth displays (Nahm et al. 1997; Gothard et al. 2004). Our results also highlight some differences between facial features that are important for facial expression discrimination in rhesus monkeys and chimpanzees, where upper facial features and brows appear to be important for discrimination in rhesus monkeys but to have little or no diagnostic role in chimpanzees (Parr et al. 2008b).

Despite the specific features described above, the discrimination performance for expression dyads in experiment 2 was often quite poor (see Table 1), and considerably lower than the performance of chimpanzees using similar procedures (Parr et al. 1998, 2008b). Of the 12 possible dyadic expression combinations, subjects' performance exceeded 75% on only five, with reasonably consistent performance observed only for the play face (mean 80% across foil categories). In fact, subjects' performance revealed a moderately strong stimulus bias for the

play face, in that they selected it over 50% of the time when it was the foil. For example, in the open-mouth threat and play face combinations, where the play face was the foil, subjects selected the play face over 77% of the time despite never being reinforced. Subjects also had difficulty discriminating bared-teeth displays from screams, possibly because both expressions share lip movements that expose the teeth, particularly the raised upper lip (AU10) and lip corner puller (AU12). In contrast, chimpanzees never confused these two expressions (Parr et al. 2008b), even though they share the greatest number of features in common. The function of screams in chimpanzees and rhesus monkeys appears to be quite similar in signalling the intensity of the conflict (Gouzoules et al. 1984; Slocombe & Zuberbühler 2005); however, use of the bared-teeth display has notable differences (de Waal & Luttrell 1985; Waller & Dunbar 2005). Whether these species differences can account for our results, however, is unclear. Moreover, performance discriminating open-mouth threats and screams in both dyadic directions was around 50%, despite there being no clear shared feature between these two expressions other than an open mouth, which is stretched to a lesser degree in the threat (AU26-jawdrop) than in the scream (AU27-mouth stretch). Previous authors have speculated that the visual scan patterns of macaques can be grouped according to the affective quality of the display, where similar scan patterns may be observed for threatening and fearful expressions (open-mouth threat and bared-teeth displays) versus submissive ones (lipsmacks) (Nahm et al. 1997). Thus, subjects might have difficulty discriminating between open-mouth threats and screams because they use similar scan patterns for both, but our results do not support this distinction because subjects had little difficulty discriminating bared-teeth displays from open-mouth threats, which both fall in the threatening/fearful category.

Among humans, facial expression discrimination is accomplished primarily using configural information (Calder et al. 2000; Bimler & Paramei 2006). However, the presence of a single characteristic features can increase recognition rates several fold over instances where that feature is absent (Kohler et al. 2004). Moreover, while single features do not reliably exemplify a particular expression, changing a single feature can dramatically affect the judgment of a particular expression, and recognition rates between different expressions may suffer if they share too many key features in common (Wallbott & Ricci-Bitti 1993). Based on subjects' overall performance on the expression dyads in experiment 2, and the MDS analysis, it does not appear that the monkeys were attending to specific, unique (or diagnostic) features during these tasks. This was confirmed by their ability to rapidly and accurately discriminate facial expressions from a neutral portrait when posed by different individuals, where the specific features of these expressions were subject to individual variation. As has been argued for chimpanzees and humans, it appears that a combination of featural and configural strategies may be used by monkeys. The development of the Maq-FACS, an objective tool for describing facial movement in the rhesus monkey, will be critical for future studies because it will provide an objective tool for standardizing facial expressions according to discrete movements. These standardized associations can then be used to guide the development of a more prototypical stimulus set where each individual expression can be compared according to the presence or absence of specific facial features.

Finally, it should not be concluded from these experiments that facial expressions are not salient, emotional stimuli for rhesus monkeys. This experiment presented only static pictorial representations of facial expressions, which are normally dynamic, multimodal stimuli occurring within a specific social context. While it seems intuitive that monkeys are able to recognize expressions in a natural context, and perhaps even gain information about the sender's emotional state, there is virtually no existing data to show how monkeys are able to accomplish these perceptual tasks or whether these mechanisms are similar to those in humans. In contrast, humans (and chimpanzees) perform exceptionally well discriminating facial expression from similar two-dimensional static pictures, and even from computer-generated cartoons of expression categories (Wallbott & Ricci-Bitti 1993; Kohler et al. 2004; Parr et al.

2008b). At this early stage of inquiry, it is unclear whether facial expressions are less representational to monkeys or whether the lack of standardized stimuli and high degree of individual variation may best explain these species differences. Thus, it is important that future studies build on the data presented here to create more standardized examples of facial expressions, quantify the individual variability across expression categories, and ultimately incorporate other ecological factors such as familiarity, social context and multimodal cues to provide a more complete picture of how monkeys are able to recognize and discriminate these important social stimuli.

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Figure 1.
Example of four facial expressions in rhesus monkeys. From left to right, the bared-teeth display, scream, open-mouth threat and the relaxed open-mouth face (play face).

Figure 2.
Example of a matching-to-sample trial used in experiment 1.

Figure 3. Mean performance by subjects on each facial expression category during experiment 1, assessed at two criteria.

Figure 4.

Example of a matching-to-sample trial used in experiment 2. Three individuals are shown. In the correct pair, each individual is making a scream face, while the nonmatching stimulus is a third individual making an open-mouth threat (bottom right).

Figure 5.

Cluster plot created through multidimensional scaling analyses showing the perceived dissimilarity of facial expressions in experiment 2. The distance between the expressions represents their perceived dissimilarity.

Table 1

Mean performance (+SE) on each expression dyad in experiment 2

Sample expression	Foil expression			
	PF	BT	TH	SC
Play face (PF)		86.16+6.24	68.75+9.79	86.16+3.91
Bared-teeth (BT)	58.93+6.59		77.23+5.00	29.91+7.62
Open-mouth threat (TH)	22.32+7.10	80.36+5.53		55.80+6.00
Scream (SC)	56.70+10.19	76.34+5.49	48.66+6.85	

Table 2

Confusion matrix for performance on each expression dyad in experiment 2

Sample expression	Foil expressions			
	PF	BT	TH	SC
Play face (PF)	80.36	23.48	53.03	23.48
Bared-teeth (BT)	30.67	55.36	17.00	52.33
Open-mouth threat (TH)	54.89	13.88	52.83	31.23
Scream (SC)	36.60	20.00	43.40	60.56

Overall percentage correct for each expression category is given in bold. Rows show the distribution of errors for each foil expression based on the overall number of errors for each sample expression.

Table 3

Mean performance (+SE) on neutral face trials in experiment 2

Subject	Expression category			
	PF	BT	TH	SC
Rocket	96.43	98.21	96.43	51.79
Samosa	100.00	100.00	91.07	75.00
Olive	98.21	96.43	51.79	69.64
Onion	98.21	100.00	89.29	66.07
Chewey	100.00	98.21	89.29	67.86
Lemon	98.21	94.64	98.21	42.86
Caramel	91.07	94.64	96.43	89.29
Mean	97.45	97.45	87.50	66.07
SE	1.16	0.86	6.11	5.73

Each expression type was paired with a neutral portrait. Every stimulus showed a different individual.