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Monkeys and Mug Shots: Cues Used By Rhesus Monkeys (*Macaca mulatta*) to Recognize a Human Face

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We investigated the cues rhesus monkeys (*Macaca mulatta*) use to recognize a familiar human face. To manipulate facial cues, schematic faces were constructed with Identi-Kit materials derived from mug shots. The monkeys ($N = 4$) spontaneously classed Identi-Kit stimuli as faces on initial presentations. The monkeys then learned to distinguish one Identi-Kit face, the standard, from others. Panel presses indicated recognition of the standard face. Eye movement recordings revealed that the monkeys predominantly fixated on the eyes of the standard face. When the standard face was transformed by removing, altering, or reorienting its features, only alterations of eyes or brows lowered recognition; removal of eyes, brows, nose, or lips did not. Responses to rotated, inverted, and scrambled versions of the standard face varied but generally disrupted recognition. We concluded that features and configuration were used to recognize the human face.

Primate social relationships depend on the ability to identify individual animals. The conspicuous way in which primate facial features cluster about the front of the head corresponds with the importance of quick and reliable recognition (Gregory, 1929/1965). Facial features and their configural relationships provide the basic input for the identification process among humans (Bruce & Young, 1986; Ellis, Shepherd, & Davies, 1979; Shepherd, Davies, & Ellis, 1981) and perhaps among other primate species, as well (Boysen & Berntson, 1986; Rosenfeld & van Hoesen, 1979). In our research we anticipated cross-species parallels in the face-identification process by examining the role of physiognomic cues in a face-recognition task performed by nonhuman primates.[1]

In our study rhesus monkeys were trained to identify a familiar, schematic human face constructed from police Identi-Kit materials. Researchers use these materials because they provide a controlled, systematic means of varying facial features and configuration. To date, stimuli created from Identi-Kit (and Photofit) have been used in studies of face recognition with only human subjects (e.g., Hines & Braun, 1990; Matthews, 1978; Walker-Smith, Gale, & Findlay, 1977; see also Davies, Ellis, & Shepherd, 1981). We used these materials to alter facial information systematically for studying face recognition in monkeys.

We expected our nonhuman primate subjects to respond to Identi-Kit faces much as they would any other facial stimuli. Past research has shown that monkeys are adept at a wide variety of facial judgment tasks. Laboratory studies have demonstrated that (a) monkeys and apes respond to photographs of nonhuman primate and human faces as faces (Boysen & Berntson, 1986, 1989; Keating & Keating, 1982; Overman & Doty, 1982), (b) they recognize conspecifics and humans from portrait photographs (Boysen & Berntson, 1986, 1989; Rosenfeld & van Hoesen, 1979), and (c) monkeys class monkey and human faces together in a *face* category (Perrett et al., 1988; Sands, Lincoln, & Wright, 1982). Neuropsychological studies indicate that face perception relies on similar brain mechanisms in nonhuman primates and humans (Perrett et al., 1988).

Our aim was to determine the facial information monkeys use to recognize a familiar face. First, the monkeys learned to distinguish one Identi-Kit face, the *standard*, from 24 others. The standard face was then corrupted in a controlled fashion by sequentially removing one of five features (eyes, eyebrows, nose, lips, or chin) in order to test the importance of single features in the recognition process. We also explored the elasticity of the monkeys' template of the face by substituting the familiar features of the standard with others that varied in size and shape. Additional experimental manipulations altered the placement and orientation of familiar features. Eye-movement records and recognition responses were made as the monkeys judged the succession of faces.

On the basis of earlier studies of human and nonhuman face recognition, we hypothesized that eyes would be the primary recognition cue and capture a disproportionate share of fixations (Cook, 1978; Keating & Keating, 1982; Kyes & Candland, 1987; Mendelson, Haith, & Goldman-Rakic,

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[1] Whether monkeys perceive facial stimuli as *faces* the way humans do may be debated. Much like the conventions *triangle* or *square* are used to describe shapes, the use of *face* to describe facelike stimuli functions as the standard convention used to communicate what we infer the monkeys perceive.

1982; Yarbus, 1967). Features internal to the standard face (e.g., eyes, brows, lips, and nose) were predicted to attract more fixations than external facial features (e.g., foreheads and chins); such a result would reflect a greater reliance on internal structures for the recognition process (Ellis et al., 1979; Walker-Smith, Gale, & Findlay, 1977).

Recognition of the standard face was expected to be affected by some facial transformations but not by others. Theorists have argued that elasticity in the internal representation of familiar faces is required in order to maintain recognition when visual access to facial regions is restricted, for example, when faces are partially occluded or seen in degrees of profile (Bruce & Young, 1986; Diamond & Carey, 1986; Ellis, 1981). Thus, monkeys were not likely to behave as single-feature detectors (Carey & Diamond, 1977), and we did not expect the absence of a single feature to reduce recognition rates significantly.

Recognition was expected to rely as much on information about relations among features (configuration) as on information about the distinctive properties of the features themselves (Bruce & Young, 1986; Diamond & Carey, 1986; Haig, 1984; Sergent, 1984). In practice, it may even be difficult to distinguish between feature properties and configuration (Bruce & Young, 1986), especially when experimental transformations of the size and shape of familiar features consequently alter spatial relations among them.

Transformation of a familiar feature by changing its size and shape was predicted to disrupt recognition of the standard face, although removal of the feature was not. The more extreme the feature transformation, the greater the violation of featural and relational cues and, therefore, the greater the expected disruption in recognition rates. The disruptions in recognition created by feature transformations were expected to correspond with shifts in visual fixation patterns as the monkeys scanned for reliable facial cues (Walker-Smith et al., 1977).

We also explored the impact of inverting and rotating the standard face and scrambling its features. In humans, inverting faces apparently alters the way in which facial information is processed and lowers identification rates when faces are presented upside down during recognition or learning trials (Diamond & Carey, 1986; Sergent, 1984; Valentine, 1988, 1991; Yin, 1969). In monkeys (*Macaca mulatta*), Bruce (1982) and Rosenfeld and van Hoesen (1979) have reported that inversion had little effect on the face recognition of conspecifics. However, Overman and Doty (1982) found that macaques had greater difficulty matching inverted compared to upright monkey and human faces. More recently, Perrett et al. (1988) presented behavioral (reaction-time) data and neurophysiological evidence that suggested that face processing in the monkey is most efficient when faces are presented in the upright orientation.

Thus evidence bearing on the effect of transformations that reorient facial features is inconsistent for monkeys. We explored recognition responses to inverted, rotated, and scrambled versions of the familiar face and tracked the fixations that accompanied them. On the basis of recent research, we predicted that these reoriented facial arrays would interfere with recognition (Overman & Doty, 1982; Perrett et al., 1988). Fixations patterns were expected to reveal the cues monkeys relied on to make judgments about the reoriented, facial stimuli.

Method

Subjects

The subjects were 2 male and 2 female adult rhesus monkeys (*Macaca mulatta*).

Apparatus

Facial stimuli were created with the Smith-Wesson Identi-Kit Model II. The Identi-Kit contains transparencies of hundreds of physiognomic elements originally sketched from thousands of human facial photographs, actually, from mug shots taken of convicted criminals. Law enforcement personnel typically use the Identi-Kit to construct the facial appearance of alleged criminals from eyewitness accounts. The faces we created were photographed and rear-projected onto a screen from a 35-mm carousel slide projector.

Eye movements were recorded with the scleral coil technique. Position of the eye was transduced from current induced in three turns of wire wound about the sclera of one eye as it rotated in a two-dimensional magnetic field. The horizontal and vertical position of the eye was sampled every millisecond and digitized. A microprocessor separated fixations from saccades by a velocity criterion. Before testing, the monkey was required to fixate a matrix of calibration lights on the viewing screen. The eye coil voltages collected during this task allowed the computer to plot the location of fixations with reference to pictures of faces later presented to the monkey. The system calculated the location of fixations to within 1° of visual angle.

Eye movements were recorded in 3 of the subjects. As they sat in a primate chair, a head position toward the center of the screen was maintained by a head holder. The fourth subject was free to move its head, although the primate chair prevented it from turning its back on the screen. Eye position at the start of the trial could not be controlled in this subject.

A pair of push panels were located in front of the primate chair and below the projection screen.

General Procedure

Two blocks of 100 trials composed a typical daily testing session. During testing, the monkeys faced the projection screen and press panels depicted in Figure 1. Subjects initiated a stimulus presentation by fixating a red spot at the center of the projection screen for 500 ms. The red spot was then replaced by a stimulus face accompanied by a warbling tone that lasted for 5 s. The tone signaled a forced viewing time. A panel press during this period aborted the trial without a reward. The delay prevented monkeys from pressing a panel without scanning a face.

The stimulus appeared until the monkey responded to it with a panel press or for 30 s if no response was made. Under reinforcement conditions, if the response was correct, the monkey received 0.1 ml of juice through a tube at its mouth, the stimulus disappeared, and an intertrial period of 0.8 s was imposed before the next trial. No juice and a longer, 1.2-s interval between trials penalized an incorrect response. On critical probe trials reward was given randomly and was not determined by the monkey's response.

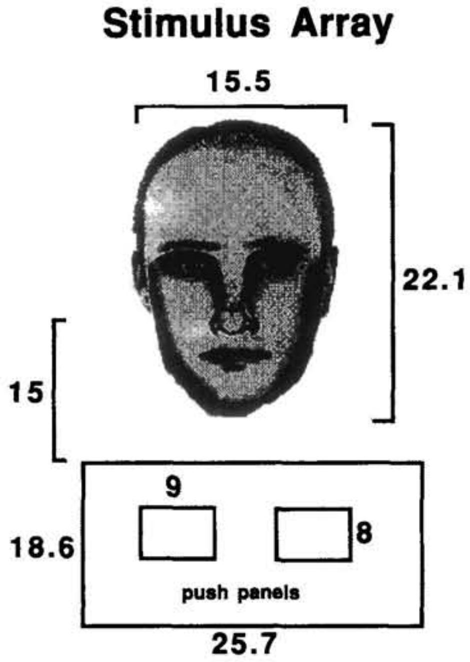

Figure 1. Schematic representation of the stimulus array depicting degrees of visual angle.

Pretraining and Experimental Training

Color. The monkeys learned the basic elements of the task by training on a color discrimination task. Appearance of a blue field required them to push the left panel, a red field the right panel. They were judged to have learned this when they responded correctly in 90 of 100 trials of a block.

Faces versus nonfaces. The monkeys learned to distinguish photographs of faces from photographs without faces in them. Half of the photographs contained faces of humans, chimpanzees, or various monkey species. The other half contained body parts or inanimate objects but no faces. After the monkeys learned to sort one set of such photographs into face and nonface categories to a criterion of 90% correct, they were retested on a novel set to confirm they had not just memorized a sequence of individual photographs.

Classing Identi-Kit faces. This task determined whether monkeys classed Identi-Kit mug shots as faces: That is, on initial presentations (rewarded at random), would monkeys place Identi-Kit faces into the same face category as human, ape, and monkey faces? Thus, after the monkeys had learned to distinguish face from nonface photographs, they were given a novel set of these slides, this time with 12 Identi-Kit faces mixed into the block of trials.

Standard versus random Identi-Kit faces. A standard face was composed with features randomly selected from the Identi-Kit with the restriction that each facial element be of intermediate size. The standard face was to be distinguished from 24 *random* Identi-Kit faces. Each random face was constituted of features selected at random with the restriction that none of the standard face elements were used. A press on the left panel in response to the standard face was rewarded, and a press on the right panel earned a reward for the appearance of any random face.

When the monkeys had learned the standard versus random face discrimination to criterion of 90% correct in a block, they were retested with a novel set of random faces to establish that they had not merely memorized a particular set of slides. Another retest presented the faces at different positions on the screen to confirm that the monkeys' did not rely on local luminance cues.

Experimental Manipulations

Once they had learned the standard face to a criterion of 90 correct presses in 100 trials (and across two different sets of random faces), the main experiment began. These trials repeated the standard versus random discrimination but included 12 probe trials embedded into every 100 trials in the same random order. A group of 44 random and 44 standard faces completed the set.

On probe trials the standard face appeared, but it was distorted in some way that tested the limits of the monkey's template of that face. To the extent that the monkey chose the left panel on the 12 probe trials, it judged the distortion to still be the standard face. To avoid guiding the monkey's choices, the panel presses on probe trials were rewarded 50% of the time according to a random sequence. The experimental manipulations proceeded in a set order.

Feature removal. Each of five features (eyebrows, eyes, nose, lips, and chin) was individually removed from the Standard.

Feature substitutions. Each of five features (eyebrows, eyes, nose, lips, and chin) was individually substituted with one of a different type and size. The most obvious dimension along which the features varied was size: Two were dramatically smaller or larger and two were slightly smaller or larger than the standard feature.

Rotated, inverted, and scrambled features. The spatial arrangement of the standard face's features was systematically altered in four different ways: The Standard face was rotated or inverted, and its features were scrambled in two separate arrays.

Results

Training

Classing Identi-Kit faces as faces. Before training on the standard face, each monkey performed a sorting task to establish whether it classed Identi-Kit portraits as faces distinct from objects and other body parts. When interspersed among the complement of 16 other face and 24 nonface phot graphs, Monkeys 1 and 4 spontaneously classed the Ident Kit stimuli as faces on 8 of 8 initial presentations, and Mo keys 2 and 3 did so on 7 of 8 initial trials ($ps < .04$, one-taile binomial tests). These results are comparable with those r ported by Perrett et al. (1988). In addition, all subjects class nonface photographs correctly 85% of the time or better.

We then trained our subjects to distinguish one Identi-K portrait, the standard, from an array of others. They conti ued to train until achieving a rate of 90 out of 100 corre trials for two 100-trial blocks.

Fixations on the standard face. At the conclus training, we analyzed fixations from the 3 subjects wit movement data in order to test predictions about the r importance of different facial features for the identifi of the standard face. We first partitioned the face stimu sectors representing the forehead, brows, eyes, nose, li chin. No part of the face was left undefined: Every o fixation was assigned to one of these regions. A re measures analysis of variance (ANOVA) to compare t centage of fixations on each of six facial regions (av across each monkey's 12 trials) indicated significant differences in the amount of visual attention directed toward each feature of the standard face, $F(5, 10) = 3.87, p < .033$.[2] As predicted, the region of the eyes captured the greatest percentage of fixations ($M = 64\%$). On average, the brow, nose, and lip regions accumulated few fixations ($Ms = 14\%$, 14%, and 7%, respectively). The outer regions of the face (forehead and chin areas) attracted the lowest percentages of fixations ($Ms = 1\%$ and 0%, respectively), as predicted.

These differences in fixation rates were not simply proportional to the relative sizes of feature regions. For each of the 3 monkeys, the percentage of fixations in the eye region exceeded the value expected from the relative size of the eye area ($ps < .05$).

The monkeys' scans of the standard face differed from those of other stimulus faces. Figure 2 plots fixations, collected late in training, for Monkeys 1, 2, and 3 as they scanned the standard (averaged across 10 randomly selected presentations) and random faces (a composite of fixations averaged across presentations of 10 different random faces). Figure 2 demonstrates that each monkey displayed fixation patterns in response to random faces that differed from their scans of the standard one.

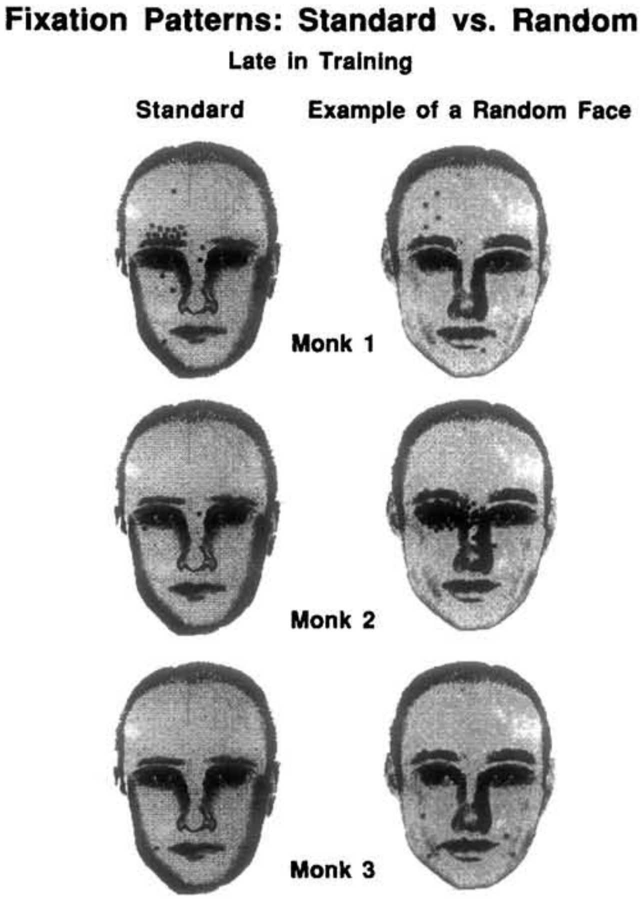

Figure 2. Fixations on the standard and random faces for 3 monkeys.

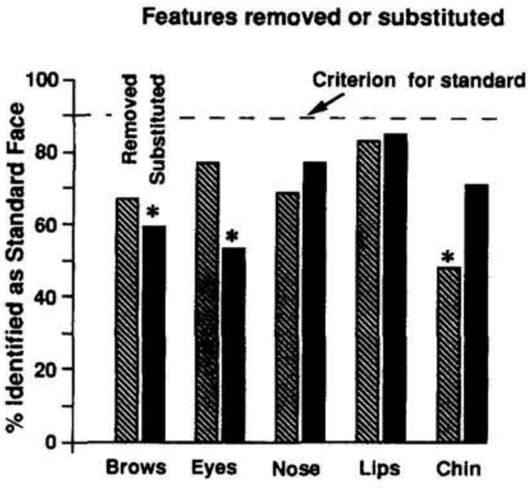

Figure 3. Mean identification rates for the standard face with features removed and substituted. (*p < .05.)

Experimental Manipulations

Feature removal and feature substitution. For each feature three analytic strategies were designed to address hypotheses about the effects of manipulating the standard face by removing a feature or by replacing a feature with one of four graded substitutes. First, we tested the prediction that feature substitution (and not removal) would disrupt identification of the standard face. The average percentage of left-panel presses (identifications) for feature removal and for feature substitution (averaged across all four graded substitutions) was compared with criterion identification (90%) of the standard face. Second, we tested whether the graded substitutions had a graded effect: Did the feature substitutions most deviant from the standard face derail identification the most? Third, to determine whether facial transformations produced shifts in fixation patterns, we compared the percentages of fixations toward designated facial regions for the standard and transformed faces.

Identification responses for feature substitution and removal. Figure 3 displays the mean percentages of identifications across all 4 subjects in response to the two types of facial manipulations. The results for eyes and brows supported our hypotheses: Substitutions of eyes and of brows reduced recognition rates significantly from criterion (90%; $Zs = -2.46$ and -2.07, $ps < .02$ and $.04$, two-tailed tests, respectively). Comparable tests for feature substitutions in the lower half of the face (nose, lip, and chin substitutions) were not statistically reliable ($Zs < 1.27$, $ps > .20$).

Feature removal was not expected to disrupt recognition significantly and generally did not: Absence of the brows, eyes, nose, and lips did not reduce identification rates reliably across monkeys ($Zs < 1.54$, $ps > .12$). However, when the chin was removed identification rates declined significantly

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[2] Statistical tests based on percentages were repeated with arcsine transformations of the data. The results of these tests were virtually identical to those we report.

($Z = -2.80$, $p < .01$, two-tailed test; see Figure 3). Perhaps the absence of a completed facial outline disrupted the integration of information about features or their spatial relations.

Identification responses for graded feature substitutions. One-way repeated measures ANOVAs comparing the effects of the four feature substitutions on identification rates were calculated separately for brows, eyes, nose, lips, and chin manipulations. Means for these analyses are depicted in Figure 4. Eye substitutions produced the pattern of identification disruption we predicted: The more the eyes deviated from the standard feature, the less often the monkeys judged the distorted face to be the standard, $F(1, 3) = 9.74$, $p < .003$. A similar pattern emerged for brows but was not statistically reliable, $F(1, 3) < 1.00$ (see Figure 4). Substitutions of the nose had a variable effect on recognition, $F(1, 3) = 18.37$, $p < .001$: Replacing the standard nose with a very large one reduced identification rates. Lip substitutions did not affect recognition differentially, $F(1, 3) < 1.00$. Responses to graded substitutions of the chin revealed an unanticipated pattern, $F(1, 3) = 4.71$, $p < .03$: The less extreme alterations degraded identification more than the extreme alterations did (see Figure 4).

Fixation patterns for feature substitution and removal. For each of five features, we compared the percentages of fixations on six facial regions (forehead, brow, eye, nose, mouth, or chin) when the feature was removed and when it was substituted (averaged across all four grades) to fixation patterns for the standard face (averaged over 12 trials late in training).

Inspection of Figure 5 reveals that in relation to the standard face, removing or substituting features generally drew the monkeys' gaze away from the eyes and toward other areas of the face. Similar to the results for identification responses,

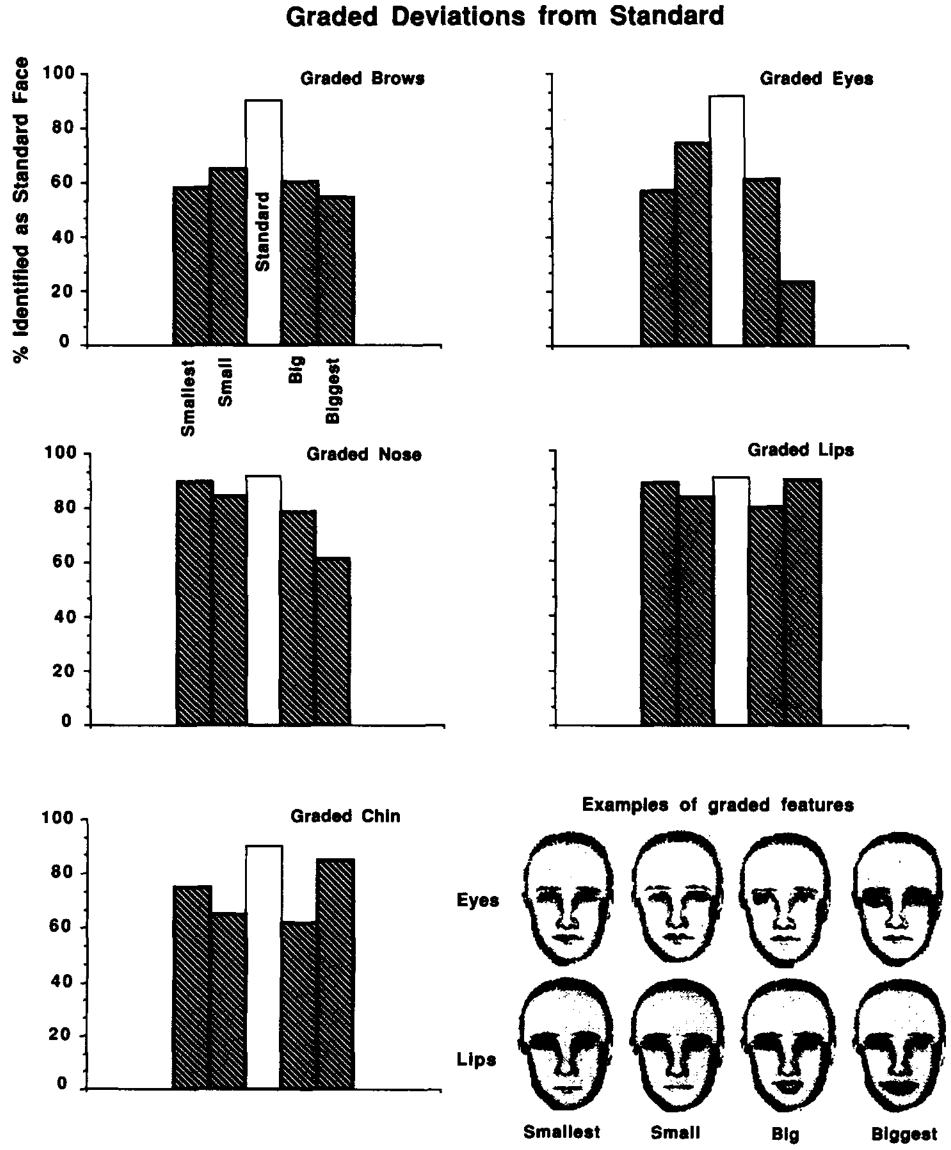

Figure 4. Mean identification rates for the standard face with graded feature substitutions.

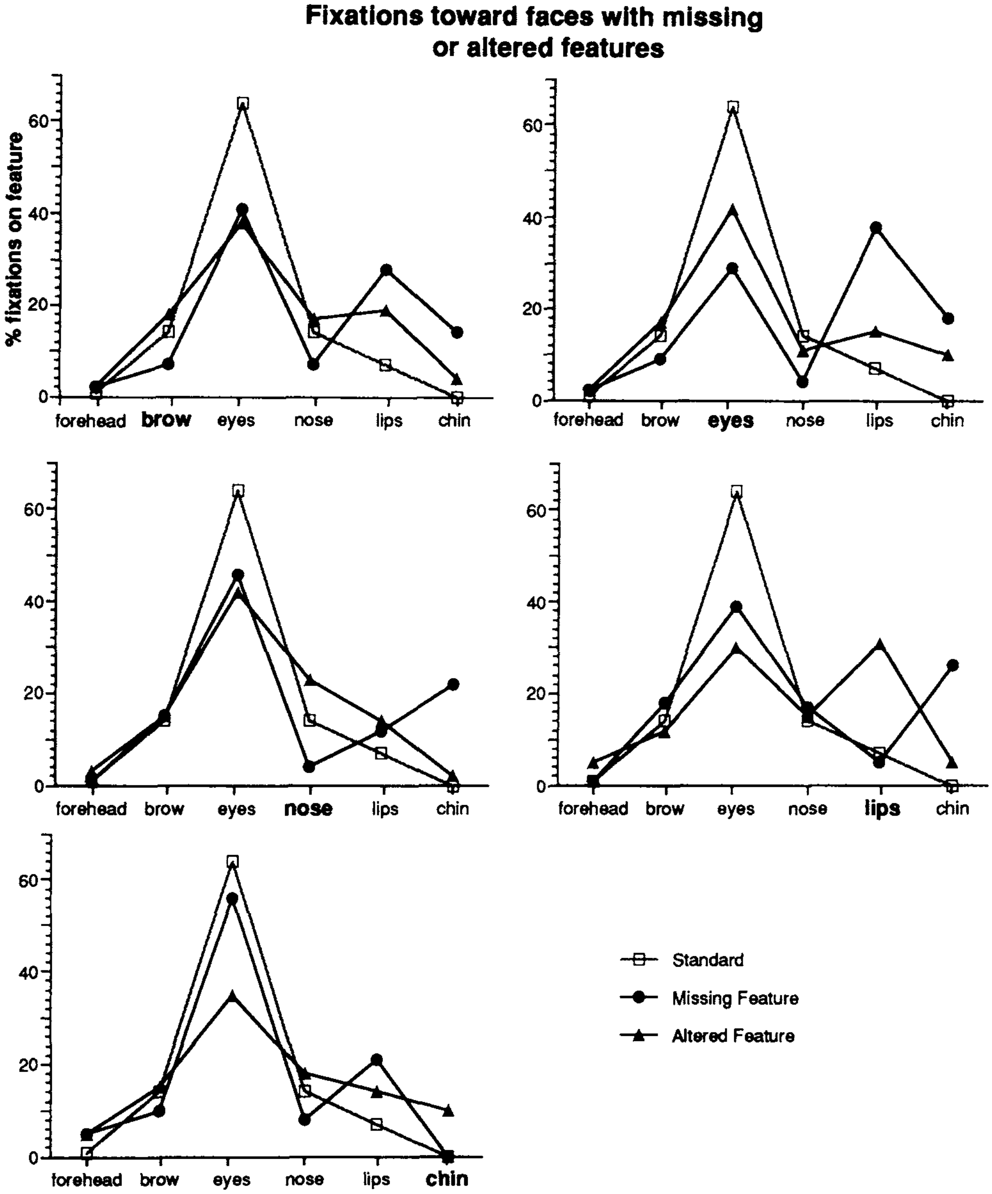

Figure 5. Mean percentage of fixations on feature regions for the standard face and two transformations.

substitutions had the greatest impact on behavior, in this case by attracting fixations to the region in which the transformation occurred. To quantify this impression we compared the percentages of fixations on each facial area from which the feature had been removed or substituted. A Wilcoxon sign rank test confirmed that across facial areas the percentages of fixations were significantly larger when the feature was substituted rather than removed ($T = 0$, $p < .05$.)

Spatial arrangement of features. How important was the spatial arrangement of features to the recognition process? Figure 6 depicts mean identification rates (averaged across all 4 subjects) for the rotated, the inverted, and the two scrambled versions of the standard face: Each rate fell significantly below criterion (90%; Zs = −2.53, −2.42, −2.80, and −2.12, respectively, $ps < .034$). A one-way repeated measures ANOVA on the percentage of identifications for each of the four manipulations indicated that there were no systematic differences in the degree to which the different distortions affected responses, $F(1, 3) < 1.0$: Identification rates generally dropped to chance levels (see Figure 6). These results were consistent with some reports (Overman & Doty, 1982; Perrett et al., 1988) but diverged from others (Bruce, 1982; Rosenfeld & van Hoesen, 1979), and so we probed each subject's responses in finer detail.

Inspection of individual identification rates revealed that although reactions to the four spatial distortions were consistent for each monkey, they varied greatly between monkeys. For example, Monkeys 1 and 3 judged none or few of

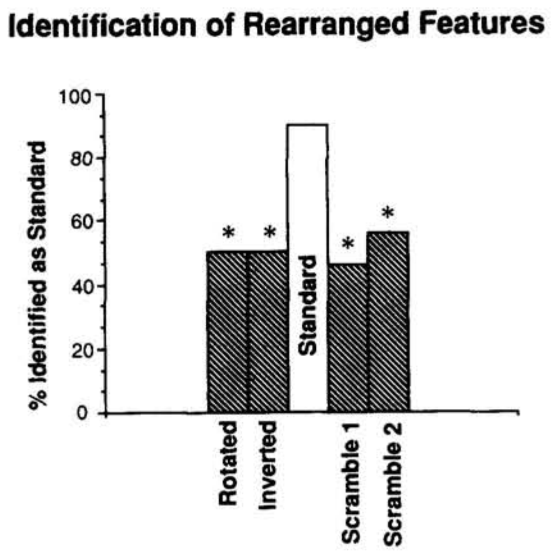

Figure 6. Mean identification rates for the rotated, inverted, and scrambled transformations of the standard face. (*p < .05.)

the four distortions to be the standard, Monkey 2 identified virtually all four distortions as the standard, and Monkey 4's responses fell consistently inbetween these extremes.

When individual gaze patterns were examined for clues, it appeared that the monkeys relied on different scanning strategies for their judgments. Figures 7, 8, and 9 depict fixation patterns and identification responses for each individual subject with eye movement data. Across the four spatial arrangements, Figure 7 indicates that Monkey 1 concentrated fixations in the area of the standard's right eye, the same area used to identify the standard. Not finding the right eye, Monkey 1 rejected all four distorted faces as the standard (see Figure 7). The fixation patterns depicted in Figure 8 suggest that Monkey 2 relied on a familiar feature in isolation: Across all but one of the four spatial rearrangements (Scramble 2), Monkey 2 fixated on the same cue associated with criterion identification of the standard (the standard's left eye), regardless of where it appeared, and judged each rearranged face to be the standard. Monkey 3's fixation patterns across the four spatial arrangements, illustrated in Figure 9, revealed that the consistent disruption in this animal's identification responses corresponded with fixation patterns very different from those associated with criterion performance on the standard face.

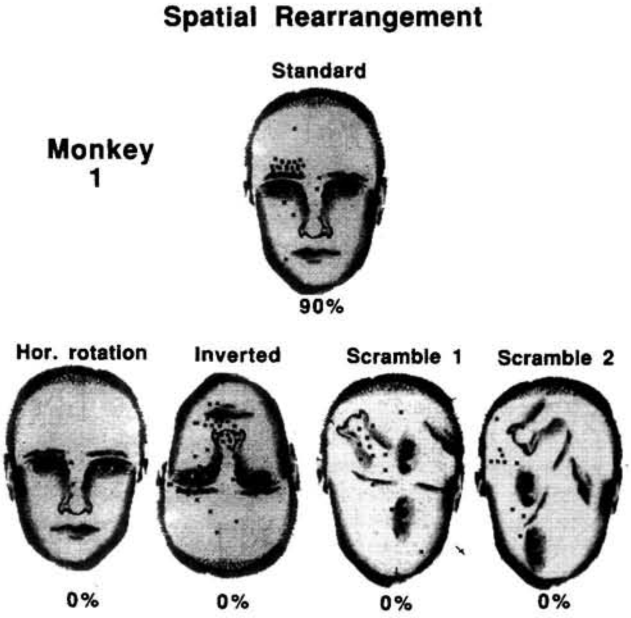

Figure 7. Fixation patterns in response to the spatial rearrangement of the standard face for Monkey 1.

Discussion

Like others (Perrett et al., 1988; Sands et al., 1982), we found that monkeys readily acquired a face category of shapes. Moreover, once learned, the category extended without further training to include some fairly abstract stimuli, Identi-Kit mug shots. We also confirmed the ability of monkeys to perform a face recognition task (Rosenfeld & van Hoesen, 1979) and extended their repertoire to include schematic faces of a different species.

The prediction that face recognition would be disrupted by altering, but not removing, familiar features was confirmed for features in the upper regions of the face. Absence of an upper region feature appeared to trigger a shift in visual attention to structures in the lower facial areas for solving the recognition puzzle. Moreover, removing any single interior facial feature (brows, eyes, nose, and lips) failed to derail recognition, which suggests that the monkeys were not single-feature detectors in the simplest sense (Diamond & Carey, 1977). Did recognition thus hinge on configurational cues? Or were multiple, independent features processed in parallel? Unfortunately, our results do not conclusively distinguish between these two processing strategies.

When deprived of information about a single feature, our subjects generally responded as if the face resembled the standard. This kind of response bias may serve some function in nature, as when animals encounter situations in which visual access to all parts of the face is constrained. Faces may not be unique in this regard. In other situations, as well, missing information causes rather little disruption in the identification of familiar patterns (Warren, 1970).

Of the facial features we tested, the eyes were most important to the recognition process. The monkeys predominantly fixated the eyes of the standard face, which corroborates previous reports (Keating & Keating, 1982; Kyes & Candland, 1987). Recognition of the standard face was disrupted by changes in eyes; the more dramatic the change, the greater the disruption. Changes in eyebrows elicited a similar, though weaker pattern; changes appearing in the lower half of the face had no systematic effect on recognition. Assuming that the responses of our subjects were inspired by facial processing strategies internal to the organism, and not simply by aspects peculiar to the Identi-Kit stimuli we used (see Ellis, 1981), it may be argued that nonhuman primates share with humans a special sensitivity to changes in features

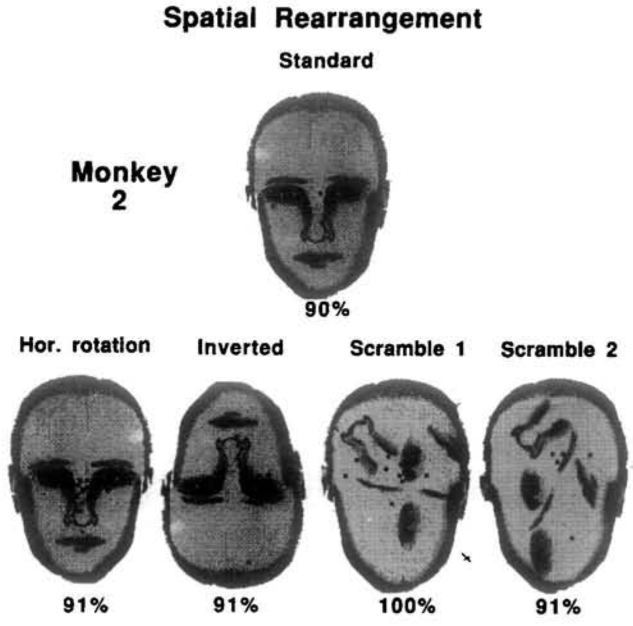

Figure 8. Fixation patterns in response to the spatial rearrangement of the standard face for Monkey 2.

in the upper portion of the face (Shepherd et al., 1981).

Several theorists have emphasized the contribution configural information makes in the face-recognition process (e.g., Diamond & Carey, 1986; Sergent, 1984; Yamane, Kaji, & Kawano, 1988; Yin, 1969). At first glance, results for the spatially distorted stimulus faces reinforce this view: Without altering the standard features per se, changing their orientation and spatial relationships by inverting, scrambling, or rotating them lowered recognition rates across all four monkeys combined. In contrast to researchers who have reported no inversion effect for monkeys (Bruce, 1982; Rosenfeld & van Hoesen, 1979), our data generally supported those who have argued that monkeys, like humans, are specialized to process faces most effectively in the upright orientation (Overman & Doty, 1982; Perrett et al., 1988).

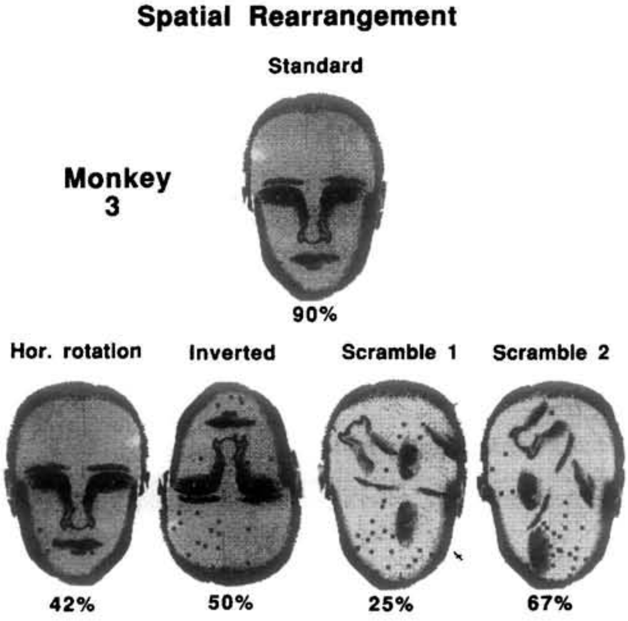

Figure 9. Fixation patterns in response to the spatial rearrangement of the standard face for Monkey 3.

To shed some light on these discrepant reports, we probed each of our individual monkey's responses to the spatially rearranged faces and discovered that although recognition was generally depressed for 3 of our 4 animals, 1 monkey identified each of the spatially distorted stimuli as the standard. From the eye fixations that accompanied identification responses, it appeared that this animal used a distinctive strategy to resolve the recognition question. The monkey that judged all of the spatial distortions to be the standard persistently fixated the single feature (an eye) it used to identify the standard, regardless of where it appeared on the face. From the monkey's point of view, it was as if we had asked for the identification of a single, isolated feature rather than a face.

In contrast, the animal that judged none of the spatial transformations to be the standard predominantly fixated the facial area it typically relied on for reliable cues. The cues this monkey found in their place were discrepant both in structure and in relation to surrounding features. Given this processing strategy, a manipulation as subtle as horizontal rotation was enough to disrupt identification of the standard.

Though the data are not unequivocal, it appears that monkeys can rely on isolated, distinctive features or configuration to make facial discriminations. Perhaps this is why laboratory studies of facial inversion effects in monkeys have produced such diverse results (e.g., Bruce, 1982; Overman & Doty, 1982; Perrett et al., 1988; Rosenfeld & van Hoesen, 1979). In more natural settings, it is difficult to believe that both feature properties and configuration would not play a role in face recognition: Individual recognition seems too critical to primate social life to rely on only a single processing strategy.

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