Why Faces May Be Special: Evidence of the Inversion Effect in Chimpanzees

Lisa A. Parr and Tara Dove
Emory University

William D. Hopkins
Emory University and Berry College

Abstract

■ Five chimpanzees were tested on their ability to discriminate faces and automobiles presented in both their upright and inverted orientations. The face stimuli consisted of 30 black and white photographs, 10 each of unfamiliar chimpanzees (*Pan troglodytes*), brown capuchins (*Cebus apella*), and humans (*Homo sapiens*). Ten black and white photographs of automobiles were also used. The stimuli were presented in a sequential matching-to-sample (SMTS) format using a computerized joystick-testing apparatus. Subjects performed better on upright than inverted stimuli in all classes. Performance was significantly better on upright than inverted presentations of chimpanzee and human faces but not on capuchin monkey faces or automobiles. These data support previous studies in humans that suggest the inversion effect occurs for stimuli for which subjects have developed an expertise. Alternative explanations for the inversion effect based on the type of spatial frequency contained in the stimuli are also discussed. These data are the first to provide evidence for the inversion effect using several classes of face stimuli in a great ape species. ■

INTRODUCTION

Faces are one of, if not the most important and salient class of stimuli involved in social communication. They provide invariant information about age, sex, individual identity, and emotion (Brothers, 1990; Buck, 1988; Tomonaga, Itakura, & Matsuzawa, 1993). The perception of faces appears to involve specialized processes at the perceptual, neurobiological, and cognitive levels, although the exact mechanisms that underlie these specializations remain elusive (Bruce & Young, 1986).

One of the more puzzling aspects of face processing is the general recognition impairment that occurs when faces are inverted 180°. This impairment, appropriately termed the *inversion effect*, has been widely studied in humans and is often used as a marker supporting evidence of a specialized face-processing mechanism (Carey & Diamond, 1977; Diamond & Carey, 1986; Farah, Tanaka, & Drain, 1995; Yin, 1969). In addition, the inversion effect provides evidence that faces are not recognized simply by their specific features but rather that individuals are sensitive to the precise configuration and orientation of these features, which are unique in every face. When faces are inverted, their configuration of features is altered and recognition becomes impaired, but the relationship between the individual features to one another remains the same (see Diamond & Carey,

1986; Farah et al., 1995, and Tanaka & Farah, 1991 for a review of the debate between first- and second-order relational properties).

Only a few studies have attempted to investigate whether the face inversion effect is present in nonhuman primate species that share a similar visual processing system with humans. Vermeire and Hamilton (in press) reported a left visual field, right-hemisphere advantage in split-brain macaques for both learning and discriminating conspecific's faces. When these faces were inverted, subjects showed impaired discrimination performance when the faces were presented to the left visual field, or right hemisphere. No deficits were reported for discriminations involving the same inverted stimuli presented to the right visual field, or left hemisphere. This suggests that face recognition is primarily a function of the right hemisphere and that the recognition of inverted faces is impaired when stimuli are laterally presented to this hemisphere.

Tomonaga (1994) tested five Japanese macaques (*Macaca fuscata*) for their ability to discriminate photographs of both conspecifics and rhesus monkeys (*Macaca mulatta*). The duration that subjects viewed each stimulus face in its upright or inverted orientation was presented as a dependent variable that subjects could control by pressing a lever. Slides that were viewed for longer durations were considered more meaningful than

those that were viewed for shorter periods. Subjects showed significantly shorter viewing durations for slides of inverted monkeys than slides that depicted monkeys in their upright posture. No differences were found for the viewing preferences between the different macaque species.

Several problems with this study stem from the fact that the subjects had little social experience with conspecifics or other macaque species: They had been separated from their mothers at 1 week of age and were raised by humans. The stimuli used in the experiment were not exclusively faces, but many depicted several monkeys in whole body poses. Therefore, viewing preferences for upright stimuli may not have been dependent on monkey faces but may have been influenced by objects in the environment or the animal's body parts.

Tomonaga et al. (1993) failed to find evidence of an inversion effect for familiar faces in one chimpanzee. Parr, Hopkins, and de Waal (1996), however, reported finding the inversion effect in four of five chimpanzees when discriminating unfamiliar conspecific's faces using a simultaneous, matching-to-sample paradigm. The chimpanzee's performance was significantly better for discriminations involving faces in their upright compared to inverted orientations. Moreover, only two of the five subjects showed better performance when discriminating abstract shapes in their upright compared to inverted orientations. This study suggests that chimpanzees do show evidence of the inversion effect for viewing unfamiliar faces of their own species.

Diamond and Carey (1986) attribute the inversion effect not to faces themselves but to a specialization of the visual processing system that develops when an individual becomes an expert with a specific class of stimulus. As this occurs, the visual system becomes specialized to process those stimuli using a holistic strategy, a predominantly right-hemisphere activity, that allows stimuli to be recognized using the configurational arrangement of their features. Stimulus processing based on configurational cues tends to be more rapid than that achieved through feature matching or serial processing techniques, functions typically associated with the left hemisphere (Benton, 1980). According to the expertise effect hypothesis, the inversion effect should not be thought of as an impairment unique to processing facial stimuli. Rather, it should be viewed as a consequence of the way the visual system becomes specialized for processing familiar stimuli: using a holistic strategy based on the configurational arrangement of features. This strategy is sensitive to the stimuli being viewed in their normal, or typically viewed, orientation (Farah et al., 1995).

Several recent studies support some aspects of Diamond and Carey's study, primarily that the inversion effect may not be specific to faces per se. These studies also suggest that the inversion effect is not sensitive for classes of stimuli for which subjects have developed an expertise (Phelps & Roberts, 1994; Wright & Roberts,

1996). Instead, they suggest that the inversion effect results from the visual system's sensitivity to specific classes of stimuli that contain homogeneous feature information, such as the low-frequency information that is predominantly found in human faces. In a study of three rhesus macaques, Wright and Roberts (1996) demonstrated the inversion effect only for human faces. Similarly, Phelps and Roberts (1994) documented the inversion effect only for human faces in one squirrel monkey. Neither study reported evidence of the inversion effect for the faces of other nonhuman primate species. Therefore, these authors concluded that the type of spatial frequency information contained in faces, rather than faces as a category of familiar stimuli, was responsible for the inversion effects.

Human faces may be considered more homogeneous than other primate faces because they are not marked by distinctive features or high-contrast facial markings and consist primarily of low-spatial frequency information (Benton, 1980; Moscovitch & Radzins, 1987). Processing stimuli that contain only low-spatial frequency information is predominantly accomplished using a configurational, right-hemisphere strategy (Keenan, Whitman, & Pepe, 1989). Wright and Roberts (1996) do not imply that subjects need to have any expertise with human faces, as the expertise effect hypothesis suggests. Instead, they conclude that the inversion effect should be observed for any discrimination involving stimuli that contain low-spatial frequency information and are, therefore, processed using configurational, orientation-dependent cues. These two interpretations of the inversion effect present an interesting paradox: Is the inversion effect evidence of a specialization developed by the visual system for processing classes of stimuli that are very familiar, or is it evidence that the brain differentially processes classes of stimuli according to the type of spatial information they contain?

The studies of Phelps and Roberts and Wright and Roberts, however, have not adequately provided their subjects with the range of stimuli necessary to clearly dissociate between these two alternative explanations: Is the inversion effect dependent on expert-level processing of certain classes of stimuli, or is it sensitive only to stimulus types that share a similar physical homogeneity that results from the predominance of low-spatial frequency information? The stimuli used by Phelps and Roberts and Wright and Roberts consisted of exemplars from the same general categories: human faces, nonhuman primate faces, and environmental scenes. The nonhuman primate category consisted of species ranging from prosimians to great apes. Therefore, this did not represent a single species or class of stimuli for which subjects had developed an expertise. In addition, the subjects in both of these experiments were all experts with human faces, having a long history of interaction with researchers and caretakers. The fact that subjects did not show evidence of the inversion effect for view-

ing faces of nonhuman primates in these two studies may have been due to the subject's lack of expertise with any individual species in the wide variety that were represented, and not based on the fact that the face inversion effect is specific to human faces.

The present study is the first to test for the inversion effect in chimpanzees using the faces of three different primate species, including a nonface control: chimpanzees, humans, capuchin monkeys, and automobiles. An overall prediction is that chimpanzees will perform better on all categories of stimuli presented in their upright versus inverted orientations. More specific predictions are as follows. Should the inversion effect be sensitive only to stimuli that are defined by homogeneous, low-spatial frequency information, as predicted by Wright and Roberts, the inversion effect should be found only for human faces and not for the other three stimulus categories. If, however, the inversion effect is dependent on a period of social learning when the visual system matures and individuals develop an expertise for processing the faces of familiar individuals, species, or objects, the inversion effect should be demonstrated for those classes of stimuli that subjects are familiar with: in this case chimpanzee faces and human faces. It should not be observed for capuchin monkey faces or automobiles, for which subjects had no prior experience. Finally, an additional explanation may be that evolution has favored a face-processing strategy in the primate order to enable rapid and accurate recognition of individuals. This strategy should favor stimulus processing using configurational cues and result in a right-hemisphere advantage for face processing as opposed to a left-hemisphere advantage that would be expected if subject's searched for individual, distinctive features. This hypothesis would be supported if the chimpanzees demonstrated the inversion effect for all face stimuli, regardless of the type of spatial information they contain or their expertise with the faces of that species. They should, however, have no difficulty discriminating inverted automobiles, the nonface control stimulus.

RESULTS

The total number of upright trials given to each subject before reaching criterion and their percentage of correct responses upon reaching criterion for each stimulus type are presented in Table 1. Subjects reached criterion fastest for the human faces and required the most trials to reach criterion for discriminations involving the automobiles. The number of trials needed to reach criterion for the four different stimulus types, however, was not significantly different, $F(3, 12) = 1.24$, ns.

During the test phase, the mean percentage of correct responses for the upright and inverted test trials were 80.6 and 68.2% for chimpanzee faces, 77.6 and 72.4% for capuchin monkey faces, 85.4 and 76.2% for human faces, and 73.6 and 68.4% for automobiles. Figure 1 shows the mean differences (DI) for performance on each of the four stimulus types, including the standard error of the mean (SEM). At the individual level, all five subjects showed better performance on the upright chimpanzee and human faces. Four of five subjects were better at discriminations involving upright automobiles, and only three of five subjects showed better overall performance when discriminating the upright capuchin monkey faces.

The first hypothesis predicted that chimpanzees would perform better on discriminations involving stimuli in their upright versus inverted orientations. To test this, a paired t test (two-tailed) compared the combined performance of subjects on all categories of stimuli in their upright versus inverted orientations. This analysis revealed that stimuli presented in their upright orientation were discriminated significantly better than stimuli presented in their inverted orientation, $t(4) = 12.96, p < 0.001$.

To test the specific hypotheses for the nature of the inversion effect, the relative performance of upright versus inverted presentations within each stimulus category were compared. This was done using a priori contrasts (t tests) where the relative performance of upright ver-

Table 1. The Total Number of Trials Given to Each Subject Before Reaching Criterion on the Upright Training Trials and Their Percentage of Correct Responses upon Reaching Criterion for the Four Stimulus Types

	Stimulus Type[a]			
Subject	Chimpanzee faces	Capuchin faces	Human faces	Automobiles
Jarred	50/88	50/88	80/78	100/78
Katrina	250/80	150/76	50/88	50/76
Kengee	80/82	55/75	140/77	250/76
Lamar	50/86	50/86	87/96	300/76
Scott	50/88	150/80	50/82	150/78

[a] The number of trials to criterion/percentage correct upon criterion.

Figure 1. The mean difference (DI) values for all subjects and the standard error of the mean (SEM) for all four stimulus types. The DI values were calculated by subtracting the mean percentage of correct responses on the inverted trials from the mean percentage of correct responses on the upright trials (% upright − % inverted). Positive scores indicate better performance on upright compared to inverted trials.
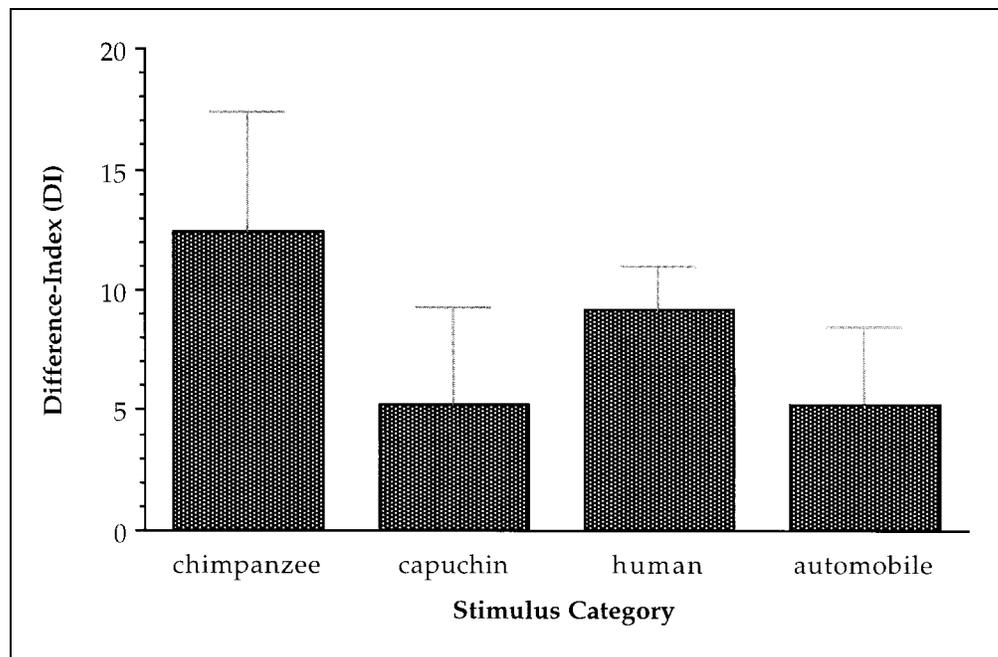
sus inverted presentations within each stimulus category was compared. These analyses revealed that for both chimpanzee and human faces the mean percentage of correct responses was significantly better when the faces were presented in their upright orientation compared to their performance when the faces were inverted, $t(4) = 2.20$, $p < 0.05$, and $t(4) = 4.52$, $p < 0.01$, respectively. No significant differences were found for discriminations involving capuchin monkey faces or automobiles in either orientation.

It is possible that these inversion effects occurred because the subject's performance for some categories was so low that performance on the inverted trials could not be significantly lower, revealing a floor effect. In contrast, if performance on other categories was very high, their relative performance on inverted trials would have an opportunity to be lower. To examine whether the inversion effect occurred because subjects showed better overall performance discriminating some categories, the absolute means for discriminations involving each stimulus category were calculated and compared to every other category. The mean performances were 74.4% for chimpanzee faces, 80.8% for human faces, 75% for capuchin monkey faces, and 71% for automobiles. Paired t tests comparing every possible combination of these means revealed only one significant difference between human faces and automobiles, $t(4) = 3.15$, $p < 0.05$.

DISCUSSION

These data provide evidence for the inversion effect in chimpanzees when discriminating specific classes of face stimuli, chimpanzee faces and human faces. These represent classes of stimuli for which subjects could be considered experts, although the individuals depicted in the stimuli were not known to subjects. These results support the expertise effect hypothesis proposed by Diamond and Carey (1986): The inversion effect occurs for stimuli for which subjects have developed a familiarity, or expertise. According to this hypothesis, when a class of stimuli becomes very familiar, the visual system shifts from a processing strategy that favors the identification of individual features to one where stimuli are recognized by the overall configuration of these features. The accurate discrimination of stimuli using configurational information is dependent on viewing those stimuli in their typical orientation. When the stimuli are inverted, the information provided by configurational cues is disrupted, and recognition becomes impaired. The recognition of unfamiliar stimuli, however, is accomplished primarily through the identification of characteristic features. According to the theory, the recognition of such features is not disrupted even when the stimuli are presented in an unfamiliar orientation. Whether these results are specific to faces or any familiar category of stimuli is not evident in this study. This question may become clearer if future studies provide nonhuman primate subjects with the opportunity to develop an expertise with a nonface class of stimuli and then test for the inversion effect with these and other face categories. This could easily be accomplished using the matching-to-sample paradigm presented here.

These results do not support an explanation of the inversion effect according to the hypothesis proposed by Wright and Roberts (1996): The inversion effect may be the result of confusion caused by discriminations involving classes of stimuli that contain homogeneous

features or those defined by low-spatial frequency information. Visual discriminations of homogeneous stimuli also involve a configurational strategy rather than one based on the identification of distinctive features. Although subjects did show the inversion effect for human faces, as predicted by the Wright and Roberts hypothesis, they also showed the inversion effect for chimpanzee faces. Testing this hypothesis is problematic, however, because no study has quantified the degree of homogeneity present in face stimuli. Homogeneity may simply indicate the absence of facial cues, such as distinctive, high-contrast facial markings or facial hair. Chimpanzee faces may indeed be as homogeneous as human faces. Capuchin monkey faces, however, contain a distinctive pattern of facial coloration that may be characterized by high-spatial frequency. Even though these faces were presented as black and white stimuli, sharp contrasts in facial markings were noticeable where these colors bordered the face. The chimpanzee and human faces lacked any type of distinctive, high-contrast facial markings and were assumed to be composed mostly of low-spatial frequency information, although this remains to be quantified.

Finally, this study does not support the general assumption that the visual system is selective for facial stimuli in general because the inversion effect was not demonstrated for the capuchin monkey faces. It is possible that the inversion effect is best explained as an interaction between factors that enhance the visual system's ability to perform complex discriminations based on a configurational strategy. First, faces contain a very distinctive configurational pattern. Second, human and chimpanzee faces appear to be more homogeneous than the other types of stimuli presented and may, therefore, contain predominantly low-spatial frequency information. Third, expertise with specific categories of stimuli may emphasize a reliance on configurational information. Further research is needed to dissociate the interdependency of these possible mechanisms for the inversion effect.

Another explanation for these results may be that the morphological features that are characteristic of chimpanzee and human faces are more similar than those shared between New World and Old World monkey species. The inversion effect may not be the result of an individual's familiarity with the faces of that species but may be the result of an evolutionary familiarity for all species in a closely related phylogenetic lineage. If this were true, the expertise effect may be extended to closely related species that share a morphological similarity in facial features. Humans and chimpanzees share a more recent common ancestor than chimpanzees and monkeys or humans and monkeys. They are, therefore, more likely to share a morphological similarity in the size, composition, and perhaps even spatial frequency of facial features that likely contributes to the way these faces are processed at the perceptual and cognitive lev-

els. Impairments due to the inversion of stimuli may be seen in those species that are evolutionarily the most closely related to humans, such as the apes and some Cercopithecine monkeys but not New World monkeys like the capuchins. Testing for the face inversion effect across categories of Old World monkey species for which subjects have varying familiarity may help eliminate explanations for these results based on an evolutionary similarity in the facial morphology of species tested.

Finally, one last point concerns the pattern of cerebral asymmetry observed in humans when processing familiar versus unfamiliar faces. Many studies have reported a right-hemisphere advantage for face processing using the faces of unfamiliar conspecifics as stimuli (De Renzi, Perani, Carlesimo, Silveri, & Fazio, 1994; Gilbert & Bakan, 1973; Rizzolatti & Buchtel, 1977; Sergent, 1988). These results have been replicated for some species of monkeys (Hamilton & Vermeire, 1988) and apes (Morris & Hopkins, 1993). This pattern reportedly shifts to a left-hemisphere advantage when the stimuli become familiar (Ross & Turkewitz, 1982; Turkewitz & Ross, 1983). This laterality shift has been attributed to differences in the way familiar versus unfamiliar faces are recognized and processed at a cognitive level. When faces are unfamiliar, for example, they are primarily recognized using a configurational strategy: the strategy predominantly associated with a right-hemisphere superiority. When the faces are familiar, such as when individuals are known to subjects or are faces that subjects learn through repeated exposures, the asymmetry shifts to one that favors the recognition of distinctive facial features. This type of serial, feature-based processing is superior in the left hemisphere (Bradshaw & Wallace, 1971; Patterson & Bradshaw, 1975). No study has investigated this laterality shift involving familiar versus unfamiliar faces in a nonhuman primate species, although a left-hemisphere advantage for processing familiar nonface stimuli has been demonstrated in chimpanzees (Hopkins, Morris, & Savage-Rumbaugh, 1991; Hopkins, Morris, Savage-Rumbaugh, & Rumbaugh, 1992).

The expertise effect is inconsistent with the data supporting this lateralized shift in the processing of familiar versus unfamiliar stimuli. If, according to the expertise effect hypothesis, faces for which subjects have little expertise are recognized by individual, distinctive features that are not disrupted when the face is inverted, how can it reconcile the preponderance of data that support evidence of a right-hemisphere advantage for unfamiliar face processing? Similarly, when faces are processed at the level of an expert, such as the familiarity that comes when individuals are known, the asymmetry shifts to one that favors the left hemisphere and involves the detection of individual, characteristic features. According to this latter explanation, Tomonaga et al. (1993) should have found an inversion effect in the one chimpanzee subject they tested. This individual was person-

ally familiar with all stimulus individuals presented in the experiment: The chimpanzee subjects were cage mates, and the humans were familiar researchers. The recognition of these faces should be disrupted when presented in an inverted orientation according to the expertise effect hypothesis, but they were not. It is reasonable to assume, based on the human literature and studies demonstrating a shift in lateralized processing of nonface stimuli, that the chimpanzee in this study had developed a recognition strategy based on the identification of distinctive features. This type of recognition does not involve a configuration strategy and should not be disrupted if stimuli are presented in atypical orientations. Furthermore, Parr et al. (1996) presented the faces of unfamiliar conspecifics to chimpanzees and demonstrated the inversion effect in four of five subjects. Further studies should investigate the degree of familiarity that is necessary to demonstrate the shift in hemispheric specialization for face recognition in nonhuman primates. An understanding of the reliance on configurational and feature-based processing strategies for faces in their normal orientation would facilitate a better understanding for how recognition becomes impaired when these stimuli are inverted. It may be that the inversion effect occurs as a result of a disruption in a configurational processing strategy for faces, but the extent to which expertise is needed before this configurational strategy develops remains unclear. In contrast, the human literature suggests that a familiarity with faces should remove any impairment resulting from inversion because recognition of familiar individuals appears to be more dependent on the detection of distinctive features than on the configurational properties of those features.

METHODS

Subjects

Data were collected on five chimpanzees (*Pan troglodytes*), three males and two females between 8 and 9 years of age, housed at the Yerkes Regional Primate Research Center, Atlanta, Georgia. All subjects were reared by humans in the Yerkes Primate Center nursery and then moved into social groups (see Bard, 1994 for a description of the rearing history). Subjects were tested in their home cage with minimal group disturbances. All subjects had received previous training with matching-to-sample tasks using a computerized, joystick-testing apparatus, including several months of experience with conspecific face-matching tasks prior to this study (Hopkins, Washburn, & Hyatt, 1996; Parr et al., 1996).

Stimuli

Four classes of unfamiliar stimuli were used: chimpanzee faces, capuchin monkey faces, human faces, and automobiles. The chimpanzee and capuchin monkey faces con-

sisted of males and females of all ages. They were obtained from black and white photographs taken with a hand-held camera. The human faces were obtained from magazines and a high school yearbook from 1993 and consisted of males and females approximately 18 to 35 years of age. The photographs of automobiles, representing several recent models and varieties, were obtained from a local trade magazine.

The stimuli were scanned into a Pentium-133 computer using a Hewlett-Packard Deskjet scanner at a resolution of 75 dots per inch (dpi) and saved as bitmap files. The presentation size of these images was 5.00 to 6.25 cm × 5.00 cm. All external cues such as the presence of background objects and obvious differences in lighting were removed from the photographs by homogenizing the background using a nonprofessional graphics software package (PhotoFinish). Facial stimuli were all black and white and depicted only the head and face but included head orientations and eye positions that were both direct and averted. Twenty black and white photographs of automobiles were combined so that their general style was conserved within each stimulus set. Trucks, for example, were paired with other trucks, and sedan-style cars, with others of that type. Figure 2 illustrates an example of each of the four stimulus types.

Procedure

The stimuli were presented to subjects in a SMTS format using software written in QuickBasic 4.0. Images were displayed on a 17-in. SVGA color monitor. The computer and monitor were mounted on a moveable cart covered in clear Plexiglas that was wheeled to the front of the subject's home cage prior to the beginning of a testing session. The monitor was positioned approximately 60 cm from the subject. The joystick was then mounted to the front of the home cage in a vertical position so that the stick, approximately 5 cm in length, protruded into the cage and could be manipulated by the subject. Figure 3 illustrates this testing situation.

At the onset of each trial, a sample stimulus and a white, cross-shaped cursor (1 × 1 cm) appeared on the monitor on a black background (see Hopkins et al., 1996). The sample was centered at the top of the monitor with the cursor positioned in the center of the monitor, slightly below the sample. Subjects were required to make an orienting response by moving the joystick-controlled cursor until it contacted the sample stimulus. If this condition was met, the sample was cleared from the screen and two comparison stimuli appeared in laterally displaced positions below the center of the monitor. A correct response was recorded if the cursor was moved into contact with the comparison stimulus that matched the sample. Correct responses were rewarded with food and followed by a 3-sec inter-trial interval (ITI). An incorrect response was recorded if subjects moved the cursor into contact with the com-

Figure 2. One example of each of the four stimulus types in their upright orientation. From left to right these are a chimpanzee face, a capuchin monkey face, a male human face, and an automobile.
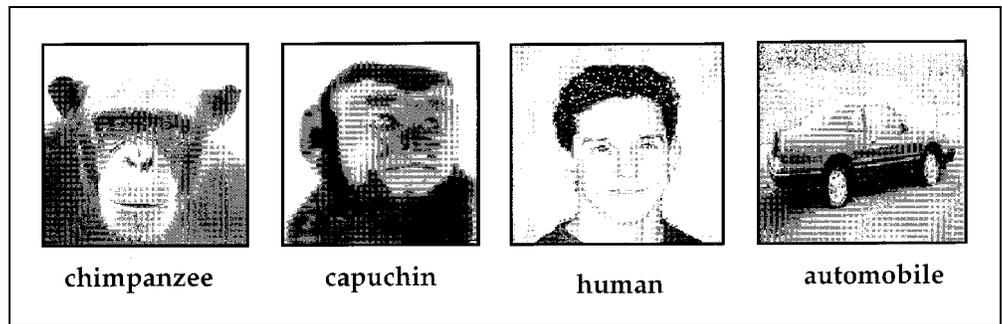
parison stimulus that did not match the sample (the foil stimulus). Incorrect responses were not food rewarded and were followed by a 7-sec ITI. During the ITI, the screen was black.

The three stimulus images together were referred to as a stimulus set and, when presented to subjects, represented one trial. On no trial was a sample stimulus, or the stimulus individual, repeated as a foil. Therefore, there were 20 different individuals represented in the three primate face categories and 20 different automobiles: 10 were the sample stimuli and 10 served as the nonmatching foils. Subjects were tested on one class of stimuli at a time. Each of the four categories of stimuli were presented to subjects in a random order that was counterbalanced across subjects. In the upright trials, the sample and the two comparison stimuli were presented in their upright orientations. In the inverted trials, the sample was presented upright, and the two comparison stimuli were presented upside-down, or inverted 180°. Each subject received daily sessions of 50 trials of the

10 upright stimulus sets until they reached a criterion of greater than 75% correct in a single session. The 10 inverted stimulus sets were then added, and data were recorded on each subject's performance on 100 randomly presented test trials (50 upright and 50 inverted) given in a single session wherever possible. After this, the subject was moved on to the next stimulus category beginning with 10 upright trials until criterion was met for that stimulus type. Testing was terminated when each subject had completed the 100 test trials on all four stimulus categories.

Data Analysis

A difference-index (DI) was calculated for each subject's performance on the upright and inverted trials during the 100-trial test sessions. This was done by subtracting the percentage of correct responses for the 50 inverted trials from the percentage on the 50 upright trials (% correct upright − % correct inverted = DI). Positive

Figure 3. An example of the testing situation illustrating the position of the computer and cart, the attachment of the joystick to the home cage, and the position of the experimenter. (Photo courtesy of F. B. M. de Waal.)
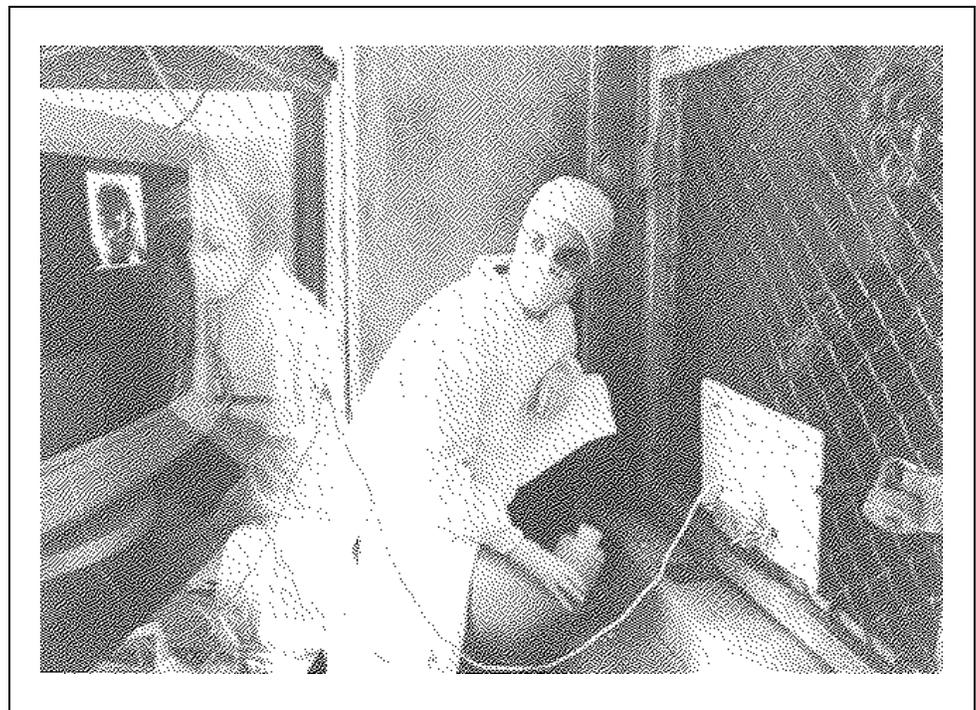
scores indicate better performance on upright trials, whereas negative scores indicate better performance on inverted trials. These data were then analyzed using parametric statistics.

REFERENCES

Bard, K. A. (1994). Evolutionary foundations of intuitive parenting: A special case of maternal competence in chimpanzees. *Early Development and Parenting, 3,* 19–28.

Benton, A. L. (1980). The neuropsychology of faces. *American Psychologist, 35,* 176–186.

Bradshaw, J. L., & Wallace, G. (1971). Models for the processing and identification of faces. *Perception and Psychophysics, 9,* 443–448.

Brothers, L. (1990). The neural basis of primate social communication. *Motivation and Emotion, 14,* 81–91.

Bruce, V., & Young, A. W. (1986). Understanding face recognition. *British Journal of Psychology, 77,* 305–327.

Buck, R. (1988). The perception of facial expression: Individual regulation and social coordination. In T. R. Alley (Ed.), *Social and applied aspects of perceiving faces* (pp. 141–165). Hillsdale, NJ: Erlbaum.

Carey, S., & Diamond, R. (1977). From piecemeal to configurational representation of faces. *Science, 195,* 312–314.

De Renzi, E., Perani, D., Carlesimo, G. A., Silveri, M. C., & Fazio, F. (1994). Prosopagnosia can be associated with damage confined to the right hemisphere—An MRI and PET study and a review of the literature. *Neuropsychologia, 32,* 893–902.

Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General, 115,* 107–117.

Farah, M. J., Tanaka, J. W., & Drain, H. M. (1995). What causes the face inversion effect? *Journal of Experimental Psychology: Human Perception and Performance, 21,* 628–634.

Gilbert, C., & Bakan, P. (1973). Visual asymmetry in perception of faces. *Neuropsychologia, 11,* 355–362.

Hamilton, C. R., & Vermeire, B. A. (1988). Complementary hemispheric specialization in monkeys. *Science, 242,* 1691–1694.

Hopkins, W. D., Morris, R. D., & Savage-Rumbaugh, E. S. (1991). Evidence for asymmetrical hemispheric priming using known and unknown warning stimuli in two language-trained chimpanzees. *Journal of Experimental Psychology: General, 120,* 46–56.

Hopkins, W. D., Morris, R. D., Savage-Rumbaugh, E. S., & Rumbaugh, D. M. (1992). Hemispheric priming by meaningful and nonmeaningful symbols in language-trained chimpanzees (*Pan troglodytes*): Further evidence of a left-hemisphere advantage. *Behavioral Neuroscience, 106,* 575–582.

Hopkins, W. D., Washburn, D. A., & Hyatt, C. W. (1996). Video-task acquisition in rhesus monkeys (*Macaca mulatta*) and chimpanzees (*Pan troglodytes*): A comparative analysis. *Primates, 37,* 197–206.

Keenan, P. A., Whitman, R. D.., & Pepe, J. (1989). Hemispheric asymmetry in the processing of high and low-spatial frequencies: A facial recognition task. *Brain and Cognition, 11,* 229–237.

Morris, R. D., & Hopkins, W. D. (1993). Perception of human chimeric faces by chimpanzees: Evidence for a right hemisphere advantage. *Brain and Cognition, 21,* 111–122.

Moscovitch, M., & Radzins, M. (1987). Backward masking of lateralized faces by noise, pattern, and spatial frequency. *Brain and Cognition, 6,* 72–90.

Parr, L. A., Hopkins, W. D., & de Waal, F. B. M. (1996). A preliminary report on face recognition in chimpanzees (*Pan troglodytes*). A paper given at the ASP/IPS Joint Congress, Madison, WI, August 11–16.

Patterson, K., & Bradshaw, J. L. (1975). Differential hemispheric mediation of nonverbal visual stimuli. *Journal of Experimental Psychology: Human Perception and Performance, 1,* 246–252.

Phelps, M. T., & Roberts, W. A. (1994). Memory for pictures of upright and inverted faces in humans (*Homo sapiens*), squirrel monkey (*Saimiri sciureus*) and pigeons (*Columba livia*). *Journal of Comparative Psychology, 108,* 114–125.

Rizzolatti, G., & Buchtel, H. A. (1977). Hemispheric superiority in reaction time to faces: A sex difference. *Cortex, 13,* 300–305.

Ross, P., & Turkewitz, G. (1982). Changes in hemispheric advantage in processing facial information with increasing stimulus familiarization. *Cortex, 18,* 489–499.

Sergent, J. (1988). Face perception and the right hemisphere. In L. Weiskrantz (Ed.), *Thought without language* (pp. 108–131). Oxford: Clarendon Press.

Tanaka, J. W., & Farah, M. J. (1991). Second-order relational properties and the inversion effect: Testing a theory of face perception. *Perception, & Psychophysics, 50,* 367–372.

Tomonaga, M. (1994). How laboratory-raised Japanese monkeys (*Macaca fuscata*) perceive rotated photographs of monkeys: Evidence of an inversion effect in face perception. *Primates, 35,* 155–165.

Tomonaga, M., Itakura, S., & Matsuzawa, T. (1993). Superiority of conspecific faces and reduced inversion effect in face perception by a chimpanzee. *Folia Primatologica, 61,* 110–114.

Turkewitz, G., & Ross, P. (1983). Changes in visual field advantage for facial recognition: The development of a general processing strategy. *Cortex, 19,* 179–185.

Vermeire, B., & Hamilton, C. (in press). Inversion effect for faces in split-brain monkeys. *Neuropsychologia.*

Wright, A. A., & Roberts, W. A. (1996). Monkey and human face perception: Inversion effects for human faces but not for monkey faces or scenes. *Journal of Cognitive Neuroscience, 8,* 278–290.

Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology, 81,* 141–145.