Anim Cogn (2001) 4 : 191–205
DOI 10.1007/s100710000076

ORIGINAL ARTICLE

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Face processing in cotton-top tamarins (*Saguinus oedipus*)

Received: 5 August 1999 / Accepted: 28 November 2000 / Published online: 1 February 2001

Abstract Current research on face processing in primates has focused on a few species, mostly macaques and chimpanzees; to date, only one New World monkey, the squirrel monkey, has been tested. We explored face processing, and the inversion effect in particular, in a New World primate species, the cotton-top tamarin (*Saguinus oedipus*). In phase 1 of our study, we trained subjects to discriminate between two faces and two scrambled faces; we then presented the tamarins with a series of novel probes in order to determine the features underlying classification. Results showed that the tamarins relied on the external contour of the face for discrimination more than the internal features and their configuration. Statistical analyses revealed no differences in accuracy or response times to upright versus inverted stimuli, and thus no inversion effect. In phase 2, we provided subjects with additional training on the face versus scrambled face discrimination task in order to focus their attention on the configuration of the internal features. Accuracy data revealed individual differences in how tamarins classified these stimuli, even though each subject was trained in the same way. In phase 3, we tested for generalization to a new set of face stimuli, as well as for the capacity to show an inversion effect. For one subject who attended to the configuration of internal features, we found significant evidence of generalization, but no evidence for an inversion effect.

Key words Face processing · Inversion effect · Discrimination learning · Nonhuman primates · Cotton-top tamarins

Introduction

Faces serve many critical functions for nonhuman primates. Research has shown that face processing plays a role in both individual and species recognition (e.g., Fujita 1987; Dasser 1987). In addition, facial expressions may be important for mediating many types of social interactions and relationships (e.g., Perrett et al. 1995; Preuschoft 1995; Hauser 1996). Given the importance of faces, one would expect that, like humans, nonhuman primate species may have a dedicated mechanism for processing faces (Kanwisher et al., in press).

Studies with humans suggest that face recognition depends more on holistic processing than does processing of non-face objects (Bruce and Humphreys 1994). It has been posited that the neural mechanisms for face processing in humans have been designed to handle the configuration of upright faces (e.g., Perrett et al. 1988; Haxby et al. 2000). In fact, face processing is significantly affected by orientation. When subjects are shown an inverted face, they are impaired in recognition tasks, showing both a decrease in accuracy and slower response times (Yin 1969, 1970). Many researchers believe that subjects actually encode faces differently when they are inverted (e.g., Farah et al. 1995). Upright faces are processed in terms of the configuration of critical features (e.g., the “triangle” formed by the eyes and nose) whereas inverted faces are encoded in a piecemeal fashion, feature by feature (Yin 1969, 1970; Carey and Diamond 1977). Furthermore, the right hemisphere bias for face recognition (Hilliard 1973) disappears when an inverted face is presented.

From a comparative perspective it is important to explore whether other species (especially nonhuman primates) also show an inversion effect for faces. Evidence for an inversion effect in other primates would give further support to the hypothesis that humans and nonhuman primates share a comparable mechanism for face processing, one that presumably evolved from a common ancestor. To set up the experiments reported here, we have summarized in Table 1 some of the studies that have tested for in-

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Table 1 A list of some of the inversion effect studies conducted with nonhuman primates and their sample sizes

Study	Species	Subjects (*n*)	Results
Phelps and Roberts (1994)	Squirrel monkey (*Saimiri sciureus*)	2, 1 per condition	Inversion effect for human and great ape faces
Bruce (1982)	Longtailed macaque (*Macaca fascicularis*)	6	No inversion effect[a]
Dittrich (1990)	Longtailed macaque (*M. fascicularis*)	4	No inversion effect[b]
Perrett et al. (1988)	Rhesus macaque (*M. mulatta*)	2	Inversion effect for human and conspecific faces
Keating and Keating (1993)	Rhesus macaque (*M. mulatta*)	4	Inversion effect for human faces in 3 out of 4[b]
Tomonaga (1994)	Japanese macaque (*M. fuscata*)	5	Inversion effect for conspecifics and rhesus macaque faces[c]
Wright and Roberts (1996)	Rhesus macaque (*M. mulatta*)	3	Inversion effect only for human faces
Tomonaga et al. (1993)	Chimpanzee (*Pan troglodytes*)	1	Inversion effect for human and conspecific faces
Parr et al. (1998)	Chimpanzee (*P. troglodytes*)	5	Inversion effect for human and conspecific faces

[a] No reaction time data reported
[b] Used line drawings/schematic faces, no reaction time data
[c] Looking time procedure; stimuli consisted of scenes with monkeys

version effects in nonhuman primates. Table 1 highlights the uncertainty of whether or not this effect exists in any nonhuman primate species and also underscores the fact that most experiments in this area involve small sample sizes. More importantly, given the mixed evidence for an inversion effect, it is difficult to assess whether this pattern is due to differences between or within species, or to methodological approaches that differ in terms of training and the kinds of stimuli presented.

The aim of the present studies is to explore the precise features underlying face processing in primates, and to extend the comparative work that has focused almost exclusively on macaques and chimpanzees to New World monkeys. Although a number of studies (e.g., Perrett et al. 1988; Phelps and Roberts 1994; Wright and Roberts 1996) suggest that some form of inversion effect exists in nonhuman primates, few studies (e.g., Perrett et al. 1988; Keating and Keating 1993) have attempted to specify which features of the images are directly responsible for the subjects' responses. Not only is such information critical for our understanding of the similarities and differences in face processing mechanisms across species, but also, in terms of providing a clean test of the inversion effect; as studies of humans, and at least one macaque species (Perrett et al. 1988) have shown, a test of the inversion effect should include a condition where subjects attend to the configuration of internal features.

With these brief introductory comments in mind, we can summarize our general experimental approach as follows. We first trained the tamarins to respond to a small set of faces and scrambled faces. When they had learned this discrimination, we presented the tamarins with several face and non-face images in an attempt to explore which features were most directly responsible for the discrimination and whether the subjects could generalize to novel faces; we also tested for the inversion effect. In phase 1, as well as in later phases of our experiments, we used both response accuracy and response time to assess the mechanisms guiding classification. We predicted that if our task engaged a spontaneously available face processing mechanism, then even though our training set was relatively impoverished, tamarins would generalize to a new set of face stimuli. In contrast, if the small set of training stimuli enabled the tamarins to focus on a narrow range of features in order to solve the discrimination task, then they would show only weak evidence of generalization. Thus, if they adopted this latter strategy, we predicted they would not show an inversion effect. These predictions are based on the findings reported by Perret et al. (1988) for rhesus macaques, and are described below. In phase 2, we trained the tamarins to discriminate between one face image and a number of systematically manipulated scrambled faces. This phase was designed to train the tamarins to use configuration in order to discriminate faces from scrambled faces. In phase 3, we first presented the tamarins with several novel faces in order to test for generalization following the training from phase 2 and then presented them upright and inverted faces together with upright and inverted scrambled faces. In parallel with our predictions from phase 2, we predicted that if the face processing mechanism in tamarins and humans is similar, and if tamarins learned to use the configuration of internal features to discriminate faces from non-faces, then they would generalize to novel stimuli, and would show an inversion effect.

Our study was designed, in part, on the basis of the findings of Perrett et al. (1988) with rhesus macaques. In the first phase of this work, macaques were trained to distinguish between faces (human and macaque) and common objects (including human and macaque non-face body parts). Following a generalization phase (in which novel faces were presented), the stimuli were then presented upright or inverted. Subjects showed no difference in response time for correctly identifying the face images, and thus no inversion effect. Although this result paralleled an earlier report by Bruce (1982), Perrett and colleagues hypothesized that the failure to show an inversion effect may have been due to a failure by the macaques to attend to the internal configuration of facial features, focusing instead on single, distinctive features like external contour.

To further explore the possibility of differences in processing upright versus inverted images, Perrett et al. (1988) ran a second experiment designed to test whether macaques can use configuration to discriminate faces and, if so, whether they will then show an inversion effect. Subjects were first taught to discriminate sets of human and macaque faces from scrambled images where all the features were present but not in their proper position; this training procedure was designed to encourage subjects to use the configuration of features to classify the images. The monkeys were then trained with horizontally presented stimuli and finally, with inverted stimuli. In order to test for inversion effects, Perrett and colleagues used the original training images presented randomly in four orientations (0°, 90°, 180°, 270°) and then retrained the subjects on another face presented in the same way. Once subjects reached criterion (90% accuracy on all images), they showed a significant increase in reaction times to both horizontal and inverted orientations compared with the upright orientation; this orientation effect was replicated with a second set of face stimuli. Perrett and colleagues concluded that prior failures to find an inversion effect may be attributed to a lack of constraints on processing strategies rather than to a fundamental difference between humans and nonhuman primates in the mechanisms underlying face processing.

Our study was largely motivated by Perrett and colleagues' conclusions, as well as the fact that most work on face processing in nonhuman primates comes from experiments on Old World monkeys and great apes, and in particular, rhesus macaques and chimpanzees (Table 1). Of the New World monkeys only the squirrel monkey has been studied (Phelps and Roberts 1994). The following experiments were designed to extend our understanding of face processing in New World monkeys by testing cotton-top tamarins on a task that systematically explores how faces are discriminated from non-faces.

Methods

Subjects

The experimental subjects were four cotton-top tamarins (*Saguinus oedipus*). All subjects were captive-born at the New England Regional Primate Research Center, Southborough, Massachusetts, United States. At the time of these experiments, all animals were maintained at 85% body weight in order to maintain their motivation. These weights fall within the range of cotton-top tamarins in the wild (Savage et al. 1993). The study was conducted and approved under the Harvard University's Assurance of Compliance 92-16.

Materials

All animals were tested within an Acoustic Systems "Tracoustics Acoustical Enclosure", measuring 86 cm(height)×86 cm(length) ×61 cm(width). An 46×46 cm glass panel was placed at one end of the enclosure. Below the glass panel, two response buttons were mounted with infrared sensors (Fig. 1). Noyes banana pellets (45 mg) were dispensed as food rewards. Outside the chamber, a Macintosh PowerPC (7100, 66 MHz) computer controlled a 21-inch (53 cm) Sony Trinitron color monitor and an I/O interface manufactured by Electronic Energy Control, Inc. This interface was used to monitor the tamarin's responses and deliver food pellets from a Gerbrands pellet dispenser. Software written in FutureBasic (Zedcor, Inc.) allowed us to display stimuli and control the interface.

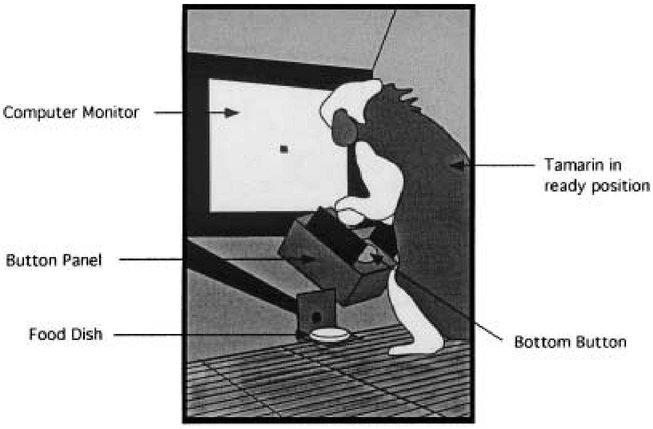

Fig. 1 Diagram of the testing apparatus. Subjects sat in front of a button panel and computer screen

The tamarins were shown digitized images of human and nonhuman primate faces together with faces whose features had been rearranged. The images were digitally acquired, and standardized for size (320×240 pixels) and resolution (72 dpi).

Subjects were trained to hold onto a round knob, one for each hand, and fixate on the center of the screen in order for the trial to begin (Fig. 1). Fixation was trained by placing a square at the center of the screen (1.0×1.0 cm) and rewarding subjects for correct fixation (fixation was monitored via two video cameras). At the start of a session a pellet was provided to the subject once the ready position was achieved (hands on knobs, looking at center of screen). Subjects were required to press one of the two buttons once an image flashed on the screen. For all trials, subjects were required to press the top button when presented with face stimuli and bottom button for scrambled face stimuli. Correct responses resulted in the screen turning yellow and a food pellet delivered as a reward. Each stimulus was presented for 5 s or until the subject pressed a button. Inter-trial interval varied according to how long it took the monkey to eat the pellet (during correct trials) and then resume the ready position. Incorrect responses resulted in a high frequency tone of 2-s duration and thus longer latencies before beginning the next trial. Normally, trials began as soon as the subjects sat upright facing the screen with both hands on the knobs. Subjects were run on one or two sessions per day, each session consisting of 60 trials.

Phase 1

In the first phase of the experiment, we trained the monkeys to discriminate two different human faces from two different scrambled human faces (Fig. 2, top row). After the tamarins reached criterion (80% correct for three sessions in a row), test sessions started. During the test sessions, six unrewarded trials were inserted into the session. Thus, a session included 54 rewarded trials of familiar faces and scrambled faces and 6 unrewarded probe trials

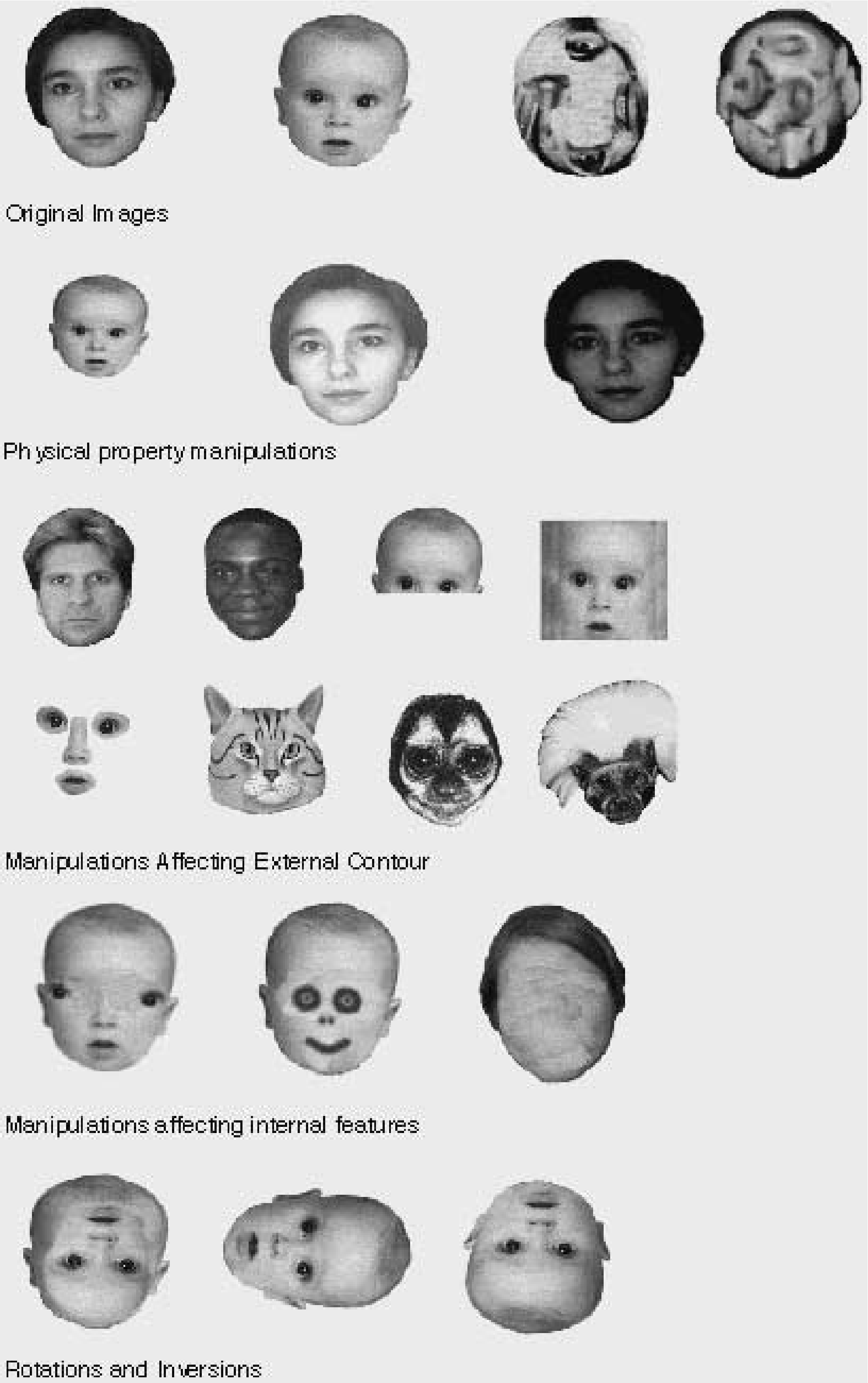

Fig. 2 Sample images drawn from the different classes of stimuli used in phase 1. It should be noted that the actual experimental images had much higher resolution

of unfamiliar faces and manipulated faces. The probes were novel images designed to reveal how tamarins classified the original images. Some probes consisted of the original images with specific features manipulated (e.g., eye position, brightness, overall texture). These manipulations allowed us to explore, which features were most important in classifying the original stimuli, using both response accuracy and response time. For example, if the tamarins relied on eye position to classify face stimuli, then altering this feature should cause them to press the button associated with scrambled faces. Given the similarity to the face category, this stimulus should cause an increase in the tamarin's response time. We also showed the tamarins a set of novel faces (both conspecific and heterospecific) to determine whether they would generalize to a broader category of faces. Evidence of generalization would be demonstrated by responses to the button associated with the face category. Finally, we tested the tamarins with inverted and rotated faces. If tamarins process an inverted or rotated face in the same way that they process the original upright face, then response accuracy should be high, and response times comparable to the original upright face. Overall, then, we used our probe trials to understand the basis for the tamarins' original discrimination.

In each session, the tamarins were presented with 30 face stimuli (15 of a baby face and 15 of an adult female face) and 30 manipulated stimuli (15 of an adult male face scrambled and 15 of a different female adult face scrambled; Fig. 2). For the manipulated face stimuli, all of the internal features of the face were present but randomly placed within the external contour. At the beginning of training, images were presented in stimulus blocks (e.g., 6–12 images from the face category followed by 6–12 images from the manipulated-face category), and then presented in a random order. Once randomized presentation started, the only constraint was that the same category could not be presented more than three times in a row. Subjects moved on to probes once they reached a criterion of 80% correct on three consecutive sessions.

Procedure

In test sessions, 54 of the original images (27 face, 27 nonface) were presented together with six probe trials interspersed in the session. The six unreinforced probe trials consisted of two probe stimuli presented three times each during the session. The probe trials started after ten nonprobe trials had passed and were presented in a quasi-random order; the only constraint was that at least three nonprobe trials were presented between probe trials.

Each probe was presented a total of six times (three per session). If, however, the subject could not finish the session (usually due to behavioral difficulty), then the session was rerun; we nonetheless included in the overall data all probes that were presented in such aborted sessions. Due to illness or behavioral difficulty, some subjects were only tested on a subset of all probes.

Group A probes involved manipulations of the external contour of the image, and included: conspecific faces (6 images; i.e., 6 faces and 6 scrambled faces), novel human faces (8), novel ethnic faces (4; including African and Asian faces), other species (2; cat and owl monkey), profiles of the original images (2), modified external contour probes (4; including square contours and shaved contours), half faces (1 each for top and bottom, as well as left and right), embedded face probes (2 images of one of the original faces embedded in the contour of a different face), original images in opposite condition (i.e., original faces presented as scrambled faces and visa versa), features alone with no external contour (4), eyes alone with no external contour (2) and schematic faces (2). Group B probes involved manipulations of the internal features. These probes included: blank faces (4), interocular distance manipulations (2; eyes closer or further apart), square features (3 images in which squares replaced original features, and combined or morphed faces (3). Group C probes explored the importance of physical properties of the original images. This group included: size manipulations (2), texture images (2), changes in location on monitor (2), original images presented in color (2), brightness manipulations (2), and blurred images (2). Group D probes consisted of images that were rotated or inverted. This group included inverted faces (2), inverted features (2), and images rotated 90° (1). The inverted faces were shown both at the beginning and end of the first condition (to see if there was any change over the course of the condition.

As noted above, each probe stimulus was presented a total of six times, three per session, for two sessions (excluding aborted sessions). The trials lasted approximately 20 min, with the longest session lasting 50 min.

Accuracy data were analyzed using a one-sample sign test (two-tailed), a nonparametric statistic that tested whether the results were significantly different from chance. Data from trials with no response were not included in calculating the overall accuracy scores. Response time was calculated using a paired *t*-test, comparing response times of probes against response times of original images.

Note that performance will be reported as accuracy. The score for accuracy (*a*) was calculated as *a*=percentage correct/100. The Bonferroni procedure was applied to each group. Thus, the *P*-value needed to assign significance for face probes was 0.007 for physical feature probes, 0.0125 for internal feature probes, 0.0038 for external feature probes, and 0.0167 for inverted or rotated probes. For scrambled face probes, the *P*-value needed to assign significance was 0.008 for physical feature probes, 0.017 for internal feature probes, 0.005 for external feature probes, and 0.01 for inverted or rotated probes.

Results

Results from the first phase are divided into four main probe categories: physical manipulations, manipulations of the internal features, manipulations of the external contour, and rotation and inversions (Table 2).

Throughout the experiment, subjects consistently responded on probe trials. In particular, there was little change in the proportion of probe trials responded to across this condition, with the range in response varying from 70 to 100%. Overall, the average percentage of trials aborted after one probe had been presented was 10.3% (SD=6.75). This percentage was influenced by one individual who aborted a relatively high percentage of sessions (19%).

Manipulations of the physical features appeared to have the least affect on performance. In fact, for many of these probes performance was similar to that of the original im-

Table 2 Accuracy results for face probes from phase 1. The accuracy scores reflect the number of times the subjects pressed the top or bottom button divided by the number of trials for that probe category. Each category may contain multiple probes (e.g., *Combined or morphed*) and therefore the sample size for each probe category is different (see Methods for additional information as to how number of probe presentations can differ). When there is a *blank space* in the table, it signifies that the subject never received that probe category

	Probe type	WQ	RM	PC	NC	Average	*n*, *P*
Top button accuracy data for phase 1							
Physical feature probes	Blurred faces	1.00		1.00		**1.00**	*n*=12, *P*=0.0005
	Size	0.95	1.00	0.82		**0.93**	*n*=42, *P*<0.0001
	Brightness – BRIGHTER	0.87	0.88	1.00		**0.92**	n=41, P=0.001
	Location	1.00	0.56	1.00		**0.84**	*n*=25, *P*=0.0009
	Color faces	0.44	0.56	0.93	1.00	0.72	
	Texture	1.00	0.23	0.33		0.47	
	Brightness – DARKER	0.33	0.38	0.33		0.35	
Internal feature probes	Interocular distance	0.75	0.83	0.89	1.00	**0.86**	*n*=49, *P*<0.001
	Combined or Morphed	0.94	0.67	0.83		**0.81**	n=54, P<0.0001
	Blank faces	0.33	0.83	0.83	1.00	**0.69**	*n*=48, *P*=0.01
	Square features	0.50	0.46	0.25		0.34	
External feature probes	Top half of face	1.00	0.50	0.56	1.00	0.74	
	All features, no ext. contour	0.50	0.25	1.00		0.71	
	Bottom half of face	0.50	0.16	0.67	1.00	0.57	
	Schematic faces	0.29	0.67	0.73		0.54	
	Left and right half faces	0.73	0.33	0.31	1.00	0.50	
	Novel faces	0.52	0.30	0.56	0.80	0.42	
	External contour probes	0.56	0.33	0.45		0.42	
	Eye features, no ext. contour	0.50	0.20	0.29	0.78	0.37	
	Novel ethnic faces	0.41	0.42	0.21		0.34	
	Conspecific faces	0.00	0.20	0.62		0.33	
	Embedded probes	0.67	0.19	0.50	0.03	0.28	
	Profile	0.00	0.22	0.50		0.23	
	Other Species	0.00	0.00	0.20	0.67	0.14	
Inversions and rotations	Inverted features	1.00	1.00	1.00		**1.00**	*n*=15, *P*<0.0001
	Inverted faces	0.89	1.00	0.55	0.83	**0.82**	n=32, P<0.001
	Rotated face	0.83	0.30	0.50	0.87	0.62	
Bottom button accuracy data for phase 1							
Physical feature probes	Blurred faces	1.00		1.00		**1.00**	*n*=8, *P*=0.0078
	Location	1.00	0.88	1.00		**0.97**	*n*=30, *P*<0.0001
	Brightness – BRIGHTER	0.89	1.00	1.00		**0.96**	n=23, P<0.001
	Brightness – DARKER	1.00	0.75	1.00		**0.92**	*n*=23, *P*<0.001
	Size	0.87	0.78	1.00		**0.89**	*n*=44, *P*<0.0001
	Texture	0.40	0.88	0.60		0.65	

Table 2 (continued)

	Probe type	WQ	RM	PC	NC	Average	n, P
Internal feature probes	Blank faces	1.00	0.89	0.83		**0.91**	$n=21$, $P=0.0002$
	Combined or Morphed	0.80	1.00	0.75		**0.86**	$n=14$, $P=0.01$
	Square features	0.67	0.64	0.85		**0.73**	$n=30$, $P=0.01$
External feature probes	Other species	0.88	1.00	0.75	1	**0.88**	$n=24$, $P<0.0001$
	External contour probes	0.83	0.83	0.92		**0.86**	$n=42$, $P<0.0001$
	Novel ethnic faces	0.53	0.89	0.90		**0.80**	$n=54$, $P<0.0001$
	Eye features, no ext. contour	1.00	1.00	0.33	0.33	0.65	
	Conspecific faces	0.90	0.78	0.40		0.65	
	Novel faces	0.46	0.72	0.69	0.375	0.64	
	Schematic faces	0.00	0.00	0.77		0.45	
	Embedded probes	0.67	0.50	0.38	0.0625	0.37	
	Original faces – opposite condition	0.08	0.25	0.28	0.5	0.24	
	All features, no ext. contour	0.00	0.50	0.00		0.11	
Inversions and rotations	Inverted scrambled features	1.00	1.00	1.00		**1.00**	$n=15$, $P<0.0001$
	Inverted scrambled faces	1.00	1.00	1.00	0.83	**0.96**	n=32, P<0.0001

ages. For the physical manipulation probes (group C), four sets of face probes yielded results significantly above chance. This indicates that the tamarins' categorization of these images was most likely based on the probes having the relevant features for category membership. These probes included blurred faces ($a=1.0$, $n=12$, $P=0.0005$), size ($a=0.93$, $n=42$, $P<0.0001$), brighter faces ($a=0.92$, $n=41$, $P=0.001$), and location ($a=0.84$, $n=25$, $P=0.0009$). For the scrambled face probes, five sets were significantly above chance. These included blurred faces ($a=1.0$, $n=8$, $P<0.008$), location ($a=0.97$, $n=30$, $P<0.0001$), brighter faces ($a=0.96$, $n=23$, $P<0.0001$), darker faces ($a=0.92$, $n=23$, $P<0.001$), and size ($a=0.89$, $n=44$, $P<0.0001$). Overall, changes in the physical features of the stimuli had little affect on the tamarins' performance.

For manipulations involving internal features (group B), three sets of face probes yielded accuracies significantly above chance: inter-ocular distance ($a=0.86$, $n=49$, $P<0.001$), combined or morphed ($a=0.81$, $n=54$, $P<0.0001$), and blank faces ($a=0.69$, $n=48$, $P=0.01$). The square features probes yielded a lower accuracy ($a=0.34$, $n=32$). Three sets of scrambled face probes were significantly above chance: blank versions of the original scrambled stimuli ($a=0.91$, $n=21$, $P=0.0002$), combined or morphed scrambled ($a=0.86$, $n=14$, $P=0.01$), and square features ($a=0.73$, $n=30$, $P=0.01$). In general, the tamarins tolerated changes to the internal features, demonstrating that they relied on other features to classify the original images.

There were no face probes that reached statistical significance for the external feature probes (group A). The subjects' performance on probes with novel contours was generally poor as evidenced by low accuracy scores for novel faces ($a=0.42$, $n=125$), conspecific faces ($a=0.33$, $n=30$), and novel species' faces ($a=0.14$, $n=22$). For the scrambled face probes, three sets were significantly above chance: other species ($a=0.88$, $n=24$, $P<0.0001$), external contour probes ($a=0.86$, $n=42$, $P<0.0001$), and novel ethnic faces ($a=0.80$, $n=54$, $P<0.0001$). The overall accuracy scores for external contour manipulations were lower than any other category of probes showing that the tamarins relied on these features for classifying the original images. This is further demonstrated by subjects' failure to correctly categorize probes in which the original faces were scrambled ($a=0.24$).

For the rotations and inversions category (group D), two sets of face probes were significantly above chance: inverted features ($a=1.0$, $n=15$, $P<0.0001$) and inverted faces ($a=0.82$, $n=32$, $P<0.001$). For the scrambled face probes, both sets were also significant: inverted scrambled features ($a=1.0$, $n=15$, $P<0.0001$) and inverted scrambled faces ($a=0.96$, $n=32$, $P<0.0001$). Response times to inverted faces and inverted features were comparable to response times for the original images (664 ms and 697 ms respectively). Thus, the tamarins showed no inversion effect in this condition.

For the response time data, paired t-tests were run comparing each individual's response to probes against their response to the original images. Using this method, only one set of response time data revealed a significant performance effect on the original images. Specifically, response time for other species' faces (1955 ms) was significantly slower than for the original images (764 ms; *t*=3.91, *P*<0.0005). Thus the response time data failed to significantly distinguish between performances on different probes. However, the trends that emerged from these data may provide some insight into the subjects' performance. For example, the response times for inverted face and inverted feature probes were nearly identical to the response times for original images (664 ms and 697 ms respectively). This supports the conclusion that given a relatively impoverished set of training exemplars, tamarins do not show an inversion effect.

Discussion

Results from phase 1 suggest that the external contour of the image was the most important feature for categorization. This finding resembles that of the study of Dittrich (1990) on the representation of faces in long-tailed macaques, using line drawings. The most important feature for face recognition in that species was the external contour of the face, followed by the eye region, and then the mouth. In our study, the manipulations imposed on the external contour caused the most errors. No probes from this group were associated with a statistically significant accuracy score. Further, when the original face images were scrambled, the tamarins continued to categorize the image as a face. This shows that the basis for the categorization of those images depended mostly on the external contour and not the internal features. In addition, using only the external contour as a cue, the tamarins were able to categorize correctly blank faces and blank scrambled images at 75% and 91% respectively.

The tamarins failed to generalize from the original images to novel conspecific and human images. The failure to generalize may be explained by the fact that the external contours of the novel images differed from the original. Supporting this hypothesis is the observation that the tamarins had greater difficulty categorizing faces of novel species and conspecifics, images with radically different external contours, than they did categorizing other human faces (see Results). Results from previous studies have found that nonhuman primates may process conspecific faces differently from human faces (e.g., Wright and Roberts 1996). Thus, it is not surprising that the tamarins performed poorly with conspecific faces given that the original task utilized human faces. The tamarins' apparent inability to generalize may indicate that our task failed to fully engage their face processing mechanism. This issue is addressed in phase 3.

In general, the tamarins' ability to categorize images with manipulated features was compromised less than images with the external contour altered. However, substituting squares in place of the original internal features had a significant affect on performance (see Results). This demonstrates that although specific features of the face may not be as important as contour in facilitating categorization during this phase, the tamarins nonetheless attend to these features while categorizing the images.

Manipulations of the physical features (such as size or location) appeared to have less of an affect on classification accuracy than the internal features or contour. Performance on these probes was similar to that on the original images (see Results); exceptions included face images that were significantly darkened or altered by imposing a salient texture change. The poor performance on darkened faces was surprising given that the external contour was intact. Again, this suggests that although the internal features did not play as great a role as contour, they were nonetheless important for categorization.

It is worth mentioning that the conclusions drawn thus far are from scores averaged across subjects. There was, however, variation between individuals. Notable exceptions to the general patterns mentioned above include the observation that subject NC classified all probes consisting of half faces as face images. It is possible that when even a small proportion of the external contour was visible this was sufficient for classifying the image as an exemplar of the face category. Since the top and bottom halves of a face contain different internal features, it seems unlikely that our subjects relied on internal features to classify the original stimuli. A second exception to the group performance results was the fact that subject PC performed well below the average on inverted (55%) and rotated (50%) faces. This result is difficult to interpret since PC's performance on other probes was consistent with the group's performance. Despite the exceptions, the overall trends noted above seem to capture the general mechanisms underlying categorization in the first phase of our experiments.

The tamarins' performance on inverted faces and inverted scrambled faces was generally high. However, like rhesus monkeys in the first condition of the experiment of Perrett et al. (1988), it is likely that the tamarins were using a simple strategy in categorizing the inverted and scrambled faces. For example, given that the tamarins relied on external contour, it is unlikely that inversion caused a sufficient deviation to cause a change in performance from upright images. The lack of an inversion effect is also evident from the response time data. In contrast to the 180° rotation, accuracy performance on probes with 90° rotation was not significantly different from chance; such rotations appear to result in a relatively more salient change in external contour. This pattern of results confirmed our hypothesis that the subjects would not show an inversion effect if they did not use the configuration of features in order to discriminate between faces and scrambled faces. However, as mentioned in the results, response time data were difficult to interpret because of high variance. Such variance was not only evident between subjects, but also within subjects across separate sessions.

Phase 2

Phase 1 failed to reveal an inversion effect for faces and scrambled faces. Again, this is not surprising if the face

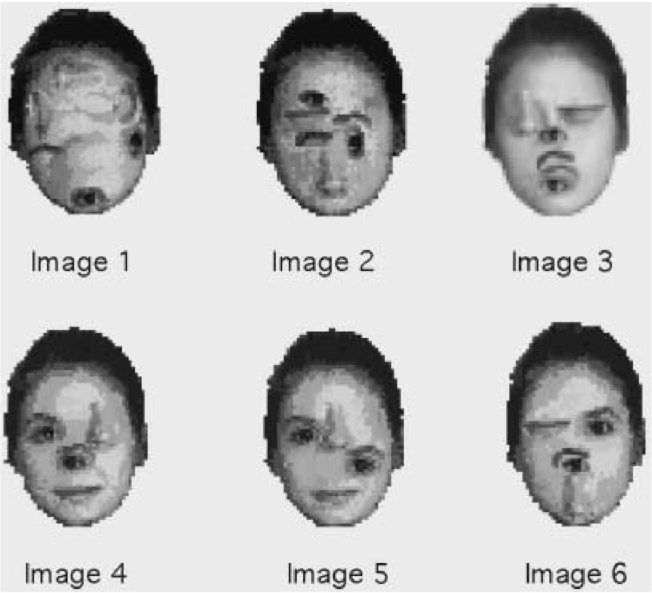

Fig. 3 Sample of different images shown during phase 2. *Image 1* scrambled face with the features located at the periphery, *Image 2* features scrambled in the center, *Image 3* all features scrambled with T configuration maintained, *Image 4* two features switched, *Image 5* two features switched and the T configuration disrupted, *Image 6* 3 features switched, T configuration maintained

inversion effect depends on using the configuration of facial features (Perrett et al. 1988). Since there are many different ways to scramble a face (Fig. 3), and these may effect the process of classification, phase 2 of our experiment was designed to examine how tamarins respond to a greater variety of scrambled faces, involving systematic manipulations of the internal features of the face. Specifically, we attempted to determine how the particular position of features within a scrambled face influenced the tamarins' classification. In addition, our training was designed to shift the tamarins to a configurational strategy of classification in order to determine they would then show an inversion effect.

Methods

In phase 2, we presented the tamarins with one face image for the top button and a progressive series of scrambled face images for the bottom button. The first set of bottom button images were scrambled faces, but with all features located on the periphery of the face (see example in Fig. 3). For the second set of scrambled images, we moved the features toward the center (Fig. 3). After reaching criterion (80% correct for two consecutive sessions) on each of these two sets, we presented the tamarins with a variety of scrambled images in which the features and their configuration were manipulated. Two images were presented in which all of the individual (local) features were displaced, but the global configuration of the face stayed the same (i.e. the T configuration normally made by the two eyes, nose, and mouth was preserved; Fig. 3). In an effort to focus the tamarins' attention on the specific configuration of the eyes, nose, and mouth, we presented images where two features switched position, but the overall configuration of the face was maintained (Fig. 3). Based on the tamarins' responses to these images, we created new images to examine the kind of strategy used while discriminating between face and scrambled face images. Image 5 of Fig. 3 provides an example of this kind of probe, involving a switch of two features and a disruption of the T configuration; this image helps us assess the salience of the T configuration. If tamarins categorize this image as a scrambled face, but classify as a face a similar image with the T configuration preserved, then we may conclude that maintaining the T configuration is a necessary feature for categorizing an image as a face. Other images were constructed with the T configuration intact, but with three features switched (Fig 3). These images helped us establish the degree to which tamarins tolerate variation within a face image, while maintaining the T configuration.

The level of experimental detail outlined above is necessary to determine the extent to which tamarins use featural configuration in classifying stimuli. By carefully analyzing which features or configuration of features are being used, we may be able to make a more accurate assessment of similarity between face processing in nonhuman and human primates.

We ran only two individuals in this condition. Subject NC's performance was too variable and subject RM became ill.

Results

Figure 4a, b shows that both subjects were able to categorize correctly scrambled faces when the features were placed toward the periphery of the face (see Fig 4a, b). PC was influenced by the presence of the right eye, as indicated by the lower scores for images in which the right eye was present (Fig. 4a). When the left eye was in its correct location, performance improved (Fig. 4a). Although the presence of the right eye does not provide a complete explanation of this subject's performance, it clearly influenced categorization of face and scrambled face images.

WQ showed a different pattern of responses given the same set of face and scrambled faces. Unlike PC, WQ was apparently not influenced by the presence or absence of a specific feature (Fig. 4b). WQ's performance did, however, appear to be affected by the presence or absence of the T configuration, as well as the position of at least one feature. When the T configuration was maintained WQ had greater difficulty categorizing it as a scrambled face than when the T configuration was disrupted (Fig. 4b). However, the T configuration alone was insufficient to account for WQ's ability to distinguish faces from scrambled faces. When shown an image with all features scrambled but the T configuration maintained, WQ's accuracy was high (97%). Overall, as the resemblance between the scrambled and original face increased (in terms of both

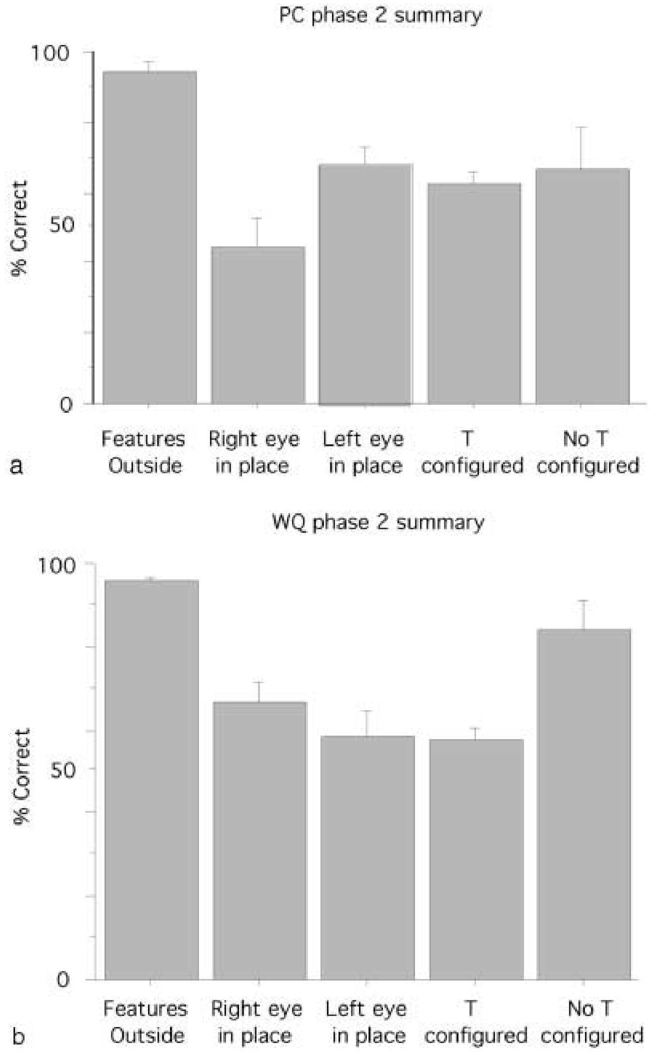

Fig. 4 **a** Mean accuracy data (+SD) for subject PC across different classes of stimuli presented in phase 2. Note the difference between *right eye* versus *left eye in place*. **b** Mean accuracy data (+SD) for subject WQ across different classes of stimuli presented in phase 2. Note the difference between *T configured* and *no T configured*

configuration and the location of features), WQ was more likely to make classification errors.

Response time data are not discussed because of the high variance during training.

Discussion

A primary goal of phase 2 was to examine the features that tamarins use to distinguish faces from scrambled faces. Though our analyses are limited to two subjects, it seems clear that different featural manipulations within the scrambled face category had a significant effect on how the images were classified. One subject, WQ, appeared to respond to the configuration of facial features. The other subject, PC, seemed to attend more closely to the presence or absence of an individual feature. This shows that when two animals view the same set of scrambled faces, they may process them in completely different ways even when they have the same history of training. Previous studies have asserted that when animals are required to categorize faces and scrambled faces, they automatically use configuration (e.g., Perrett et al. 1988). Although our sample size is small, our results suggest that individual variation can sometimes swamp this effect. Thus, at each training phase, each subject should be probed with regard to the features guiding classification.

Depending on which scrambled faces are used, an animal does not necessarily need to use a configurational strategy in order to correctly categorize the image. This is consistent with the work of Keating and Keating (1993) on macaques. Clearly, if one were only to show scrambled faces with the features on the periphery, the subjects could use a relatively simpler response strategy (Herrnstein 1990). It is also important to distinguish between different configurational strategies, such as the relationship between two features and the T configuration of the eyes, nose and mouth. By carefully manipulating both kinds of features and their relative positions (i.e., configuration), we will be in a stronger position to assess how each subject classifies the experimental stimuli. This approach will provide a more relevant data set for comparing the mechanisms underlying human and nonhuman primate face processing.

Phase 3

Phase 3 was designed to test whether the tamarins would generalize to novel faces given the training they received in phases 1 and 2. Evidence of generalization is critical for the claim that our experimental tasks tap a face processing mechanism in tamarins. Furthermore, since one subject learned to discriminate faces from nonfaces using a configurational strategy, we wanted to test for an inversion effect in this individual. It is possible that because tamarins spend time upside-down and often tilt their head to the side when orienting, that they are relatively insensitive to changes in orientation even when using a configurational strategy. To test this possibility, subjects were required to discriminate between upright and inverted faces, and upright and inverted scrambled faces. Once subjects reached criterion (80% for two sessions in a row) for both upright and inverted faces, response time data were examined. As reported by Perrett et al. (1988), response time is likely to provide the most sensitive measure of the inversion effect.

Methods

Generalization training

At the beginning of phase 3, we tested two subjects; one subject became sick during the course of the experiment and was unable to finish. Analyses therefore focus on only one subject.

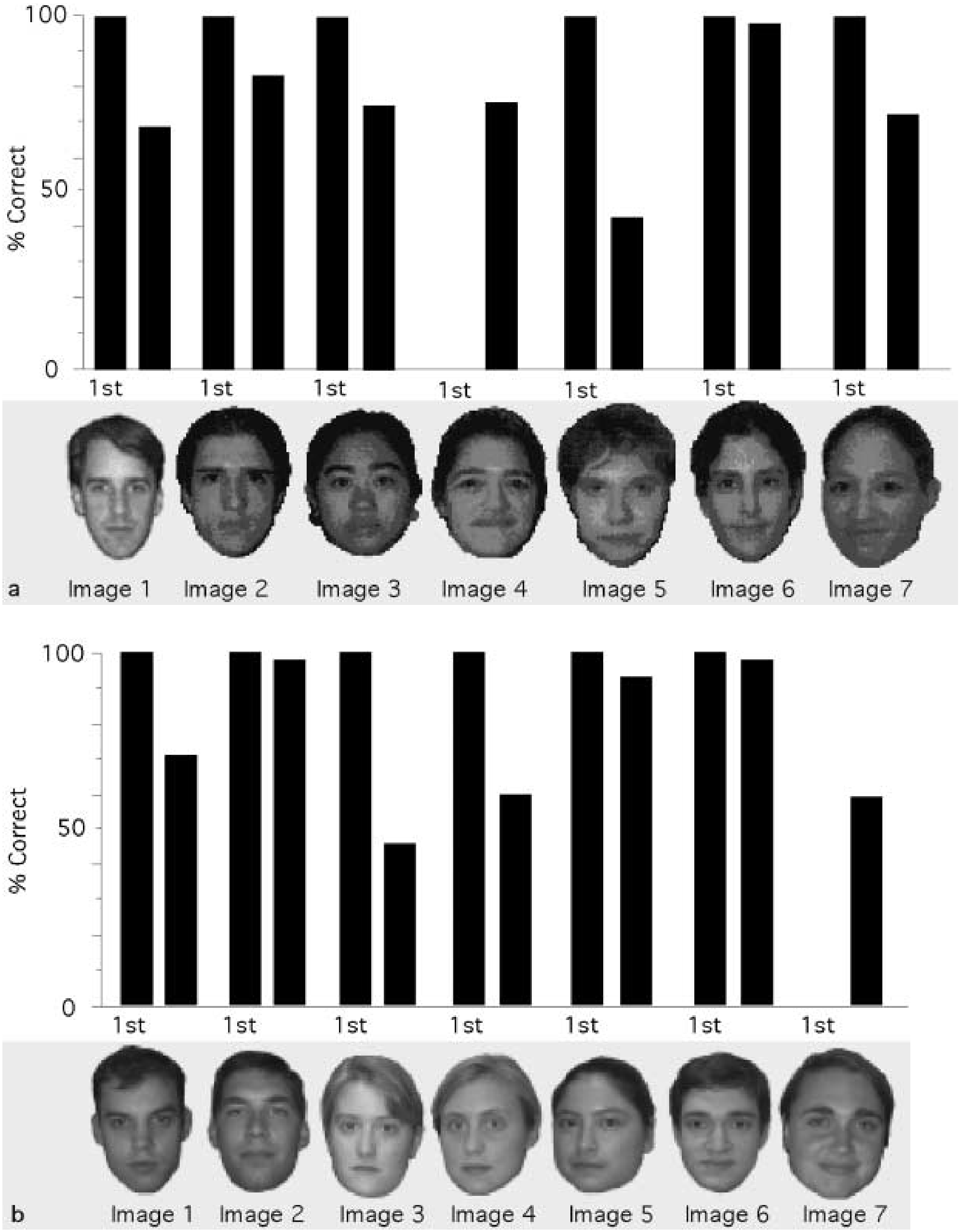

Fig. 5 **a** Percent correct on the first seven images from generalization set. The first trial data and overall accuracy scores are shown for subject WQ. **b** Percent correct on the second seven images from generalization set. The first trial data and overall accuracy scores are shown for subject WQ

We first trained the subject to discriminate an initial set of ten human faces and the same ten faces scrambled. The set of face stimuli was variable and included novel Caucasian faces, an Asian face, an African face, and an Indian face. Scrambled faces were created so that all features were located toward the center of the face. After training, we presented three novel faces and scrambled faces to determine the level of generalization. After the subject correctly classified these novel faces (80% correct on two consecutive sessions), we presented a new set of ten novel faces and scrambled faces to more thoroughly test for the level of generalization.

Testing for the inversion effect

As a final test, we trained the subject to discriminate a novel face from four scrambled faces (all features were placed in the center of the face, but the T configuration was disrupted). The subject was then trained to discriminate an inverted face from four inverted scrambled faces (Perrett et al. 1988). The stimulus sets were then combined such that each session included both the upright and inverted version of the face stimulus paired with the top button and eight scrambled faces (four in each orientation) paired with the bottom button. When the subject's accuracy on this condition reached 80% for two consecutive sessions, response time was assessed, contrasting upright and inverted stimuli.

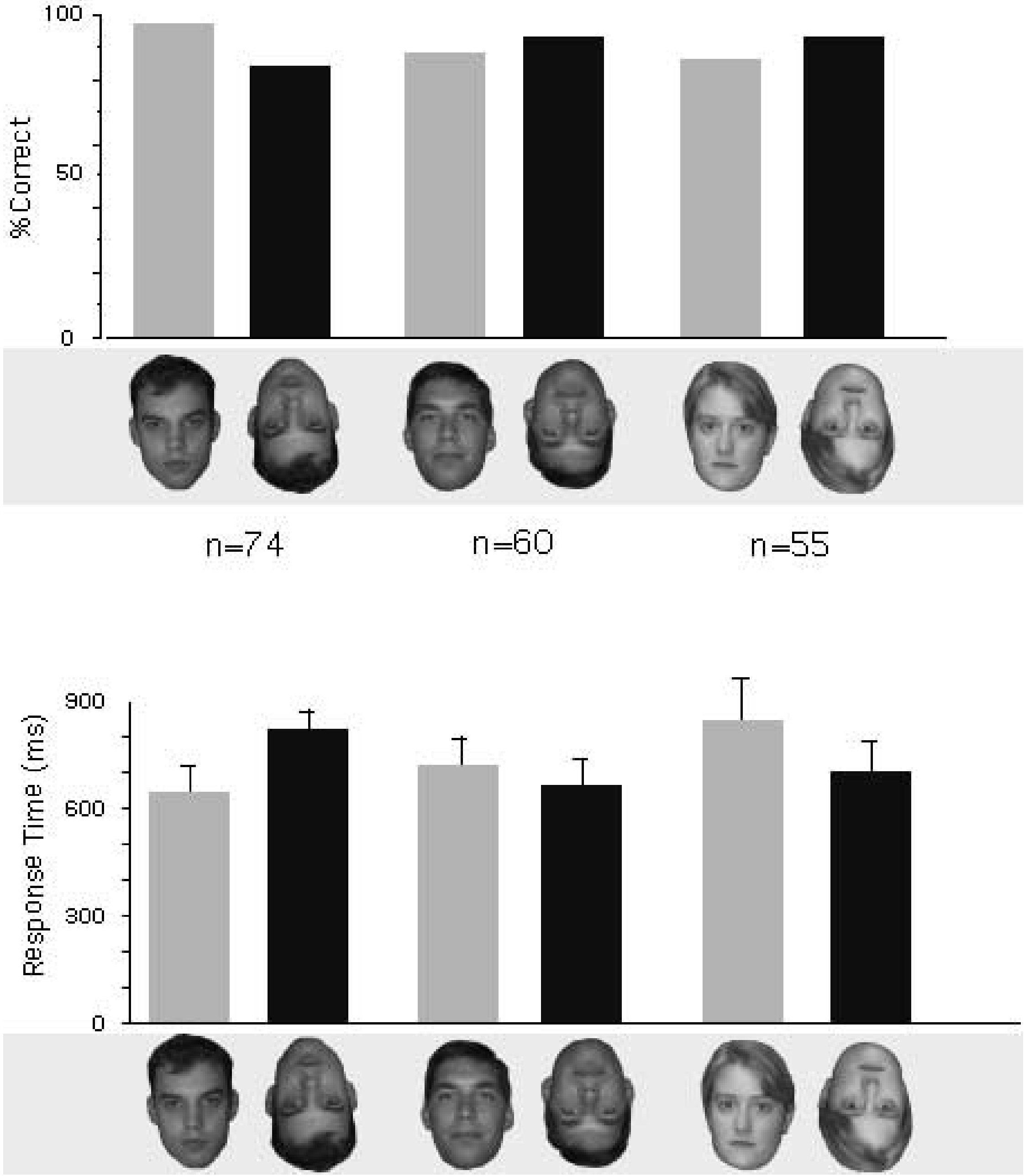

Fig. 6 Percent correct and response time scores from the three faces shown in the final condition of phase 3

Results

Results from the initial generalization condition show that subject WQ correctly categorized 12 out of 14 novel faces (86%) on the first trial; this includes the three novel faces following the training set, the second set of ten novel faces, and one novel face used in the final test for inversion (Fig. 5a, b). Over 40 or more trials, accuracy reached 70% or better on 10 out of the 14 faces (Fig. 5a, b). Overall, subject WQ seemed to perform worse on faces with lighter hair (images 3,4 and 7 in Fig. 5b).

The overall results from the inversion effect tests indicated that the mean response time for upright faces was 736 ms and 727 ms for inverted faces. Thus, there was no difference in response time (t_{183}=0.091, P>0.90) and thus no evidence of an inversion effect. The overall accuracies for the upright and inverted faces used in the final task of the experiment was above 80% for every upright and scrambled face.

Inspection of response times for specific upright and inverted faces revealed that for the first face, the upright orientation (average response time=641 ms) was processed significantly faster than the inverted orientation (average response time=818 ms; t_{73}=2.92, P<0.005). For the second and third faces, there was no significant difference in response times between the upright (average response time=720 and 846 ms respectively) and inverted orientations (average response time=663 and 700 ms; t_{59}=1.38, P<0.25 and t_{49}=1.41, P<0.10 respectively; Fig. 6).

Discussion

In contrast with our findings from phase 1, at least one tamarin subject was able to generalize to novel faces once it had been trained to discriminate faces from scrambled faces using configurational cues. Phase 3 therefore provides some evidence that tamarins can form a general face category, mediated by the configuration of the internal features. The level of generalization was not, however, complete. Results suggested that performance was influenced, to some extent, by such external features as hair and skin color. However, it is also important to note that this generalization task was far more difficult than the one used by Perrett et al. (1988) involving a discrimination between faces and common objects. As recent studies of face processing in humans suggest (Tarr and Gauthier 2000), what makes discrimination of faces potentially more difficult than other discriminations is the subtlety of within-category, as opposed to between-category, differences.

Overall our results support the conclusion that given training on configurational features of a face, tamarins fail to show an inversion effect. The fact that subject WQ responded faster to upright than inverted presentations of the first face, but not to the other face stimuli, can be partially accounted for by changes in response time across sessions. During the final stage of phase 3 involving presentation of both upright and inverted faces (see Methods), subject WQ's performance gradually improved on all three inverted faces (Fig. 6). Even though the performance criterion was reached, there was some evidence that subject WQ's responses had not yet completely leveled off. For instance, while accuracy increased for inverted faces across sessions, accuracy tended to decline slightly for upright faces. In addition, while response time generally decreased for the inverted faces across sessions, response time increased somewhat for the upright faces. Thus, although subject WQ's accuracy reached criterion for all faces, it is possible that further exposure would have continued to reduce response time to the first inverted face, eliminating the inversion effect.

The fact that there was no overall inversion effect suggests that once tamarins have sufficient exposure to inverted faces, they are adept at categorizing them, even when they are attending to the configuration of the face. At this point it is not possible to say whether the apparent lack of an inversion effect in our cotton-top tamarin subject represents a species difference between other nonhuman primates, methodological differences between studies that have examined face processing, or the effects of small sample sizes that arise in many such studies of face processing in nonhuman primates. Indeed, our own conclusions about inversion effects in cotton-top tamarins must be tempered by the fact that this condition was run on a single subject.

General discussion

In phase 1 of our experiment, we investigated whether tamarins use face configuration as a cue to discriminate a restricted sample of face images and scrambled face images. This design was implemented in order to determine the relative ease with which tamarins selectively respond to face configuration over other cues such as external contour. In other studies involving non-face object discrimination, we have found that tamarins select more complex stimulus features, such as spatial relationships, over other features such as external contour (Hauser 1997; Hauser et al. 1999). In phase 1 of the current experiment, however, the tamarins tended to use relatively simple cues, such as external contour, to discriminate the images. Thus, when spontaneously processing two-dimensional human face stimuli, tamarins do not appear to respond to featural relationships (i.e. face configuration) if other, perhaps simpler cues, can be used. As a result, they failed to show a face inversion effect. This result parallels studies with macaques showing that subjects do not readily use face configuration unless they are trained to do so (Perrett et al. 1988; Dittrich 1990).

Phase 2 of the experiment was designed to encourage the tamarins to categorize faces using face configuration. We found that even with a much more difficult and highly constrained categorization problem, subjects discriminated images in different ways, with only one subject using face configuration. Thus, phase 2 showed that individual tamarins, and by implication, individuals of other species similarly tested, may use different cues to discriminate faces from scrambled faces. Such individual variation must be accounted for when developing hypotheses about the mechanisms underlying face processing within a given species (Dittrich 1994). Phase 2 also showed that before one can conclude that subjects are responding to face configuration, one must carry out more subtle manipulations than are typically conducted in face processing studies on primates.

In phase 3, we tested one subject's capacity to generalize to novel faces and scrambled faces after being trained in phase 2 to use configurational cues. This subject showed some generalization to novel faces, suggesting a more general face category than was demonstrated in phase 1. Despite the difficulty of this phase of the experiment, the tamarin quickly learned to respond to inverted faces as exemplars within the face category. Once accuracies for all face and scrambled face images reached criterion, we examined response times and found no differences between upright and inverted faces, thereby providing no evidence of an inversion effect. To determine whether this represents a species-typical characteristic, perhaps due to locomotion or behavioral adaptations (e.g., moving upside down or head cocking), tests involving a larger sample size of tamarins, as well as other species, are necessary.

Results from our experiments suggest that studies of face processing in nonhuman primates must be designed to tease apart the specific features used by animals to classify images as faces as opposed to non-faces. If subjects are able to use cues other than face configuration, there is a strong possibility that they will do so (Herrnstein 1984; Perrett et al. 1988; Dittrich 1990). In phase 1, subjects tended to categorize faces based on features such as face contour. Only when subjects were required to discriminate faces from, for example, faces with only two features switched (e.g. nose and mouth) was there evidence that face configuration was used (phase 2). We believe that it is premature to conclude that a nonhuman primate is using face configuration unless systematic manipulations of faces are conducted, such as switching the positions of the nose and mouth; this logic has been applied in studies of species and individual recognition in longtailed macaques (Dittrich 1994). In addition, we believe that comparisons between human and nonhuman primate face processing mechanisms require explicit documentation of the features used in classifying faces. For example, if a nonhuman primate species shows an inversion effect, but individuals fail to attend to face configuration, then the mechanism underlying the inversion effect may be qualitatively different from that in humans.

The conflicting data on face inversion in primates may also be due to differences in methodological procedures across studies. As commonly pointed out in studies of animal cognition, conclusions about species differences in ability require the use of similar methods (Macphail 1987; Hauser 2000) In the experiment of Perrett et al. (1988), evidence of an inversion effect in rhesus was obtained for one training condition but not another. Specifically, differences between upright and inverted faces appeared only when the comparison stimuli included an external contour similar to the face images. Likewise, the current study has shown that different strategies may emerge based on different types of scrambled faces (as evidenced by a comparison of phase 1 and phase 2). To date, a variety of experimental methods have been used to examine the face inversion effect in nonhuman primates. Moreover, the exact procedures used to generate the scrambled face stimuli have often been unspecified, thereby increasing the possibility of variation across studies. Such variation in both testing procedures and stimuli may explain why, for example, Perrett et al. (1988) found an inversion effect in rhesus monkeys for conspecific faces, while, for example, Wright and Roberts (1996) did not.

A second consideration is the quality of the stimuli presented and the species tested. Some species (e.g., chimpanzees and rhesus) are able to perform tasks using television monitors and joysticks, while others may have more difficulty. Such inter-species variation may arise because of differences in the underlying mechanisms guiding visual perception, attentional systems, motor control, or some combination of these factors and others. Likewise, the use of two-dimensional images may have a different affect on the perception of human as opposed to nonhuman primate faces. For example, when a photograph of a tamarin's face is presented, the details of the nose, eyes, and mouth become relatively ambiguous to a human observer as depth cues are lost; fewer details are lost for human faces. As mentioned by other researchers (e.g., Wright and Roberts 1996), the stimulus properties of the different faces, as well as the species tested, must be considered when investigating face processing across species.

At present, it is unclear whether human and nonhuman primates share the same face processing mechanism. A number of theories have been proposed to account for the data on primate inversion effects. One theory is that expertise with faces causes the inversion effect. For example, Diamond and Carey (1986) showed that humans can acquire an inversion effect for dog faces if they have approximately 10 years of experience, a time scale that parallels the development of an inversion effect for human children processing human faces. The authors posit that it is the reliance on second-order relational properties (a class which includes configuration) that facilitates face recognition. Their study with dog experts shows that familiarity may facilitate the processing of second-order relational properties. In our study, the use of second-order relational properties (configuration) by subject WQ in phase 3 may explain why we found an enhanced ability to generalize across faces. Further, the data from phase 3 suggest that previous experience may play a role in the inversion effect (and may account for this subject's improved performance with inverted faces over time). In related experiments, Parr et al. (1998) suggest that captive chimpanzees show inversion effects for both human and chimpanzee faces because they have experience with both species. However, an expertise explanation alone cannot account for data from New World monkeys (i.e., squirrel monkeys) that fail to show inversion effects to conspecific faces, but do show the effect for human and chimpanzee faces. This explanation also fails to account for the lack of an inversion effect in rhesus monkeys presented with conspecific faces (Wright and Roberts 1996). In theory, the second-order relational features of conspecific faces should be particularly salient. Thus it is unclear why these species fail to show an inversion effect for conspecifics, but are able to show it for other species.

Parr et al. (1998) have further speculated, based on their own results, that the inversion effect may be the result of expertise effects that extend to "an evolutionary familiarity for all species in a closely related phylogenetic lineage". Specifically, both humans and chimpanzees show an inversion effect for human and chimpanzee faces, but not for capuchin faces. However, data from other experiments fail to support this hypothesis (e.g., Phelps and Roberts 1994; Wright and Roberts 1996). Phelps and Roberts (1994) found that a squirrel monkey showed an inversion effect for human and chimpanzee faces, but not for monkey faces. In addition, our own results failed to reveal an inversion effect at all. Interestingly, no study of any primate (humans included) has yet shown an inversion effect with a New World primate face. Furthermore, several primate species have shown an inversion effect for human faces (e.g., Phelps and Roberts 1994; Wright and Roberts 1996) and great ape faces (Phelps and Roberts 1994), but not for conspecific faces. These patterns have yet to be satisfactorily explained.

In summary, the present study has shown the importance of systematically exploring the relevance of particular features during face processing tasks, and for exerting caution in using behavioral patterns to draw inferences about the underlying mechanisms. We have also shown that when trained to attend to configurational features of the face, at least one cotton-top tamarin fails to show an inversion effect. To determine whether this represents a species-typical character, future work must increase the number of individuals tested, as well as extend the procedures used to other species, both closely and distantly related.

Acknowledgements The authors would like to thank Kofi Kankam and Renda Soylemez for help with running the experiment. For comments on the manuscript, we thank Frank Tong, William Hopkins, and two anonymous reviewers for Animal Cognition. The tamarins were provided by the New England Regional Primate Research center (PHS-P51RR00168-36). All of this research conforms to United States federal guidelines for use of animals in research, and was approved by Harvard's Animal Care and Use Committee (Assurance of Compliance 92-16, 26 February 1999).

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