

2007

Face Processing in Humans and New World Monkeys: the Influence of Experiential and Ecological Factors. *Animal Cognition*

Julie J. Neiworth
Carleton College

Janice M. Hassett
Carleton College

Cara J. Sylvester
Carleton College

Follow this and additional works at: https://digitalcommons.carleton.edu/psyc_faculty

 Part of the [Animal Studies Commons](#), and the [Psychology Commons](#)

Recommended Citation

Neiworth, J. J., Hassett, J. M., & Sylvester, C. J. (2007). Face Processing in Humans and New World Monkeys: the Influence of Experiential and Ecological Factors. *Animal Cognition*, *10*, 125-135. Available at: <https://doi.org/10.1007/s10071-006-0045-4>. Accessed via Faculty Work. Psychology. *Carleton Digital Commons*. https://digitalcommons.carleton.edu/psyc_faculty/7

The definitive version is available at <https://doi.org/10.1007/s10071-006-0045-4>

This Article is brought to you for free and open access by the Psychology at Carleton Digital Commons. It has been accepted for inclusion in Faculty Work by an authorized administrator of Carleton Digital Commons. For more information, please contact digitalcollections@carleton.edu.

Face processing in humans and new world monkeys: the influence of experiential and ecological factors

Julie J. Neiworth · Janice M. Hassett · Cara J. Sylvester

Received: 27 December 2005 / Revised: 21 July 2006 / Accepted: 21 July 2006 / Published online: 15 August 2006
© Springer-Verlag 2006

Abstract This study tests whether the face-processing system of humans and a nonhuman primate species share characteristics that would allow for early and quick processing of socially salient stimuli: a sensitivity toward conspecific faces, a sensitivity toward highly practiced face stimuli, and an ability to generalize changes in the face that do not suggest a new identity, such as a face differently oriented. The look rates by adult tamarins and humans toward conspecific and other primate faces were examined to determine if these characteristics are shared. A visual paired comparison (VPC) task presented subjects with either a human face, chimpanzee face, tamarin face, or an object as a sample, and then a pair containing the previous stimulus and a novel stimulus was presented. The stimuli were either presented all in an upright orientation, or all in an inverted orientation. The novel stimulus in the pair was either an orientation change of the same face/object or a new example of the same type of face/object, and the stimuli were shown either in an upright orientation or in an inverted orientation. Preference to novelty scores revealed that humans attended most to novel individual human faces, and this effect decreased significantly if the stimuli were inverted. Tamarins showed preferential looking toward novel orientations of previously seen tamarin faces in the upright orientation, but not in an inverted orientation. Similarly, their preference to look longer at novel tamarin and human faces within the pair was reduced significantly with inverted stimuli. The results confirmed prior findings in humans that novel human faces generate more attention in the upright than in the inverted orientation. The monkeys also attended more to faces of conspecifics, but showed an inversion effect

to orientation change in tamarin faces and to identity changes in tamarin and human faces. The results indicate configural processing restricted to particular kinds of primate faces by a New World monkey species, with configural processing influenced by life experience (human faces and tamarin faces) and specialized to process orientation changes specific to conspecific faces.

Keywords Face processing · Monkeys · Conspecific · Perception · Tamarins

Humans rely heavily on visual recognition to interact with other individuals. Our ability to identify each other by noting differences in faces is a complex process normally taken for granted. Its significance becomes salient in individuals with prosopagnosia. This perceptual deficit seems localized in the fusiform area in the right temporal hemisphere in humans (Farah 1990; McCarthy et al. 1997). Because it can be localized neurally, and because there is evidence of double dissociations by which some patients can recognize faces but not other objects, and others can recognize objects but not faces, the conclusion is that there is a specialized system for processing faces in the human brain (McCarthy et al. 1997). Important questions that remain are whether the system is specialized for faces or can be applied to other stimuli, and whether it evolved as a hardwired system in humans, or in many other primate species which share a similar social world.

Within human studies, it seems that the unique aspects of face processing extend to stimuli other than faces. For example, humans experience an inversion effect in that we cannot discriminate human faces as easily when they are presented inverted rather than upright (Ellis and Shepherd 1975; Philips and Rawles 1979). Diamond and Carey (1986) demonstrated the same inversion effect in adult humans who

J. J. Neiworth (✉) · J. M. Hassett · C. J. Sylvester
Department of Psychology, Carleton College,
Northfield, MN 55057, USA
e-mail: jneiwor@carleton.edu

acquired perceptual expertise for dog breeds, and Gauthier and Tarr (1997) found activation of the fusiform “face” area (FFA) in human subjects when discriminating “greebles” after becoming “greeble” experts. Gauthier and others also found that the FFA was activated in car and bird experts to cars and birds (Gauthier et al. 2000). Taken together, these studies suggest that the unique reliance on configural processing for faces applies to any well-practiced or extremely familiarized homogeneous stimulus set.

If it is the case that the face-processing system is not specialized to process faces, is it still unique in the sense that it is an innate system? Newborns tend to look longer at face-like stimuli than stimuli with features not configured like faces (Johnson et al. 1991). Within a few days from birth, infants recognize their mothers’ faces (Pascalis et al. 1995) and by 3 months of age, infants show evidence of integrating facial features into a whole, rather than processing the features individually (Cashon and Cohen 2003). Some have argued that such evidence in very young human infants indicates an innately specified face module in humans (Slater and Quinn 2001).

An alternative explanation is that exposure to faces in early infancy tunes cortical networks to become specialized for face processing. Developmental studies have shown that 6-month-old infants notice differences in the faces of monkeys and humans equivalently, but by 9 months of age, infants’ processing of faces is perceptually tuned to human faces alone (Pascalis et al. 2002). With regard to humans, then, face processing seems localized to a particular brain area, but that area is most likely used to process high-frequency well-experienced stimuli (such as cars by car experts; Gauthier et al. 2000). Moreover, face processing is not a purely innate system because it is cortically tuned by early experience to show greater sensitivity toward conspecific faces.

A possible explanation for the existence of a cortical network which develops an ability to process stimuli like faces configurally is that we needed to recognize other humans early on and quickly in order to survive in our complex social system. By this explanation, the cortical network should be present in other nonhuman primates which evolved in the midst of similar social systems that require early conspecific identification to survive. A review of nonhuman primates’ sensitivities to faces, eye gaze, and orientation suggests that the primate brain’s organization and primate intelligence evolved, at least in part, to meet the demands of sociality (Ghazanfar and Santos 2004).

If the face-processing system evolved to assist primates to recognize salient social stimuli, then primates should show a similar pattern of processing faces as do humans, including (1) a sensitivity toward conspecific faces, (2) a sensitivity toward particular configurations of highly practiced stimuli, and (3) an ability to generalize changes in the face that do not

suggest a new identity, such as a face differently oriented. If adult primates from various groups show these similar characteristics of face processing, then there is indirect evidence that the face-processing system evolved as a primate-general cortical network to encode configurations that are experienced at high rates, not as a human-unique face module.

Research on face processing in primates has revealed that neurons in the superior temporal sulcus of the inferior temporal cortex of macaque monkeys discharge specifically to face stimuli (Desimone et al. 1994; Perrett et al. 1982, 1985). Recent evidence from single cell recordings targeted by fMRI analyses has identified particular regions or “face patches” in macaques that are predominately face selective and respond less to body parts or to objects (Tsao et al. 2003, 2006; Pinsk et al. 2005). Cells in these areas have been identified to respond to a variety of photographs of human and monkey faces, and to respond differentially in response to repeated exposures to specific individuals, changes in facial emotional expression, eye gaze changes, and changes in facial orientation (see also Rolls 1984; Perrett et al. 1988; Desimone 1991; Gauthier and Logothetis 2000).

Given that face processing may occur in homologous brain areas in nonhuman primates and humans, the next question is whether their processing shares the same characteristics. Gunderson and Schwartz (1985) found that infant bonnet macaques recognized conspecific faces in a visual paired comparison task, and Pascalis and Bachevalier (1998) found a unique conspecific face-processing effect in rhesus monkeys in the same task. Gothard et al. (2004) found that rhesus monkeys increased attention to conspecific faces with changes in expression, changes in identity, and changes in orientation, and these results were unaffected by inverted stimuli. Their results suggested that monkeys may be more sensitive to conspecific faces but fail to process them configurally. In contrast, Phelps and Roberts (1994) tested squirrel monkeys in a matching-to-sample (MTS) task involving face stimuli and found an inversion effect to human faces. Wright and Roberts (1996) found that monkeys showed a decrement in performance when inverted human faces were shown but not when inverted monkey faces were shown in a discrimination task. Parr et al. (1998, 1999) found that chimpanzees showed an inversion effect to match human and chimpanzee faces, but not for capuchin faces or for cars, whereas rhesus monkeys showed an inversion effect to cars, rhesus faces, and capuchin faces, but not to inverted human faces or abstract shapes. Interestingly, they found a relationship between the strength of the inversion effect and the number of trials of training needed before meeting criterion, with categories that required the most training showing the strongest inversion effects. Taken together, the results from tests of the inversion effect argue for an inversion effect induced by extensive training or extensive experience with particular types of faces. An important study which tested for inversions be-

haviorally and without the use of extensive training found that rhesus monkeys processed faces faster when the stimuli were presented upright as compared to inverted. In the same study, single unit recording identified patches of neurons in one hemisphere which responded to upright faces faster than to inverted faces (Perrett et al. 1988).

This study delineates the effects of past experience and innate ability on early processing of upright and inverted faces in a New World (NW) monkey species, cotton top tamarins, in a task in which expertise for particular categories was not trained. Tamarins were selected because they are sensitive to changes in face type (Weiss et al. 2001), they show sensitivities to the gaze direction of conspecifics and of humans to find food (Neiworth et al. 2002) and they show longer looking to novel categories of animal types shown in pictures on computer screens (Neiworth et al. 2004). Their attentional reactions were compared to adult humans in the same task so that processing similarities and differences would emerge. The hypothesis was that tamarins might encode faces similarly to humans, as evidenced by a special sensitivity toward conspecific faces and to types of faces for which they have acquired extensive exposure in their life histories, but not to faces of species which are relatively novel to them. By testing a nonhuman primate species not often examined and not closely related to humans in a task that did not involve extensive training, the results test more directly any primate-general aspects of face processing.

Method

Human subjects

A total of 20 undergraduate students, 13 women and 7 men, enrolled at Carleton College ranging from 17 to 21 years of age participated in this study. None had worked or cared for the tamarins at Carleton College, and none had any extensive experience working with nonhuman primates. They were randomly assigned to one of two groups, upright (UP) or inverted (INV) testing. They received a \$10 incentive for their participation. A total of two subjects' data, one from each group, were excluded because the direction of looking could not be determined on most of the trials due to their head orientations. Results were based on nine subjects in each group.

Tamarin subjects

Twelve captive-born adult cotton-top tamarins served as subjects. They were exposed to both conditions of testing, with UP testing occurring first, and INV testing presented second. This design maximized the number of subjects whose reactions were measured in the two conditions, and the reactions measured were attentional measures so nothing was

trained during the first phase that would affect the second phase. Only 10 subjects were able to participate in the INV condition due to the death of two subjects in the interim period (Mac and Dante) and thus the 10 subjects' data were analyzed across both phases.

The tamarins were family-reared and socially housed in pairs or in family groups. The pairs were housed in 0.85 m × 1.5 m × 2.3 m cages, separated by opaque sheets. The family was housed in a 1.8 m × 3.0 m × 2.3 m cage. The subjects were on a 12-h light:12-h dark schedule and had free access to water. Their daily diet consisted of a yogurt and applesauce breakfast, a main feed of Zupreem Marmoset chow, fruits and vegetables, and an afternoon protein snack (e.g. eggs, hamburger, peanuts). Their care conformed to U.S. standards for primate care, including USDA standards and PHS standards for nonhuman primates.

Five of the tamarin subjects (Fozzy, Zhivago, Rolo, Yohoo, and Caitlin) had been exposed to the following stimuli before this experiment: mirror exposure (Neiworth et al. 2001); full-body photographs of different types of animals (Neiworth et al. 2004); gaze direction in human experimenters (Neiworth et al. 2002); and tracking food in an object permanence test (Neiworth et al. 2003). The other five subjects (Encore, Heron, Vulture, Quince, and Willow) had not been in any studies involving pictures of stimuli before this one. None had been exposed to photographs of faces of animals, including themselves.

Stimuli

A total of 162 high-quality digital photographs of 12 different adult male humans, 10 cotton-top tamarins, 13 chimpanzees, and 21 objects were used as stimuli (see Fig. 1 for examples of stimuli used). The tamarin, object, and human photos were taken using a Canon PowerShot G2 camera. Care was taken so that the tamarin subjects were presented with faces of unfamiliar tamarins. The human adult faces were unfamiliar to the human subjects because they were of male construction workers on campus over break periods or relatives of the experimenters who were not part of campus life. Two male faculty members were photographed and included in the set in the INV condition. The chimpanzee pictures were downloaded from various websites, including the Georgia State University's language project, the Environmental News Network, the San Francisco Zoo, and the World Wildlife Federation, to name a few. Objects were photographed against a black background upright in a variety of orientations. It was very unlikely that the humans in this study had seen the chimpanzee or humans depicted in the stimuli before this study, and it is certain that the tamarins had not seen any of these individuals.

Photographs were converted to black-and-white images through a program called GraphicConverter (Thorsten

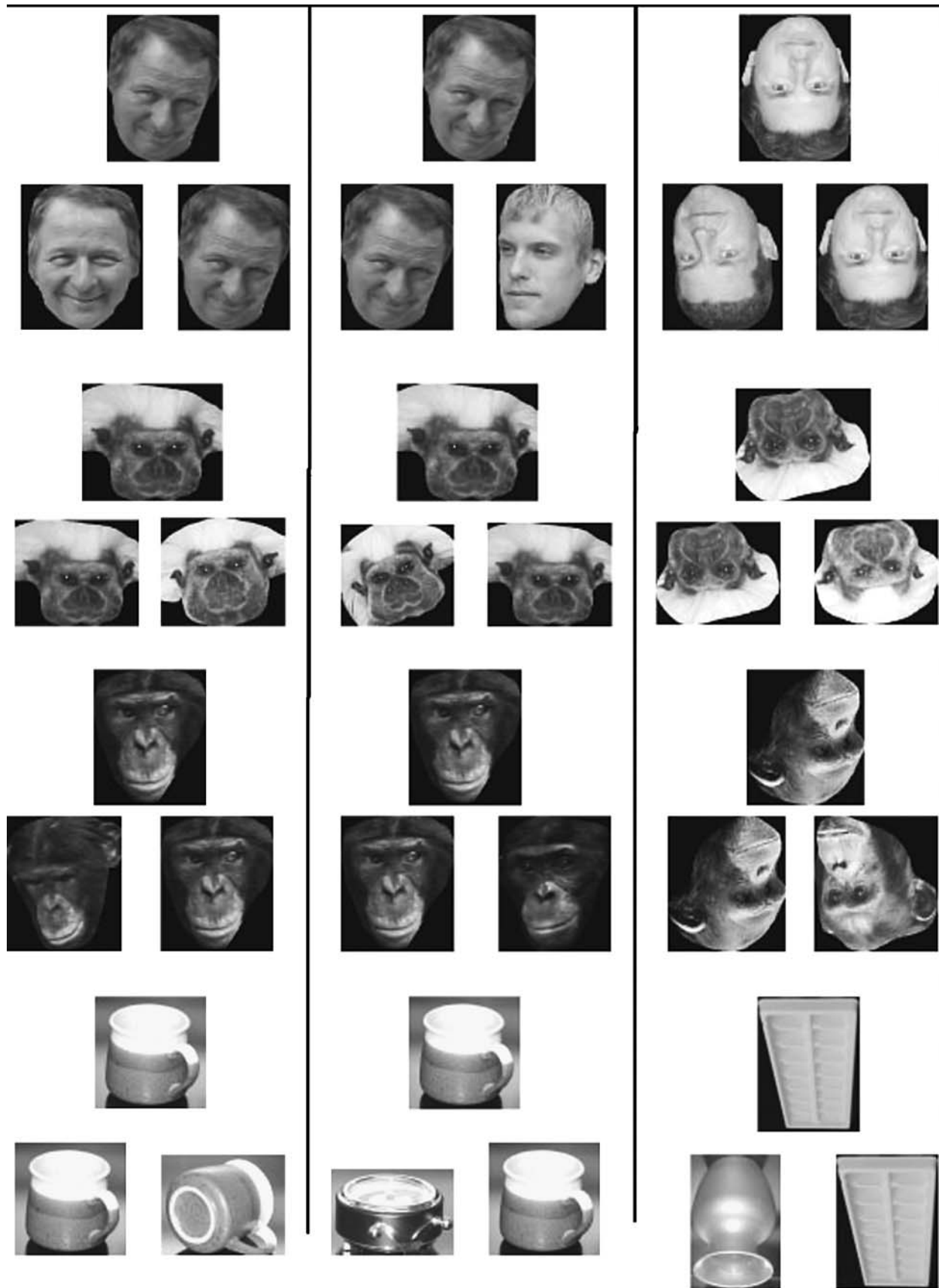


Fig. 1

Lemke, v.3.1.1). Pictures of faces were upright, showing frontal face shots which varied by approximately 60° horizontally and 30° vertically. Orientation changes (OR) were accomplished by slight shifts in the degree of looking by the face photographed. INV faces were pictures presented 180° inverted.

The backgrounds of the photographs were filled so that only the faces and some hair appeared against a black background in the visual image. Pictures were presented on a 17 in. color monitor through Microsoft Office × PowerPoint on an Apple G4 computer. The pictures were scaled to two different sizes as needed for their presentation in the experiment. The larger-sized pictures, presented as samples in the procedure, ranged from 11 to 16 cm in width and from 11 to 15 cm in height. The smaller-sized pictures, presented in pairs as test items, ranged from 6 to 11 cm in width and from 8 to 11 cm in height. Stimuli were numbered and were selected per trial using a random number generator, and trial order within a session was also randomly assigned. No stimulus was used for more than one trial type in any phase of the experiment, although each trial type was presented twice to counterbalance for side (left or right) on which the novel stimulus was presented.

Apparatus

Human participants were seated in front of a 17-inch monitor connected to a PowerMac G4 which presented the stimuli. A chair was positioned 40 cm away from the screen and at a height such that the computer monitor was at eye level for each participant and so that the camera recorded the subject's face.

Tamarin subjects were lured into a small transport cage measuring 90 cm × 90 cm × 90 cm adjacent to their home cage for daily sessions, and viewed the same monitor 10 cm from the outside of the transport cage. For both species, a Canon VC-C3 Communication video camera was centered above the computer monitor and connected to a Sony VCR to record the face of each subject, including eyes and eye movement, throughout each session. In the case of the tamarin subjects, the camera was connected to a remote system so that the animal could be tracked while it moved in the cage.

◀ **Fig. 1** Examples of different samples and pairs (including the sample repeated as a member of the pair) used in the experiment. The left panel shows orientation changes of the same face or object as the novel stimulus of the pair. The middle panel shows novel individuals of the same species or object type as the novel stimulus of the pair, shown in upright (UP) form. The right panel depicts a novel individual in each pair shown in the inverted (INV) condition

Procedure

Both procedures were approved by the relevant college committees, the Institutional Review Board for the human subjects' protocol, and the Institutional Animal Care and Use committee for the tamarin protocol. Human participants signed a consent form for participating after being told the following:

The design of this study is straightforward and you will not be required to answer any questions about what you have seen or done. Because we want to study how you process similarities and differences in pictures, we will be videotaping you for later analysis. We ask that you remain as still as possible throughout the session and that you do your best to stay focused. You will first see a yellow screen – when you are ready to begin, press the space bar. You will be presented with a single picture, and, after a delay, a pair of pictures followed by a green screen. This indicates the end of the trial and you will need to press the space bar again to continue. Feel free to take a break if needed or to stop participating at any time.

Sessions for humans and tamarins proceeded in the same manner, with a few exceptions (including the instructions, which were not read to the tamarins). For both species, the stimuli were shown in Microsoft PowerPoint presentations and each trial lasted 60 s. Each trial progressed as follows: first, a yellow observing screen was presented for 2 s, followed by a *click* sound and then a single sample stimulus was presented for 20 s centered on the screen. After the familiarization period was over, a purple delay screen was accompanied by a *click*, and remained on for 5 s. Finally, a pair of pictures (accompanied by a *whoosh* sound) was presented for 10 s, with one stimulus of the pair being the sample and the other, a novel stimulus. The trial ended with a green intertrial interval (ITI) screen, accompanied by a *whoosh* sound, which was presented for 23 s to the tamarin subjects. We kept the ITI long for the tamarins to prevent proactive interference between trials. Human subjects were exposed to much longer sessions and so we allowed them to elect to push the space bar during the ITI when they wanted the next trial to begin. Most humans elected this option within about 5 s of the ITI.

The novel stimulus in the pair was from one of three categories of change: orientation (OR) difference showing a slightly different gaze direction orientation, individual (IND) difference showing a novel individual, and a species (SPEC) difference, showing a novel type (e.g., human–chimp, human–tamarin, tamarin–chimp, or object–human, for example). The paired pictures were vertically centered and at opposite sides of the screen. The distance between

the interior vertical edges of the pictures ranged from 9 to 15 cm.

In the UP condition, the sample stimulus and the pairs were presented upright. In the INV condition, the sample stimulus and the pairs presented were all inverted. This insured that the familiarization occurred in both conditions since the sample matched exactly one of the pair in both UP and INV conditions.

The stimuli were presented in sequences consisting of 17 trial types, with 4 OR (orientation) changes, or 1 for each category (tamarin, chimpanzee, human, and object); 4 IND (individual) changes to test each category (tamarin, chimpanzee, human, and object); and 9 SPEC (species) changes to test various combinations (i.e., with sample type listed first and novel type listed second, human–tamarin, tamarin–human, human–chimpanzee, chimpanzee–human, tamarin–chimpanzee, chimpanzee–tamarin, and object – each species type). These trial types were presented twice each in each sequence with the location of the novel stimulus in the pair switched to be on the left once, and on the right once. There were a total of 34 trials in each sequence, and three different sequences were made for each condition (UP and INV). The UP condition exposed the tamarins and humans to 102 trials. The INV sequence consisted of 10 trial types (4 OR, 4 IND, and 2 SPEC) presented twice each for a total of 20 trials per sequence. The INV condition contained an abbreviated version of the SPEC trial types; only two types were shown (human–tamarin and tamarin–human). Again three sequences of INV trials were constructed for a total of 60 trials in this condition.

The procedural differences were that human subjects participated in one session either of the UP condition constructed of 102 trials and lasting about 70 min, or the INV condition constructed of 60 trials (INV) lasting about 42 min. In pilot testing, we found the task to be somewhat tedious, and in the case of the inverted trials, to cause some degree of tension and stress in perceptual processing. That was the motivation for reducing the length of session in the INV condition.

To accommodate the tamarins' short attention span within studies, the tamarin subjects were exposed to six sessions in each phase (UP and later, INV) wherein the three sequences of trials shown to humans were shown in the same order to tamarins. Each UP session consisted of the 17 trial types presented once each, with two consecutive sessions constituting counterbalanced exposure on the left and on the right sides and completing a single sequence of the trials. The INV sessions consisted of 10 trial types presented once each for a total of 20 trials across the two sessions which completed a single sequence of trials for humans. In the event that subjects were found to look for less than 2 s in any one trial in post hoc coding, more sessions were constructed per subject

to present those trials again in which the stimuli seemed not processed.

Subjects' looking rate toward the 10-s presentations of the paired stimuli were downloaded from analog videotapes to a digitized version through iMovie which allowed viewing and coding at a rate of 30 frames/s. Coding was conducted "blind" to the stimulus conditions because each coder could not see the stimuli on the iMovie clips. The coders used the auditory stimuli to determine the beginning and ending of the 10-s paired presentations. The coders' definitions of looks left and right required that the tamarin's head and eyes or the human's eyes were directed toward the left or right side of the screen. Because the camera was placed above the midline, a reference point was created readily. The accuracy and reliability of look coding was tested with regression analyses of two independent coders' data. The second coder randomly selected two subjects from each species and coded two sessions to compare with the first coder. Regression values for exact durations of looks to either side ranged from $r = +0.77$ to $+0.85$ for tamarins, with a range of $+0.73$ to $+0.95$ for humans.

The dependent variable was percent preference to novelty scores, which was the ratio of the amount of time looking toward the novel stimulus of the pair divided by the total sum of looks to both stimuli in the pair. Once we determined the length of time the subject looked left or right on any given trial, we mapped the looking times to the stimuli to calculate an averaged preference to novelty score per subject per condition/trial type. Statistical analyses were a completely repeated measures design for the tamarins, and were a mixed model design for the humans. All tests were conducted with a level of significance set at $\alpha = 0.05$.

Results

Human preference to novelty scores

A mixed model analysis of variance (ANOVA) compared humans' preference to novelty scores to the repeated measure novel stimulus (OR, IND), the repeated measure stimulus type (tamarin, chimpanzee, human, or object) and the between-group phase condition (UP, INV). The SPEC condition was excluded from the analysis because, upon further inspection, humans always looked longer at a novel category type that was different than the one familiarized, whether it was a novel animal or novel object, and this effect minimized an examination of the more subtle differences within face processing of primates and objects changed by identity or orientation. The ANOVA revealed a significant main effect for type ($F(3, 48) = 15.60, p < 0.01$) and a significant effect for the UP/INV condition ($F(1, 16) = 5.37, p = 0.03$). The

main effect of novel stimulus (OR/IND) was not significant and none of the interactions were significant.

By Bonferroni adjustments for *t*-tests for six comparisons, the main effect of stimulus type was supported by longer looking toward novel changes in faces of humans (mean = 60.93, standard error = 1.45) than at novel changes to faces of tamarins (mean = 53.18, standard error = 2.25; difference = 7.75, $p = 0.008$, adjusted $\alpha = .0083$ ¹). There was no difference in preference to notice novelty between tamarin and chimpanzee faces (mean = 54.49, standard error = 2.37). Human subjects noticed when objects changed (mean = 69.35, standard error = 2.21) significantly more than they did non-human primate face changes (difference from chimpanzee faces = 14.85, $p = 0.0001$, $\alpha = 0.0083$; difference from tamarin faces = 16.16, $p = 0.0001$, $\alpha = 0.0083$). The other pairwise comparisons were not significant. The pattern of results suggests that human face changes and object changes drew more attention than did changes in the nonhuman primate faces. The finding that variations in objects were noticed more than both species of nonhuman primates' face changes but not more than human face changes further documents the particular salience of the human face to human subjects. Figure 2a presents the mean preference to novelty scores for human subjects by animal type and novel stimulus type (OR, IND) separately for the upright and inverted conditions.

In terms of *upright* or *inverted* presentations, human subjects looked significantly longer at the novel stimuli overall when the stimuli were presented upright (mean preference = 62.59, standard error = 1.89) than when they were presented inverted (mean = 56.39, standard error = 1.81), as evidenced by the significant main effect of condition.

Independent samples *t*-tests were conducted to investigate further the differences between the UP and INV conditions within each stimulus type (human, tamarin, chimpanzee, and object). Results indicated that there were significantly higher preference to novelty scores to novel individual human faces in the UP condition (mean = 71.6, standard error = 3.51) as compared to the INV condition (mean = 58.41, standard error = 3.09; $t(16) = 2.82$, $p = 0.01$). In contrast, there was no difference between the preference to novelty scores to changes in the orientation of a human's face when presented upright (mean = 58.51, standard error = 1.84) as compared to inverted (mean = 55.22, standard error = 2.27). The inversion effect was only statistically significant with novel human individual faces; none of the other comparisons between upright and inverted primate faces or objects were significantly different from each other.

¹ The alpha level was adjusted to account for six comparisons between the four conditions, or 0.05/6 or 0.00833.

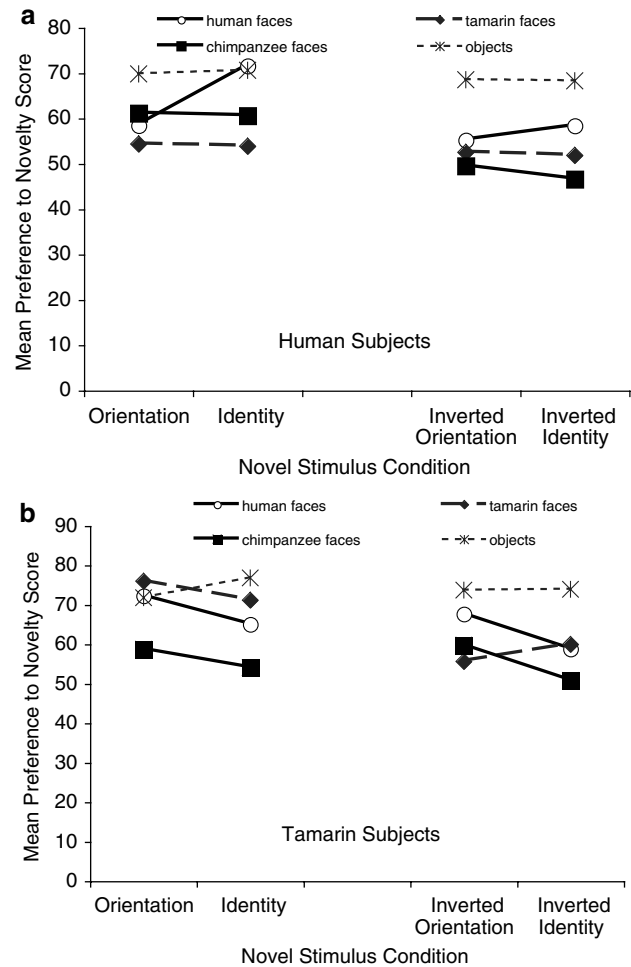


Fig. 2 Mean preference to novelty scores for human subjects (a) and for tamarin subjects (b) to each of the face/object stimulus types to look longer at the novel stimulus (defined either as an orientation or identity change), and shown in the UP and INV conditions

Tamarin preference to novelty scores

A repeated-measures ANOVA examined differences in preference to novelty scores by the repeated measure novel stimulus (OR, IND), stimulus type (tamarin, chimpanzee, human, or object), and condition (UP, INV). As in the case with humans, the preference to look when species changed was always high toward the new category type, and this change obscured an examination of the subtle differences that occurred with identity and orientation change, so the SPEC data were not included. The ANOVA revealed a significant main effect of type ($F(3,27) = 4.69$, $p = 0.009$). The main effects for novel stimulus (OR, IND) and condition (UP, INV) were not significant. The interaction between stimulus type and UP/INV was significant ($F(3, 27) = 4.17$, $p = 0.015$), indicating that some of the different species' faces and objects were treated differently in upright and inverted presentations. No other interactions were significant.

By Bonferroni adjustments for *t*-tests for six comparisons, the main effect of stimulus type was supported by a significantly longer look rate to differences between objects (mean = 74.10, standard error = 3.12) compared to look rates to differences in chimpanzee faces (mean = 55.91, standard error = 2.28; difference = 18.20, $p = 0.0001$, adjusted $\alpha = 0.0083$). Mean preferences to look at novelty within humans and tamarins were intermediate (mean for tamarins = 65.76, standard error = 1.65; mean for humans = 66.00, standard error = 1.46) and were not different from each other, nor from the other two categories. Figure 2b depicts tamarins' mean preference to novelty scores for animal type and novel stimulus (OR, IND) separately for upright and inverted conditions.

Paired samples *t*-tests compared preference scores across the condition (UP and INV) by animal type to determine the source of the interaction effect. In the UP condition, there was a significant difference in preference scores to novel orientations of tamarin faces in the upright condition (mean = 76.06, standard error = 5.05) as compared to orientations in the inverted condition (mean = 55.68, standard error = 2.59, $t(9) = 4.161$, $p = 0.002$). When the novel stimulus change was the identity of the primate face or object, novel tamarin faces provoked significantly higher preference scores in the upright condition (mean = 71.23, standard error = 4.17) than they did in the inverted condition (mean = 60.04, standard error = 1.75; $t(9) = 2.49$, $p = 0.03$) and novel human faces provoked significantly higher preference scores in the upright condition (mean = 65.08, standard error = 1.10) than they did in the inverted condition (mean = 58.84, standard error = 3.68; $t(9) = 2.37$, $p = 0.04$). The differences in preference scores between upright and inverted presentations of chimpanzees and objects when orientation or identity was changed were not significant.

Discussion

The experiment was designed to reveal similarities and differences in the face processing of primate faces for which the subjects either had expertise, a potential innate advantage, or not. Both tamarins and humans differentially encoded the different face types and objects, and this was demonstrated by significant stimulus type effects. For humans, novel changes in objects and in human faces generated more directed looking at the novel stimulus than did chimpanzee or tamarin face changes. This indicates that humans show a conspecific advantage to attending to human face changes. This advantage may be due to attributes unique to humans for humans, or it may be due to expertise acquired by humans to human faces.

For tamarins, object changes were the most attention-getting, and chimpanzee face changes drew the least directed

looking toward novel changes. For tamarins, both human and tamarin face changes drew intermediate levels of preferential attention to novel changes. Thus, tamarins show similar attention toward both human and tamarin face changes, but not to all primate faces because the chimpanzee face changes generated the least amount of attention. Because tamarins showed more sensitivity toward changes in both tamarin and human faces, the sensitivity suggests an origin of expertise rather an origin of evolved innate predisposition. The evidence does not support a primate-general module for faces, because chimpanzee faces were treated differently than were faces for which the tamarins had more experience.

The upright and inverted conditions tested for configural processing because stimuli processed configurally would generate less attention to differences when presented in an inverted manner. Overall, humans were able to note novel changes significantly more when the stimuli were presented upright as opposed to inverted, suggesting that many of the stimuli were coded by humans configurally. But, on closer inspection, the only significant change in encoding differences that supported this finding was if human faces were used and identity changed, and under that condition, humans showed a decrement in performance. Configural processing seems applied uniquely to human faces to track identity by humans. Overall, humans show a conspecific advantage to attending to human faces changes, and humans encode human faces configurally to notice the identity of individuals.

Which stimuli do the tamarins process configurally? There were significant decrements in noticing novel changes when tamarin face stimuli were inverted, whether the novel change was the orientation of the face, or the identity of the face. This finding indicated that any tamarin face change was noted more strongly in an upright presentation than in an inverted presentation. This outcome supports Gothard et al.'s (2004) findings in macaques because tamarins also show a hypersensitivity to subtle face changes in conspecific faces. It is different than the Gothard et al.'s study in that tamarins showed an inversion effect, whereas Gothard did not find one. It is possible that with very brief presentations (1.5 s) in the Gothard et al. (2004) study, monkeys tended to focus on feature changes in the stimuli and thus did not process the stimuli configurally. With 20 s of familiarization to faces followed by 10 s in which the tamarins compared two stimuli with each other, they encoded the stimuli configurally, and thus showed inversion effects. It is true that with human infants, short look times generate a focus on "local" cues or specific features, while longer looking times typically generate attention toward "global" cues in which the feature groupings are assessed (Frick et al. 2000). In this study, with longer looking times provided, we were able to tap into the configural processing strategies of tamarins and found more robust inversion effects to conspecific faces.

Another notable inversion effect emerged in the tamarins to changes in identity. For both human and tamarin faces, when a novel human or tamarin individual was presented, tamarins directed their attention much more to the identity change in the upright than in the inverted condition. This inversion effect did not occur to chimpanzee faces, so it does not support a primate-general module for configural processing of all faces by tamarins. Rather, it supports configural processing of both human and tamarin faces by tamarins, most likely the result of expertise with human and tamarin faces.

Taken together, the data suggest that tamarins use configural processing when noting the identity of faces of species with which they have had vast experience. Tamarins also show uniquely sensitive configural processing toward tamarin faces in the sense that any change (orientation or identity) to a conspecific is noted more readily in the upright position as well. So, while humans showed a unique conspecific configural processing strategy toward human faces to determine identity, tamarins show an experientially driven configural processing strategy toward human and tamarin faces to determine identity, and a conspecific configural processing strategy toward subtle changes in tamarin faces, including the orientation of the same face.

This interpretation brings together the disparate findings in the literature, if applied more broadly. It is possible that monkeys and apes show configural processing of human faces and inversion effects to human faces because they are expert at identifying humans. All the subjects in the prior studies and this one have been exposed to human caretakers throughout their lives, and thus have collected thousands of encoded representations of human faces. The evidence from this study suggests that such extensive experience can tune the face-processing system to code human faces configurally. It is also likely that faces of one's own kind are processed configurally either from extensive experience or from an inherited system that is pretuned to the conspecific face. This would explain why monkeys in other studies show a conspecific inversion effect. A lack of a conspecific inversion effect has been found in some monkey studies, and it may be due to two possibilities: (1) short presentation times that do not allow for configural processing to emerge or (2) less extensive practice, which if necessary to produce an inversion effect, would argue against an innate system for conspecific faces.

There is also evidence of a conspecific-unique configural processing by tamarins, supported by the inversion effect to orientation changes to tamarin faces. This indicates that adult tamarins are rapidly encoding in a configural way gaze direction changes in a tamarin face exclusively. Because this particular aspect of face processing in tamarins is functionally different from face processing by humans, this particular attentional strategy is probably not one that evolved from a

common primate ancestor. Rather the conspecific orientation sensitivity may be associated with the species' ecological niche and social organization, and thus may have evolved or been maintained in this species to promote survival. It is possible that the tamarins have two routes of face processing of conspecifics at their disposal—one that is a general-purpose face/stimulus system that is tuned to configural processing by experience, and one that is unique to orientations of conspecifics for survival. Because tamarins evolved in a forest canopy, it seems likely that individual identification may be accomplished by multiple routes, including auditory and visual input. There is evidence that cotton-top tamarins emit individually unique long calls (Snowdon et al. 1983) and they respond differentially to playbacks of different individuals' calls. Cotton-top tamarins also live in small social groups consisting exclusively of family members. Individual identification by visual means is probably accomplished by early experience with a small set of individuals via a general-purpose face/stimulus processing system tuned to configurations of particular individuals seen extensively and repeatedly. On the other hand, face orientation of another individual can yield life-saving information about food, about predators, and about what actions that individual will take next, aggressive, submissive, or neutral. Such encoding may have evolved for conspecific faces instinctively and early on in perceptual processing.

One may ask what has evolved if experience plays such a central role in tuning face processing, and the answer is probably that configural face processing is the rule across species of primates, but the function of face processing has evolved to support different purposes for different species of primates. A general-purpose processing system that can be tuned by experience to identify individuals seems present in both humans and tamarins here, and is likely to be present in most primates, given much of the past literature. Species-specific responding to faces may evolve if a species responds to faces at one level more uniquely than another to adapt and survive. In the case of tamarins, a New World monkey species, where a fellow monkey is looking, is just as important to encode as is the identity of the conspecific.

Acknowledgment The research presented here was funded by NIH grant 1 R15 MH62434-01A1 to Julie J. Neiwirth.

References

- Cashon CH, Cohen LB (2003) The construction, deconstruction, and reconstruction of infant face perception. In: Pascalis O, Slater P (eds) *The development of face processing in infancy and early childhood: current perspectives*. Nova Science, New York, pp 55–68
- Desimone R (1991) Face-selective cells in the temporal cortex of monkeys. *J Cogn Neurosci* 3:1–8

- Desimone R, Albright TD, Gross CG, Bruce C (1984) Stimulus-selective properties of inferior temporal neurons in the macaque. *J Neurosci* 4:2051–2062
- Diamond R, Carey S (1986) Why faces are and are not special: an effect of expertise. *J Exp Psychol Gen* 115:107–117
- Ellis HD, Shephard JW (1975) Recognition of upright and inverted faces in the left and right visual fields. *Cortex* 11:3–7
- Farah MJ (1990) Visual agnosia: disorders of object recognition and what they tell us about normal vision. MIT Press, Cambridge, MA
- Frick J, Colombo J, Allen JR (2000) Temporal sequence of global-local processing in 3-month-old infants. *Infancy* 1:375–386
- Gauthier I, Logothetis NK (2000) Is face recognition not so unique after all? *Cogn Neuropsychol* 17:125–142
- Gauthier I, Tarr MJ (1997) Becoming a “Greeble” expert: exploring the face recognition mechanism. *Vis Res* 37:1673–1682
- Gauthier I, Skudlarski P, Gore JC, Anderson AW (2000) Expertise for cars and birds recruits brain areas involved in face recognition. *Nat Neurol* 3:191–197
- Ghazanfar AA, Santos LR (2004) Primate brains in the wild: the sensory bases for social interactions. *Nat Neurosci* 5:603–616
- Gothard KM, Erickson CA, Amaral DG (2004) How do rhesus monkeys (*Macaca mulatta*) scan faces in a visual paired comparison task? *Anim Cogn* 7:25–36
- Gunderson VM, Swartz KB (1985) Visual recognition in infant pig-tailed macaques after a 24-hour delay. *Am J Primatol* 8:259–264
- Johnson MH, Dziurawiec S, Ellis H, Morton J (1991) Newborn’s preferential tracking of face-like stimuli and its subsequent decline. *Cognition* 40:1–19
- McCarthy G, Puce A, Gore JC, Allison T (1997) Face-specific processing in the human fusiform gyrus. *J Cogn Neurosci* 9:605–610
- Neiworth JJ, Anders SL, Parsons RR (2001) Tracking responses related to self-recognition: a frequency comparison of responses to mirrors, photographs, and videotape of monkeys by cotton top tamarins (*Saguinus oedipus*). *J Comp Psychol* 115:432–438
- Neiworth JJ, Burman MA, Basile BM, Lickteig MT (2002) Use of experimenter-given cues in visual co-orienting and in an object-choice task by a new world monkey species, cotton top tamarins (*Saguinus oedipus*). *J Comp Psychol* 116:3–11
- Neiworth JJ, Steinmark E, Basile BM, Wonders R, Steely F, DeHart C (2003) A test of object permanence in a new-world monkey species, cotton top tamarins (*Saguinus oedipus*). *Anim Cogn* 6:27–37
- Neiworth JJ, Parsons RR, Hassett JM (2004) A test of the generality of perceptually based categories found in infants: attentional differences toward natural kinds by New World monkeys. *Dev Sci* 7:185–193
- Parr LA, Dove TA, Hopkins WD (1998) Why faces may be special: evidence of the inversion effect in chimpanzees (*Pan troglodytes*). *J Cogn Neurosci* 10:615–622
- Parr LA, Winslow JT, Hopkins WD (1999) Is the inversion effect in rhesus monkeys face-specific? *Anim Cogn* 2:123–129
- Pascalis O, Bachevalier J (1998) Face recognition in primates: a cross-species study. *Behav Proc* 43:87–96
- Pascalis O, deHaan M, Nelson CA (2002) Is face processing species-specific during the first year of life? *Science* 296:1321–1322
- Perrett DI, Rolls ET, Caan W (1982) Visual neurons responsive to faces in the monkey temporal cortex. *Exp Brain Res* 47:329–342
- Perrett DI, Smith PAG, Potter DD, Mistlin AJ, Head AS, Milner AD, Jeeves MA (1985) Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proc Trans R Soc Lond Ser B* 223:293–317
- Perrett DI, Mistlin AJ, Chitty AJ, Smith PAJ, Potter DD, Broennimann R, Harries M (1988) Specialized face processing and hemispheric asymmetry in man and monkey: evidence from single unit and reaction time studies. *Behav Brain Res* 29:245–258
- Pascalis O, de Schonen S, Morton J, Deruelle C, Fabre-Grenet H (1995) Mother’s face recognition by neonates: a replication and an extension. *Infant Behav Dev* 18:79–85
- Phelps MT, Roberts WA (1994) Memory for pictures of upright and inverted primate faces in humans (*Homo sapiens*), squirrel monkeys (*Saimiri sciureus*), and pigeons (*Columba livia*). *J Comp Psychol* 108:114–125
- Philips RJ, Rawles RE (1979) Recognition of upright and inverted faces: a correlational study. *Perception* 8:577–583
- Pinsk MA, Desimone K, Moore T, Gross CG, Kastner S (2005) Representations of faces and body parts in macaque temporal cortex: a functional MRI study. *Proc Natl Acad Sci USA* 102:6996–7001
- Rolls ET (1984) Neurons in the cortex of the temporal lobe and in the amygdala of the monkey with responses selective for faces. *Hum Neurobiol* 3:209–222
- Slater A, Quinn PC (2001) Face recognition in the newborn infant. *Infant Child Dev* 10:21–24
- Snowdon CT, Cleveland J, French JA (1983) Responses to context- and individual-specific cues in cotton-top tamarin long calls. *Anim Behav* 31:92–101
- Tsao DY, Freiwald WA, Knutsen TA, Mandeville JB, Tottell RBH (2003) Faces and objects in macaque cerebral cortex. *Nat Neurosci* 6:989–995
- Tsao DY, Freiwald WA, Tottell RBH, Livingstone MS (2006) A cortical region consisting entirely of face-selective cells. *Science* 312:670–674
- Weiss DJ, Kralik JD, Hauser MD (2001) Face processing in cotton-top tamarins (*Saguinus oedipus*). *Anim Cogn* 4:191–205
- Wright AA, Roberts WA (1996) Monkey and human face perception: inversion effects for human faces but not for monkey faces or scenes. *J Cogn Neurol* 8:278–290