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An inversion effect modified by expertise in capuchin monkeys

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Abstract The face inversion effect may be defined as the general impairment in recognition that occurs when faces are rotated 180°. This phenomenon seems particularly strong for faces as opposed to other objects and is often used as a marker of a specialized face-processing mechanism. Four brown capuchin monkeys (*Cebus apella*) were tested on their ability to discriminate several classes of facial and non-facial stimuli presented in both their upright and inverted orientations in an oddity task. Results revealed significantly better performance on upright than inverted presentations of capuchin and human face stimuli, but not on chimpanzee faces or automobiles. These data support previous studies in humans and other primates suggesting that the inversion effect occurs for stimuli for which subjects have developed an expertise.

Keywords Oddity · Visual discrimination · Primates · Face processing · Face recognition

Introduction

Faces are an important component of social interaction for humans and other primates. Not only do they convey information about age, sex, and race, but they also contain salient emotional cues. Face processing plays a role in both individual and species recognition (e.g., Fujita 1987; Dahl et al. 2007) and serves a critical function in communication. Given how important the visual identification of

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individuals and their facial expressions likely is in the social life of primates, it is of interest to investigate whether other species besides *Homo sapiens* have specialized mechanisms for processing faces.

The inversion effect is one of the most extensively studied signatures of face-specific processing in humans. This phenomenon is defined as the general impairment in recognition that occurs when a face is inverted 180°. Yin (1969, 1970) was the first to demonstrate that when human subjects were presented with an inverted face, they were impaired in recognition memory tasks, showing both a decrease in accuracy and response times. This effect seems particularly strong for faces as opposed to non-facial visual objects, such as photographs of houses, cars, and other scenes that have comparable complexity to faces and are also typically viewed in an upright position (e.g., Yin 1969). Numerous other studies with humans have indicated a profound effect of orientation on the way faces are processed (Valentine 1988). Face recognition relies more upon global processing strategies than does the recognition of non-facial stimuli (Bruce and Humphreys 1994), meaning that faces are not processed on the basis of specific features, but rather on the basis of global arrangement of these features, which is unique for every face. The inversion effect may be due to holistic encoding of upright faces in contrast to inverted faces, which are encoded in a piecemeal fashion (Diamond and Carey 1986; Tanaka and Farah 1991; Farah et al. 1995; Carey and Diamond 1977).

Few studies have examined the presence of the face inversion effect in non-human primates. These studies have focused primarily on macaques and chimpanzees (*Pan troglodytes*) often with mixed results, making it difficult to determine whether this pattern is due to species differences, or to the variety of methodologies and stimuli used. An early study by Bruce (1982) with long-tailed macaques

(*Macaca fascicularis*) failed to find evidence of an inversion effect, as did other studies with macaques (Rosenfeld and van Hoesen 1979; Dittrich 1990; Gothard et al. 2004; Parr et al. 1999). Bruce suggested that unlike humans, macaques lack a face recognition system dependent on configuration and orientation, perhaps because macaques mature at a quicker rate than humans do. However, these claims must be re-examined in light of more recent studies that report the inversion effect in different macaque species (Overman and Doty 1982; Swartz 1983; Tomonaga 1994; Vermeire and Hamilton 1998; Perrett et al. 1988). Studies conducted with chimpanzees, on the other hand, have been relatively consistent with findings in the human literature, such that the inversion effect occurs primarily for familiar categories of stimuli, including conspecific and human faces (Parr et al. 1998; Tomonaga 1999, 2007).

Compared to other primates, few studies have investigated face processing, and especially the inversion effect, in New World monkeys. Again, findings conflict with one another, even with the same species (e.g., cotton-top tamarins, *Saguinus oedipus*: Neiworth et al. 2007; Weiss et al. 2001). Phelps and Roberts (1994) reported the inversion effect in a squirrel monkey (*Saimiri sciureus*), but this effect appeared only for human faces, and not for monkey faces or scenes.

A considerable amount of literature on the inversion effect in humans has addressed the potential effects of exposure or expertise with the stimuli involved. Non-human primate research, including Neiworth et al. (2007) and a variety of other studies with chimpanzees (Parr and Heintz 2006; Parr et al. 1998) also cite the effect of expertise as a possible explanation for the inversion effect. The expertise effect hypothesis was proposed by Diamond and Carey (Diamond and Carey 1986), who demonstrated an inversion effect in dog-show judges when presented with images of familiar breeds of dogs. The expertise effect hypothesis suggests that as stimuli become more familiar, subjects view the stimuli holistically, which enable discriminations at the individual or subordinate level (Diamond and Carey 1986; Carey and Diamond 1977). Because inverting a face disrupts this type of configural processing, impairments are likely to occur for any expert or well-practiced stimuli (though see (Gauthier and Bukach 2007; McKone and Robbins 2007) for a current debate on this topic). This makes conspecific faces special, as this is a natural category for which subjects have acquired expertise.

The question remains, however, whether or not expertise with particular stimuli influences the inversion effect in other primates. The results from Parr et al. (1998) did provide support for the expertise hypothesis in that an inversion effect was found only for those categories of face stimuli for which chimpanzees had developed an expertise: human and chimpanzee faces. In contrast, in a similar experiment with rhesus monkeys, Parr et al. (1999) found no impact of expertise on the inversion effect. This work in addition to other studies on the inversion effect and configural processing highlight important species differences.

The current study was designed to test the face inversion effect in a New World monkey, the brown capuchin. Capuchins live in complex social systems, and past research indicates that they are able to discriminate among and recognize faces of conspecifics (Pokorny and de Waal 2009a, b; Dufour et al. 2006). Given the importance of face recognition in capuchins, it is of interest to examine whether face processing is affected by inversion. This is especially intriguing in New World monkeys, given that their arboreal habitats allow them to interact with one another from a variety of different orientations. This is the first study of the inversion effect in this species and findings should yield interesting insights to the face-processing mechanisms of New World monkeys, and capuchins in particular.

Materials and methods

Subjects

The experiment took place at the Yerkes National Primate Research Center in Atlanta, Georgia. Subjects were four adult *Cebus apella* from two separately housed social groups: two females from Group 1 ("Winnie" and "Wilma") and one male and one female from Group 2 ("Mason" and "Bias"). At the beginning of the initial training phase, each social group had 15 members. During the time of testing, three individuals from Group 2, including the alpha male, were transferred to a different facility. This resulted in one subject, Mason, obtaining alpha status and becoming too distracted to test. He therefore did not complete testing on one category of stimuli (human faces) and was not included in the concomitant analyses.

The capuchin laboratory provides indoor/outdoor housing with a total floor space of 25 and 31 m^2 for each group, respectively. These enclosures are separated by an opaque panel, allowing minimal visual contact between the two groups. Monkey chow and water are available ad libitum, and trays of fruit, vegetables, bread, and protein solution are provided in the late afternoon, after testing sessions have finished. Tests were conducted once a day, midday, and 5 days per week. All subjects have considerable experience with humans as they interact with several different human researchers and caretakers on a daily basis and have for over 20 years.

Apparatus

Testing took place in a 155 × 64 × 58 cm test chamber, which was divided into separate sections with an opaque

partition allowing for the testing of two subjects simultaneously. The chamber was located in the same room as the capuchin housing and was positioned directly in front of the indoor enclosure. Subjects were removed from the group and transferred into the chamber by means of a routine process with which all individuals were familiar. The front of the test chamber, made of clear Lexan® plastic, had holes cut out so that subjects had access to the testing screen.

A 43-cm touch-sensitive computer monitor (Elo Entuitive Touchmonitor, IntelliTouch technology) was positioned directly in front of the test chamber for each subject. The screen was connected to a desktop PC and mounted on a moveable cart that also carried an automatic pellet dispenser. The pellet dispenser allotted General Mills brand Kix® or Coco Puffs® cereal, or Bio-Serv Precision Pellets as food rewards. Visual Basic 6.0 was used to control the delivery of rewards, as well as the display presentation and playback sounds. All subjects had extensive experience with the computers and testing setup (Pokorny and de Waal 2009a, b).

Stimuli: training

Four classes of stimuli, capuchin monkey faces, human faces, chimpanzee faces, and automobiles, were presented to the subjects (Fig. 1). Separate sets of stimuli were used for the training and the test phases. All training images were upright exemplars from the given category. For capuchin face stimuli, five conspecific images, representing both groups, were presented. Only five capuchins were used for training in order to reserve enough novel images for the testing phase. For human face stimuli, 10 images were obtained online from the Psychological Image Collection at Sterling (http://pics.psych.stir.ac.uk). All females were depicted in neutral, frontal poses. Chimpanzee face stimuli were composed of 10 images of different individuals obtained from the Yerkes Field Station, Ngamba Island, and the Center for Great Apes. Training car stimuli were 10 photographs of sedans and SUVs acquired from various online dealerships.

All capuchin, human, and chimpanzee face photos were originally taken as digital color photographs using a Konica Minolta Maxxum 7D digital camera. They were then edited with Adobe Photoshop 6.0 and converted to grayscale images. Face photos were cropped to only include the head, neck, and face. Further, all face images depicted neutral expressions and had forward-facing head orientations and eye positions. For all classes of stimuli, background information was removed by filling in the area around the images with solid gray. Brightness and contrast were homogenized across all images to control for obvious differences in lighting. Stimuli measured 8.4 × 8.4 cm on the monitor and had a resolution of 300 pixels per inch.

Stimuli: testing

The capuchin faces used in the test phase consisted of 20 different individuals (>5 years of age) of both males and females that were not included in the training phase. Ten photos depicted capuchins from Group 1 and 10 from Group 2, serving as both the in-group and out-group facial stimuli for each subject. Although the two colonies had minimal visual contact with each other, all subjects had previous experience with photographs of various out-group members (Pokorny and de Waal 2009a, b). This involved being presented with approximately 300 facial images (in-group and out-group) over the course of 2 years prior to performing this experiment. The number of presentations of each image varied depending on the specific task, ranging from fewer than 10 presentations to over a thousand. The images used in this study were novel, in that they were not used in any previous tasks, though the identity of the individuals depicted in the images had been presented in previous tasks. The images were always seen in color, while in the current experiment they were presented in grayscale. Subjects were never presented with a photograph of their own face.

Human face stimuli also consisted of 20 individuals. This class of stimuli was restricted to photographs of light-skinned adult females from various labs at Yerkes who had their hair pulled back and were not wearing any accessories. Ten of these were taken of individuals who never encountered the monkeys and were considered "out-group". The "in-group" subset consisted of 10 individuals who were all members of the capuchin laboratory and had regular contact with the monkeys. Subjects had never before been presented with photographs of human faces. Twenty different individual photographs of chimpanzees constituted the final class of face stimuli. Photos were

Fig. 1 Examples of the four stimulus types presented in their upright orientation. From left to right, these include a capuchin monkey face, a human face, a chimpanzee face, and an automobile

obtained from the Yerkes Field Station chimpanzees as well as from Ngamba Island (the latter photos are credited to Victoria Horner and the Chimpanzee Sanctuary and Wildlife Conservation Trust, Uganda). All of the chimpanzee faces were unfamiliar to the capuchins, as these species have never been exposed to one another, nor had the capuchins ever been exposed to chimpanzee photographs. The non-face control category, automobiles, consisted of 20 car images obtained from several different online dealerships. All cars were black, photographed from the side, and oriented in the same direction.

Procedure

The stimuli were presented using an oddity paradigm, as this is the paradigm that subjects had previously been trained on and had performed other facial recognition tasks (Pokorny and de Waal 2009a). At the onset of each trial, a black square located at the center of the screen appeared. Once the subject touched this square, it disappeared and four images appeared simultaneously on the screen in either a diamond or square layout. Three of the images were identical and one was different—this "odd" image representing the correct choice. The location of the odd stimulus was randomly chosen on each trial. When the correct image was touched, all images disappeared, a food reward was delivered, a high tone was played, and a new trial began following a four second inter-trial interval. When subjects made an incorrect selection, the images were removed from the screen, a low tone chimed, and four seconds was added to the inter-trial interval. A correction procedure was employed such that incorrect selections led to the trial being repeated four times or until the subject selected the correct response, which ever occurred first. Only the first presentation's response was used in data analysis. Subjects had 30 s to make their selection or the trial terminated and was recorded as aborted. Aborted trials were not included in the data analysis.

Colored clipart images were interspersed throughout the testing trials and were used as a baseline measure of attention. If performance on clipart trials fell below 60% correct in any given session, the data for the entire session would be discarded. However, this problem did not present itself during testing; thus, all recorded data were included in analyses. Training on the oddity task had been concluded previously as outlined in Pokorny and de Waal (2009a).

Training phase

In the current study, subjects were trained and tested on one of the four stimulus categories at a time, the order of categories being counterbalanced across subjects. The training consisted of 55 upright trials of the respective training stimuli and 25 trials of clipart in a random presentation. Training was achieved when subjects performed at 50% or above on two consecutive sessions (excluding clipart trials). Chance level in our task is 25, and 36% represents the success required for performance to be significantly above chance for 55 trials (binomial test, $\alpha = 0.05$). Training criterion was met in two to four sessions.

Testing phase

Testing consisted of 80 trials per session, which included 20 clipart, 30 upright, and 30 inverted trials. Each trial consisted of either all upright or all inverted presentations. The faces presented within the capuchin and human categories were either all in-group or all out-group within any given trial, and an equal number of in-group and out-group faces were presented in each session. Image combinations and the order in which they were presented were selected at random by the computer system. See Fig. 2 for an example of the oddity setup for both upright and inverted presentations of capuchin face stimuli. Testing concluded after subjects had completed 60 upright and 60 inverted presentations.

Data analysis

The information recorded per trial by the computer included: subject, experimenter, date, type of test, trial conditions (e.g., upright/inverted; in-group/out-group), trial number, which stimuli were used, the location of the odd stimulus, the latency to start the trial and to respond, the response of the subject, and whether the trial was correct, incorrect, or aborted.

Subjects' performance combined across all testing sessions for each stimulus category was converted to a difference-index (DI) by subtracting the percentage of correct responses on inverted trials from the percentage of correct responses on upright trials. Therefore, positive scores represented better performance on upright compared to inverted trials. The original data were then analyzed using a hierarchical logistic regression in order to determine which stimulus categories yielded significantly better performance in the upright versus inverted condition. A Wald statistic is reported as the result of the regression analysis. This approach allowed us to examine multiple independent variables, such as the familiarity conditions for the capuchin and human face categories, and permitted statistical control of the subject factor since this was a repeated design, as well as factors such as latency to respond, which may act as a confound. Analyses were conducted by condition because in one stimulus category (human faces),
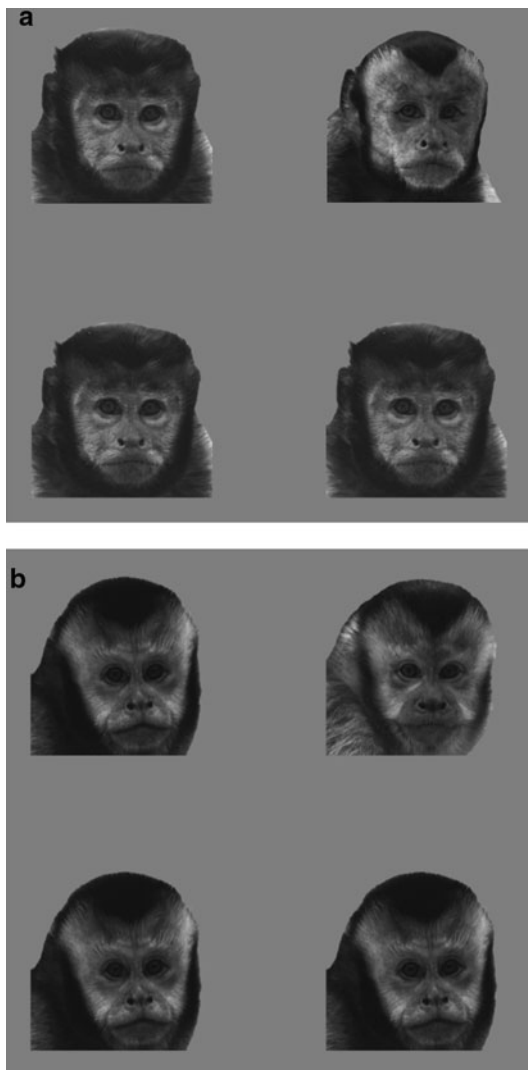
Fig. 2 a Example of an upright trial for capuchin face stimuli. The odd individual, and correct response, is the top right position. b Example of an inverted trial for capuchin face stimuli. The odd individual is depicted in the bottom left position

Fig. 3 Performance across the four subjects for each stimulus category for both upright (*black bars*) and inverted (*gray bars*) trials. The horizontal dashed line indicates chance performance (25%). *Error bars* represent the standard error of the mean

Fig. 4 The mean difference-index (DI) across the four subjects is presented for each stimulus category. *Positive DI* scores indicate better overall performance on upright trials. *Asterisks* indicate the categories for which there was a significant inversion effect, i.e., subjects performed better on the upright than the inverted trials

only three subjects had available data. Repeated measures ANOVAs were also conducted to investigate whether the latency to respond differed depending on the stimulus orientation and familiarity.

Results

During the test phase, the mean percentage of correct responses for, respectively, the upright versus inverted trials were 74% versus 55% for capuchin faces, 43% versus 31% for human faces, 58% versus 53% for chimpanzee faces, and 58% versus 56% for automobiles (see Fig. 3). Figure 4 illustrates this in the form of the mean DI values. Performance was better on upright versus inverted
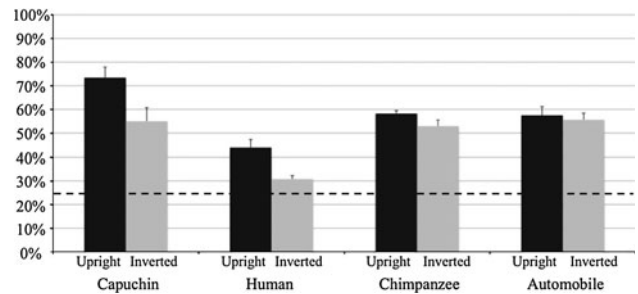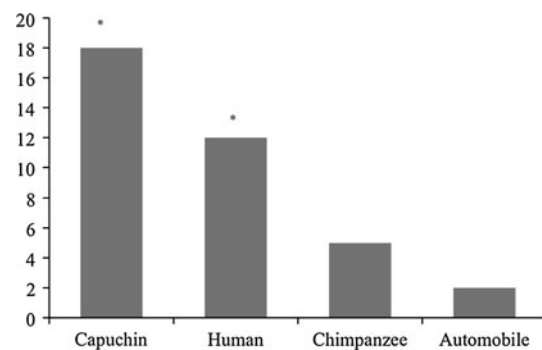
presentations in all stimulus categories. The greatest difference was found for the capuchin face stimuli and the smallest difference for the automobile stimuli.

For each stimulus category, a hierarchical logistic regression was performed on all the data with the subject entered first, followed by the latency to respond. The main independent variable of interest (the upright versus inverted orientation) was always entered last, and for the capuchin and human face categories, the effect of familiarity (in-group/out-group) was included in the regression following latency. For the capuchin face stimuli, the analysis revealed that the subject effect was not significant, $Wald = 1.278$, $P = 0.258$, indicating that there were no major differences between individual subjects' performance. The latency effect was, however, significant, suggesting that subjects took longer to respond when they chose incorrectly, $Wald = 19.794$, $P < 0.001$. Subjects' performance did not vary significantly depending on whether the depicted individuals were from the in-group or the out-group ($Wald = 0.003$, $P = 0.959$). Importantly, accuracy of response did significantly varies across the upright versus inverted condition, $Wald = 27.008$, $P < 0.001$, indicating

that after controlling for subject effects, latency, and familiarity, subjects performed significantly better on upright than inverted presentations of capuchin faces. For the human face category, no significant effects of subject ($Wald = 1.017$, $P = 0.313$) or latency ($Wald = 0.961$, $P = 0.327$) were observed. Further, no effect of familiarity was found ($Wald = 0.222$, $P = 0.638$). The effect of inversion, however, was significant ($Wald = 11.359$, $P < 0.01$), like the results for capuchin faces.

For chimpanzee face stimuli, no significant effects were observed for any of the variables in the hierarchical regression analysis (subject: $Wald = 0.155$, $P = 0.694$; latency: $Wald = 0.583$, $P = 0.445$; inversion: $Wald = 1.287$, $P = 0.257$). For the non-face control category, automobiles, there was no significant effect of subject ($Wald = 1.244$, $P = 0.265$), but the latency effect was significant, $Wald = 9.578$, $P < 0.01$. No significant effect of inversion was observed after partialling out potential subject or latency effects, $Wald = 0.072$, $P = 0.789$. Therefore, subjects' performance was not impacted by the orientation in which chimpanzee faces or cars were presented.

While there was an inversion effect for human faces, overall performance on upright trials was lower than for upright capuchin face trials. We assessed whether there was a difference in performance between upright human faces and the other three stimulus categories in their upright orientation by conducting 2-way chi-square contingency tests using the Yates' correction (Siegel and Castellan 1988). Results revealed that performance was significantly poorer on human faces compared to capuchin faces ($\chi^2(1) = 66.52$, $P < .001$), chimpanzee faces ($\chi^2(1) = 10.62$, $P < .01$), and automobiles ($\chi^2(1) = 9.61$, $P < .01$). Despite this fact, a Heterogeneity G-test found that performance on upright human faces was significantly above chance (Gh = 3.34, $df = 2$, $P > .05$, Gp = 53.70, $df = 1$, $P < .001$).

As latency can also be a sensitive measure of cognitive processing, we analyzed the data using latency as a dependent measure in a two-way (response × stimulus orientation) repeated measures ANOVA for the automobile and chimpanzee categories or in a three-way (response × stimulus orientation × familiarity) repeated measures ANOVA for the capuchin and human face categories (Table 1). As can be seen in Table 1, there was a main effect for response in the capuchin face category, such that the latency to respond (in milliseconds) in incorrect trials ($M = 2834.30$, SE = 95.88) was longer than to respond in correct trials ($M = 2499.26$, SE = 87.68). There was also an effect of orientation with upright trials being responded to faster ($M = 2460.01$, SE = 58.22) than inverted trials ($M = 2864.55$, SE = 107.18). Similar to the performance results, there was no effect of familiarity, nor were any of the interactions significant for

capuchin faces. Results in the human face condition revealed only a main effect for response, again finding that the latency to respond to incorrect trials ($M = 3136.29$, SE = 169.60) was longer than for correct trials ($M = 2481.55$, SE = 93.46). Orientation or familiarity did not have a significant effect on the latency to respond to human faces.

Automobiles also showed an effect of response, with slower response times to incorrect trials ($M = 3282.22$, SE = 193.79) than correct trials ($M = 2842.69$, SE = 161.44). Stimulus orientation did not show a main effect for automobiles, nor did the interaction of response and orientation. There were no significant effects for chimpanzee faces.

Overall, these analyses revealed a significant inversion effect in performance only for capuchin and human face stimuli. A follow-up comparison (Face Type × Orientation interaction) was performed in order to determine whether the strength of the inversion effects differed given a higher mean DI value for the capuchin faces than the human faces. Results revealed this difference were not significant ($Wald = 1.532$, $P = 0.216$). Latency analyses also found an effect of stimulus orientation in capuchin faces.

Discussion

We found evidence for an inversion effect in capuchin monkeys when discriminating among both conspecific and human faces. The subjects could be considered experts for both classes of stimuli, and therefore results are consistent with the expertise effect hypothesis proposed by Diamond and Carey (Diamond and Carey 1986). Under this hypothesis, an inversion effect is expected for any well-practiced class of stimuli, mainly because of a shift in the visual processing strategy favoring the use of configural cues over individual features. This type of processing is dependent on the stimuli being viewed in their typical orientation, explaining why inversion would impair subjects' performance. The discrimination of unfamiliar classes of stimuli is accomplished primarily by means of characteristic features. According to the hypothesis, the identification of such features is not disrupted even when the stimuli are presented in an unfamiliar orientation. This is one possible explanation for why, in the current study, subjects did not demonstrate an inversion effect for chimpanzee faces or automobiles. And although subjects did not demonstrate an inversion effect for the non-face control category, automobiles, they had never been exposed to such stimuli either. Ideally, in future studies, a class of non-face stimuli for which subjects had acquired expertise would be included to examine whether the expertise influence on the inversion effect is face specific.

Table 1 Summary of ANOVAs conducted on the latency to respond in each stimulus category

Category	Factor	Degrees of freedom	F	P
Capuchin faces	RESP	1, 56	6.263	.015*
	ORIENT	1, 56	11.240	.001*
	FAM	1, 56	.004	.950
	RESP × ORIENT	1, 56	1.082	.303
	RESP × FAM	1, 56	.314	.578
	ORIENT × FAM	1, 56	.201	.656
	RESP × ORIENT × FAM	1, 56	.572	.453
Human faces	RESP	1, 44	16.802	<.001*
	ORIENT	1, 44	.433	.514
	FAM	1, 44	.609	.439
	RESP × ORIENT	1, 44	.659	.421
	RESP × FAM	1, 44	.239	.627
	ORIENT × FAM	1, 44	.023	.880
	RESP × ORIENT × FAM	1, 44	.491	.487
Chimpanzee	RESP	1, 98	.056	.813
	ORIENT	1, 98	.264	.609
	RESP × ORIENT	1, 98	.043	.836
Automobile	RESP	1, 101	4.220	.043*
	ORIENT	1, 101	.432	.513
	RESP × ORIENT	1, 101	2.343	.129

RESP response (correct/incorrect), *ORIENT* orientation (upright/inverted), *FAM* familiarity (in-group/out-group)

Asterisks denote statistical significance

These results are inconsistent with Parr et al.'s (1999) research on rhesus monkeys, which demonstrated an inversion effect for automobiles. Furthermore, her study failed to find an inversion effect for human faces (although subjects had extensive experience with human researchers and caretakers), yet did find an inversion effect for an unfamiliar species of primate. An explanation of these discrepancies is not easy to formulate and may highlight the consequences of using different experimental paradigms. The present findings are, however, remarkably consistent with Parr et al.'s (1998) results with chimpanzees, which also found an inversion effect only for conspecific and human faces.

We did not find an effect of familiarity, for either capuchin faces or human faces when looking at performance or latency. While there is evidence that familiar and unfamiliar faces are processed differently in humans (e.g., Johnston and Edmonds 2009), this finding is consistent with our previous studies examining conspecific face recognition in these subjects (Pokorny and de Waal 2009a, b). It is possible that the familiarity effect was not found for capuchin faces since they had extensive experience with photographs of the same individuals, though they clearly have demonstrated that they know in-group from out-group members from their photographs (Pokorny and de Waal 2009b). Why a familiarity effect was not found for humans is not known, especially without further experiments, similar to what was done with capuchin faces, to determine whether they can categorize human faces as either familiar or unfamiliar.

One unexpected finding was that performance on human faces, while significantly above chance, was significantly poorer than performance on the other stimulus categories, especially considering that our subjects have ample experience with many different humans. Previously, during the course of training on the oddity task, we noticed that performance of some subjects dropped when new stimulus categories were presented, which is reflected here in that performance on all other stimulus categories was less than on capuchin faces. However, why performance was significantly worse on human faces is not known. Without further experiments, such as examining whether they recognize the identity of the individuals in the photographs and therefore understand the representational nature of the human photographs, we do not have a clear explanation for why this was the case. Even though performance was poorer than expected on upright human faces, it was significantly better than performance on inverted human faces. Given that the latency to respond to upright and inverted human faces did not differ, while it did for capuchin faces, it is difficult to determine whether subjects' expertise was a result of previous exposure to capuchin photographs or from real-life experience with conspecifics. Further studies would need to be conducted to tease apart these two possibilities.

In conclusion, the present results corroborate numerous studies in humans (e.g., Diamond and Carey 1986), in addition to several studies in non-human primates (e.g., Parr et al. 1998; Neiworth et al. 2007) and non-primates

(Kendrick et al. 1996), suggesting that the inversion effect is most pronounced for expert classes of stimuli. Although there was no significant difference between the magnitude of the inversion effect for capuchin and human face stimuli, it was more robust for capuchin faces (Fig. 4). Because capuchins have the most experience with their own species' faces, and this category revealed the greatest decrements in performance when presented upside-down, such findings provide even stronger support for at least some effect of expertise on the inversion phenomenon. Despite the paucity of inversion effect studies in New World monkeys, the current results suggest that the face-processing strategies within the primate order may not vary as much as previously thought.

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