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The perception of two-tone Mooney faces in chimpanzees (*Pan troglodytes*)

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Neurological experiments have revealed a complex network of areas in the human brain that respond more to faces than to other categories of objects and thus have been implemented in face categorization. The aim of this study was to investigate whether chimpanzees ($n = 5$), our closest living relatives, detect and categorize faces on the basis of first-order information, and whether this sensitivity is specific to faces or generalizes to other objects. In service to this aim, we created multiple categories of two-tone 'Mooney' objects (chimpanzee faces, shoes, human hands), because, by maximizing contrast, the Mooney transformation selectively degrades second-order information (the basis for individual discrimination in humans), leaving only first-order information intact. Two experiments used a 2AFC MTS procedure. The first experiment provided strong evidence that, like humans, chimpanzees categorize Mooney faces as faces. However, without second-order information, the chimpanzees could not match Mooney faces at the individual level. In Experiment 2, four of the five chimpanzees found it easier to categorize Mooney faces than Mooney shoes. Neurological evidence strongly indicates a dedicated neural mechanism for face categorization in the human brain, and our data suggest that chimpanzees share this level of specialization.

Keywords: Face categorization; Comparative data; Neural specialization.

Faces are complex visual patterns that convey an enormous range of socially relevant information. Neurological evidence strongly suggests that humans have a specialized network for analyzing and recognizing faces. This network includes the fusiform face area (FFA) (Kanwisher, McDermott, & Chun, 1997) as well as distinct areas in the lateral occipital and temporal cortices (Haxby, Hoffman, & Gobbini, 2000; Weiner & Grill-Spector, 2010). The most basic aspect of face perception that this network needs to achieve is face categorization, which refers to our ability to detect a face among non-face objects.

Humans can detect faces in natural scenes with remarkable speed and accuracy (Crouzet, Kirchner, & Thorpe, 2010; Rousselet, Mace, & Fabre-Thorpe, 2003). This ability is facilitated by the fact all faces have the same features that are repeated in the same T-shaped pattern (Diamond & Carey, 1986; for reviews, see Maurer, Mondloch, & Le Grand, 2002; Tsao & Livingstone, 2008). This basic "face" template will be from now on referred to as first-order information. A compelling demonstration of our sensitivity to first-order information is our perception of faces in Arcimboldo paintings, which are arrangements of fruit or vegetables with no explicit facial features (Moscovitch, Winocur, & Behrmann, 1997).

A number of empirical studies interested in measuring face categorization in humans have used two-tone

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Mooney faces (Mooney, 1957). By converting faces into black-and-white images, the Mooney manipulation is thought to selectively impair access to second-order information while leaving first-order information intact. Here, we define the term "second-order information" as the variance that exists between faces and, thus, forms the basis for individual identification. Examples of second-order variation include spacing between features (Diamond & Carey, 1986; Haig, 1984), feature shape (Freire, Lee, & Symons, 2000; Mondloch, Le Grand, & Maurer, 2002), and surface cues (Galper, 1970; Kemp, McManus, & Piggot, 1990). The Mooney manipulation distorts these cues, making Mooney faces more ambiguous and difficult to identify at the level of the individual. However, Mooney faces are readily categorized as faces because the first-order configuration of features is preserved (George, Jemel, Fiori, Chaby, & Renault, 2005; Latinus & Taylor, 2006; McKone, 2004; Moore & Cavanagh, 1998). In 1998, Kanwisher et al. reported that the human FFA is activated to the same extent by both upright grayscale faces and upright Mooney faces with increased blood flow in response to upright Mooney faces compared with inverted Mooney faces. This effect of inversion implicated FFA in face categorization processes.

Evidence of spared face categorization in individuals deprived of early visual experience due to congenital cataracts (Mondloch et al., 2003) converges with several studies of newborn infants to suggest that our ability to categorize faces is operational at birth or shortly hereafter (Morton & Johnson, 1991). The classic finding of infants tracking face-like configurations for longer periods of time than similar non-face configurations implies that we categorize faces as being distinct from other visual objects after only 9 min of life (Goren, Sarty, & Wu, 1975). This observation and others like it (Leo & Simion, 2009; Macchi Cassia, Turati, & Simion, 2004) strongly suggest that we are born with an ability to distinguish faces from other kinds of objects; however, it is difficult, if not impossible, to draw conclusions about the ontogenetic development of human cognition based on preferences in human infants alone. Here, we investigate first-order sensitivity in adult chimpanzees, assuming that if our ability to categorize faces is experience-expectant, then it is likely to be conserved in our closest living relative.

A recent report suggests that, like humans, chimpanzees also have a specialized neural network for processing face stimuli (Parr, Hecht, Barks, Preuss, & Votaw, 2009). Although there is a sizable body of research to suggest that chimpanzees can recognize individual faces (e.g., Parr et al., 1998), it is not known how sensitive they are to first-order information in faces. To probe this sensitivity, in Experiment 1, we used a standard, two-alternative, forced-choice match-to-sample (MTS) paradigm and designed trials that required five chimpanzees to match two classes of Mooney objects (faces or shoes) (Figure 1), using different types of information. In the image-match task, subjects were required to match identical Mooney images, using pictorial cues. In the category-match condition, the chimpanzees were asked to match the Mooney objects at the basic category level; that is, to use first-order information to match different exemplars that belong to the same object category (Figure 1c), whereas in the individual-match trials the chimpanzees were asked to match Mooney objects at the individual level; that is, to use second-order information to match different images of the same exemplar (Figure 1c). We reasoned that if chimpanzees can extract first-order cues, but not second-order cues, from Mooney objects, then accuracy would be greater in the category-match task than in the individual-match task. In Experiment 2, we asked whether there was an advantage for faces over other objects in detection tasks.

EXPERIMENT 1

Methods

Subjects

Five adult chimpanzees (*Pan troglodytes*) served as subjects in this study. Two were male. At the time of testing, the subjects were 16–23 years old and were housed at the Yerkes National Primate Research Center (Atlanta, GA). All five subjects had previously participated in many cognitive experiments involving matching faces and objects, but had never been previously presented with Mooney manipulated images (for examples of previous experiments, see Parr, Dove, & Hopkins, 1998; Taubert & Parr, 2010).

Stimuli

The digit stimuli were twelve grayscale photographs of familiar conspecifics' faces (neutral expression, full frontal) prepared with Adobe Photoshop. Six of the faces were males. Each face was positioned on a square canvas that was subsequently resized to 350 × 350 pixels. All background information was replaced with a black background. Contrast and brightness was matched as much as possible, using the preset parameters of the automatic contrast filter. From now on these faces and shoes will be referred to as the *original faces*. The *Mooney faces* were obtained by

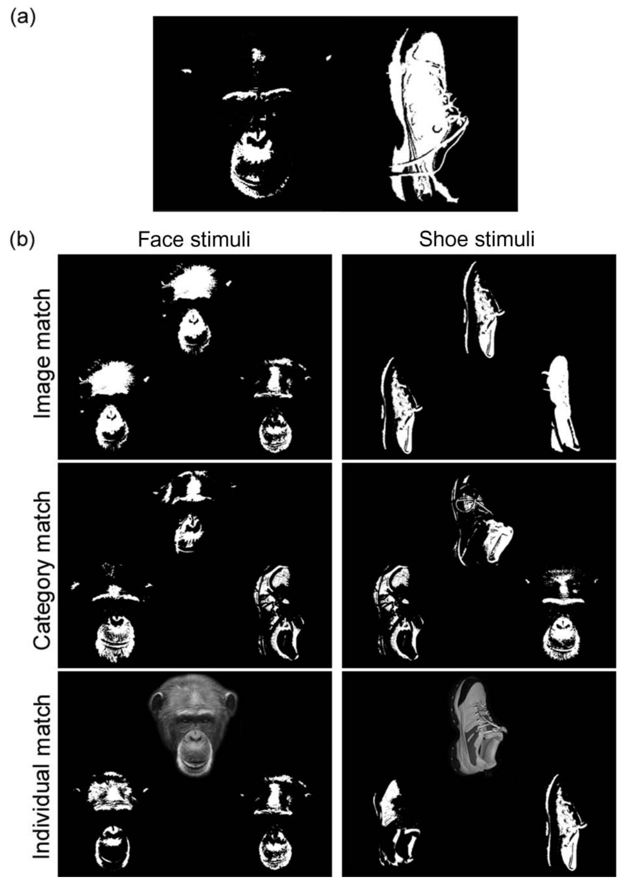

Figure 1. (a) Two examples of the experimental stimuli, one from each of the object categories. (b) Summary of the factorial design for Experiment 1 with examples of trials taken from each of the six unique conditions. In every trial, the sample was presented at the top of the screen with the two comparison stimuli below. In these examples, the correct choice is the left comparison stimulus; however, in the experiment, the position of the correct choice was selected at random.

thresholding the original stimuli so that all pixels were either black or white. The threshold level was held constant and set at 140 (Figure 1a).

Photographs were also taken of 12 shoes. Although it is difficult to select a class of objects that are equivalent to faces both in terms of complexity and familiarity, we chose shoes because the subjects had had numerous opportunities throughout their lives to see different kinds of shoes on their human caregivers. The original and Mooney shoes were prepared in the same way.

Design and procedure

The stimuli were presented to subjects in a match-to-sample format on a 17-inch color monitor. The computer and monitor were housed in an audiovisual cart covered in clear Plexiglas that could be wheeled to the front of the subject's home cage for test sessions. The monitor was positioned approximately 50 cm away from where the subject was sitting. A joystick was then attached to the front of the home cage, allowing the subject to manipulate the cursor on the computer screen.

Each trial began with the presentation of a sample stimulus (4 cm wide), centered at the top of a black screen. A white cursor appeared in the center of the screen, directly below the sample. The subject was then required to make an orienting response toward the sample. Once the cursor touched the sample stimulus, two comparison stimuli appeared at the bottom of the screen, equidistant from the sample. A correct response was recorded if the cursor was used to select the comparison stimulus that matched the sample (the target). Correct responses were reinforced with food, hand delivered by the experimenter, and followed by a 2-s intertrial interval (ITI). An error was recorded if the subject selected the comparison stimulus that did not match the sample (the foil). Incorrect responses were not reinforced and were followed by a 7-s ITI. During an ITI, the screen was black. This procedure was repeated 60 times in a single session, each of the 12 stimuli appearing as a sample/target (and a foil) an

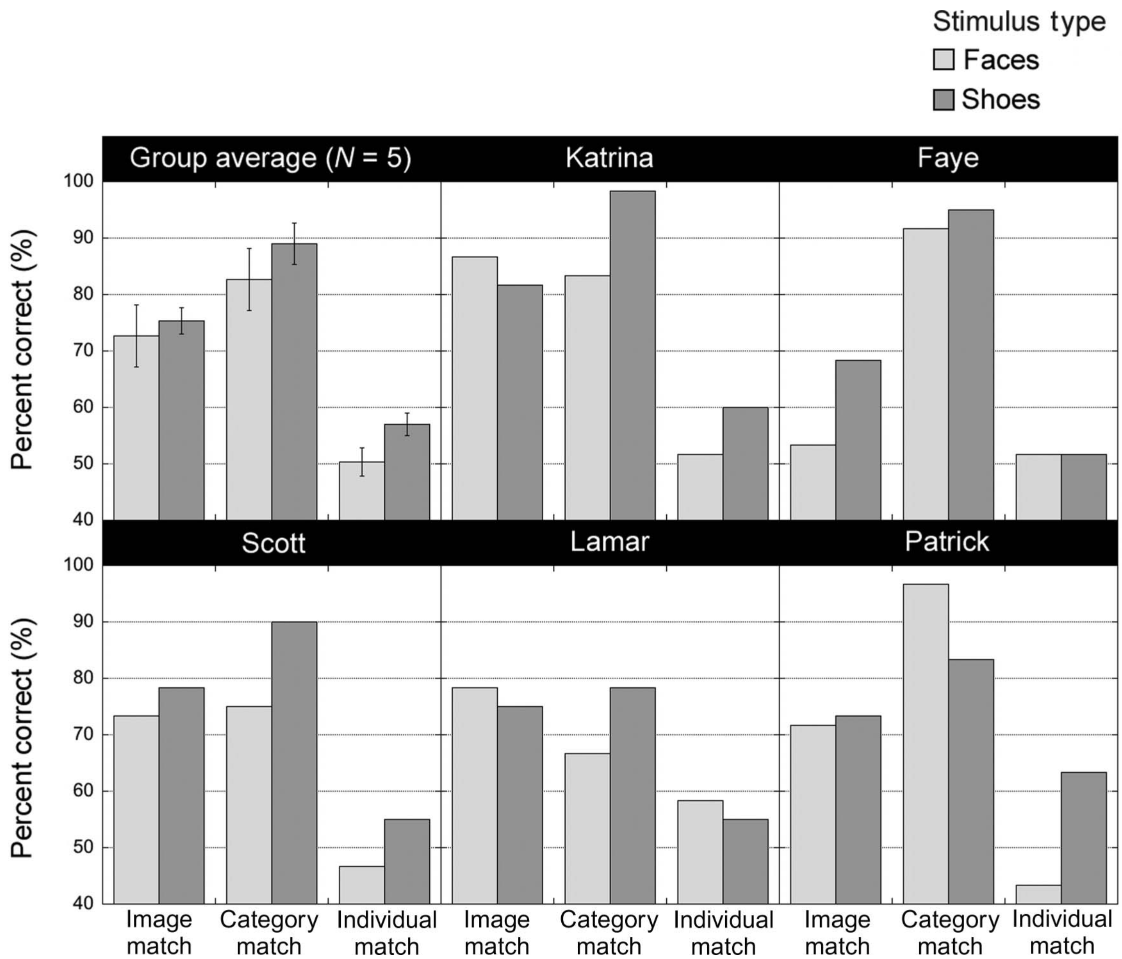

Figure 2. Accuracy in Experiment 1: Individual scores are provided with the group averages presented in the top left corner (error bars: ±1 *SEM*).

equal number of times. Subjects were tested twice a day with one session taking place at approximately 10 am and the other at approximately 3 pm.

The factorial design included six separate conditions (Figure 1b). There were two kinds of stimuli that appeared as samples (*faces* or *shoes*) and three different tasks. In the *image-match task*, subjects were asked to match a Mooney sample stimulus (a face or shoe) to the exact same image. The foil was another example from the same category. This control task was necessary to verify that the subjects understood how to respond accurately to the MTS procedure and that there was no bias against shoes.

In the *category-match task*, the subjects were required to ignore the individual identity of the sample and, instead, select comparison stimulus that belonged to the same category as the sample. For example, if the sample was a Mooney face, then the target was also Mooney face, but one belonging to a different individual, and the foil was a Mooney shoe (Figure 1b). In the third task, hereby referred to as the *individual-match* task, the subjects were given an original stimulus as the sample and were asked to match this grayscale image to the Mooney equivalent (Figure 3). Thus, even though the subjects were asked to match the same photograph, a strict image-match strategy would not facilitate performance because the Mooney transformation was only applied to the comparison stimuli. The six unique conditions were completed in a counterbalanced order.

Results and discussion

Subject performance (percent correct) was analyzed in a repeated-measures, 2 × 3 ANOVA where the within-subject factors included stimulus type (faces vs. shoes) and task (image match, category match, and individual match). The main effects of stimulus and task were significant, stimuli: $F(2, 8) = 14.34$, $p = .02$; task: $F(2, 8) = 23.25$, $p < .01$ (Figure 2). However, the interaction between stimulus and task was not, $F(2, 8) = 0.19$, $p = .83$. Thus, on average, subjects performed

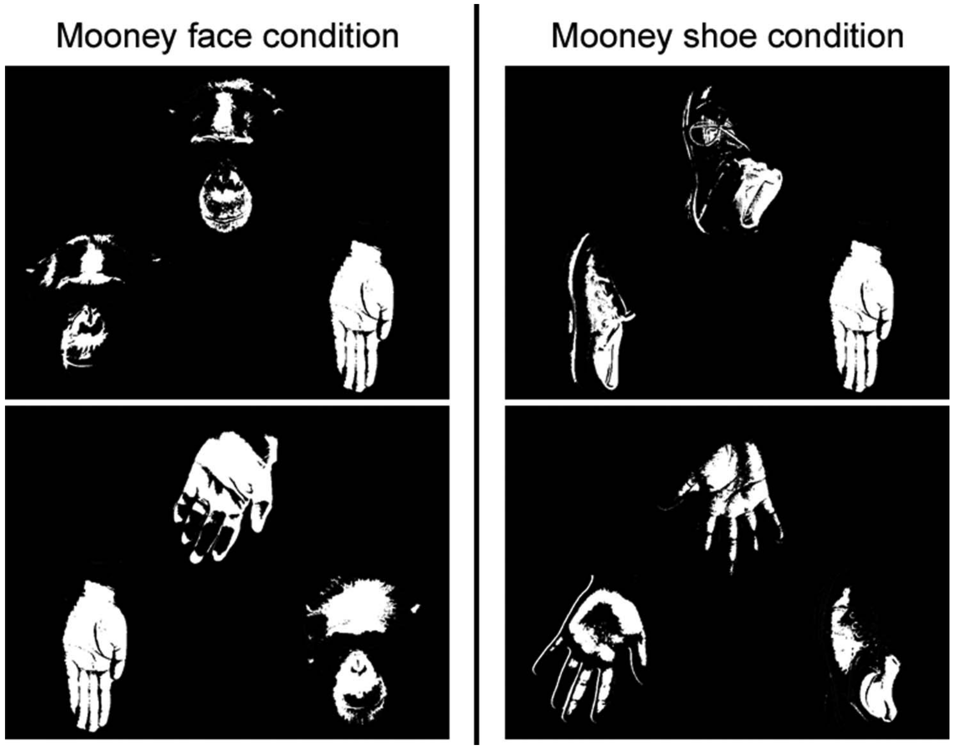

Figure 3. Experiment 2: examples of the types of trials that occurred in the two conditions. The correct response (the stimulus that matches the central sample) in these examples is on the left.

better with shoes than with faces, and there was no difference in the pattern of performance across the three tasks dependent on stimulus type. A paired *t*-test was run to check that the subjects were as accurate in the face image-matching condition as they were in the shoe image-matching condition, $t(4) = 0.75$, $p = .495$.

To follow-up on the main effect of task, the three tasks were compared in a pair-wise fashion using the Bonferroni adjustment (α / 3 = .017). As predicted, these comparisons revealed that, on average, subjects made more errors in the individual-match condition than in the image-match, $t(4) = 6.25$, $p = .003$, or category-match, $t(4) = 7.33$, $p = .002$, conditions (Figure 2). These results indicate that chimpanzees were more successful at categorizing Mooney images than identifying them. The follow-up tests did not reveal evidence consistent with a difference between the image match and category match conditions, $t(4) = 1.91$, $p = .129$.

EXPERIMENT 2

Testing the Mooney face advantage

Having established that chimpanzees can categorize Mooney objects in Experiment 1, we designed an additional task to determine whether chimpanzees are *more* sensitive to the first-order information in faces compared to other objects (Moore & Cavanagh, 1998). Experiment 2 was necessary because in the first experiment the trials that comprised the category-match task always involved a face. In the face-category trials, faces were presented as the sample/target pairs, and in the shoe-category trials, faces were presented as the foils. Thus, it is reasonable to conclude that accuracy in both the face and shoe conditions could have been based on the rapid categorization of faces, either to match, or to ignore.

In Experiment 2, we used the Mooney faces and shoes that were created in Experiment 1 and introduced a novel set of Mooney hands. Hands were chosen as a stimulus class because the chimpanzees had had daily experience with a variety of human hands as opposed to other classes of objects, such as cars or houses. The experiment was divided into two conditions; the Mooney face condition, where faces were categorized against hands and vice versa, and the Mooney shoe condition, where shoes were categorized against hands and vice versa (Figure 3). If subjects found it easier to categorize faces than to categorize shoes, as predicted, then the subjects would be more accurate in the Mooney face condition compared to the Mooney shoe condition. Alternatively, if the subjects are simply good at categorizing all Mooney objects, then they would perform similarly in both conditions.

Methods

Stimuli

The Mooney stimuli from Experiment 1 were also used in Experiment 2. In addition, 12 photographs of hands were transformed by the same thresholding procedure described above. These images will be referred to as Mooney hands.

Design and procedure

The procedure for Experiment 2 was identical to the procedure described in Experiment 1; subjects were asked to respond to a simultaneous 2AFC MTS task. In Experiment 2, however, there were only two experimental conditions (Mooney face vs. Mooney shoe), which were blocked in separate sessions that were counterbalanced across subjects. Each session comprised 60 discrete trials. In the Mooney face condition, 30 of the 60 total trials required subjects to match a Mooney face to another Mooney face, against a Mooney hand foil. In the remaining 30 trials, a Mooney hand was presented as the sample stimulus. The corresponding match was another Mooney hand and the foil was a Mooney face (Figure 3). The trial structure was the same in the Mooney shoe condition except that shoes were presented instead of faces.

Results and discussion

Subject performance in the face condition was directly compared to performance in the shoe condition, using a simple paired *t*-test. Although performance was better in Mooney face condition ($M = 77.33$, $SEM = 6.62$) than in the Mooney shoe condition ($M = 65.67$, $SEM = 4.79$), this was not statistically different, $t(4) = 1.98$, $p = .12$. However, we note that four out of five subjects demonstrated the predicted advantage for Mooney faces over Mooney shoes (Figure 4). When the Mooney face condition was run on the chimpanzee named Lamar, he

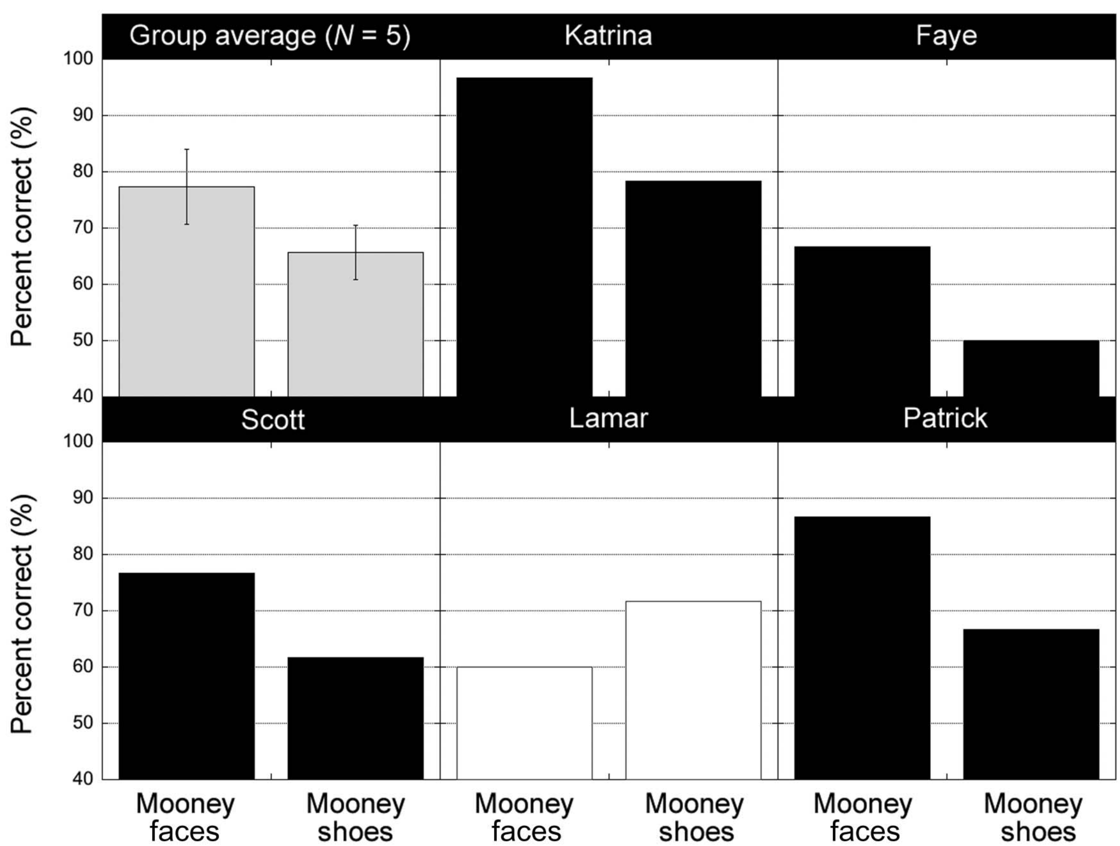

Figure 4. Accuracy in Experiment 2: The group averages are presented in the top left corner (error bars: ±1 *SEM*). Individual scores are also provided. Black bars indicate individual scores consistent with a categorization advantage for Mooney faces. The white bars indicate scores inconsistent with the predicted advantage for Mooney faces.

responded correctly only 36 times (60% correct), which was the lowest individual score and more than 1 *SD* away from the group mean. Using a binomial distribution (one-tail), we also found that Lamar was the only subject who did not perform above chance in the Mooney face condition ($p = .08$). It is possible, therefore, that his result represents an influential outlier. The same comparison was significant when Lamar's data were removed from the analysis: Mooney face condition, $M = 81.67$, $SEM = 6.45$; Mooney shoe condition, $M = 64.17$, $SEM = 5.87$; $t(3) = 16.27$, $p = .001$.

GENERAL DISCUSSION

In this paper, we investigated the ability to detect and categorize faces in chimpanzees. Experiment 1 showed that chimpanzees easily categorized Mooney faces as being distinct from Mooney shoes (category-matching task). However, while the chimpanzees demonstrated an ability to match individual faces when the sample and match were identical (image-matching task), the individual-match task revealed that the chimpanzees could not extract sufficient information from the Mooney faces to distinguish them on an individual-level. These results are consistent with Mooney face perception in human adults (George et al., 2005; Latinus & Taylor, 2006; McKone, 2004) and infants (Leo & Simion, 2009) and are consistent with the notion that individual face recognition in chimpanzees is based on the presence of second-order information (Parr et al., 1998).

In Experiment 2, we aimed to clarify whether performance on the category task was due to the rapid categorization of faces. Overall, there was no advantage for faces over shoes; however, the effect neared significance and was influenced by the performance of one subject who performed better at categorizing shoes than faces (Figure 4). Once these data were removed from the analysis, there was evidence of a profound advantage for categorizing faces. The implication is that there may be some individual variation in face categorization and potentially some competition with other object categories. It is reasonable to conclude, therefore, that while most chimpanzees are more sensitive to faces than shoes in a categorization task, this might not hold across all individuals and all situations.

In conclusion, we have provided the first clear evidence that chimpanzees are sensitive to first-order information in objects and that first-order information is not sufficient for individual discrimination. Even though it was not a significant effect across the whole group, we also found some evidence consistent with the idea that chimpanzees are more sensitive to the first-order information in faces than in another class of objects— shoes. The pattern that emerges in these data implies that chimpanzees have the same response to Mooney faces as humans (George et al., 2005; Latinus & Taylor, 2006; McKone, 2004; Moore & Cavanagh, 1998) and that face categorization is accomplished by conserved neural machinery (Kanwisher et al., 1998; Parr et al., 2009).

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REFERENCES

Crouzet, S. M., Kircher, H., & Thorpe, S. J. (2010). Fast saccades toward faces: Face detection in just 100 ms. *Journal of Vision*, *10*(4), 1–17.

Diamond, R., & Carey, S. (1986). Why faces, are and are not special: An effect of expertise. *Journal of Experimental Psychology. General*, *115*(2), 107–117.

Freire, A., Lee, K., & Symons, L. A. (2000). The face-inversion effect as a deficit in the encoding of configural information: Direct evidence. *Perception*, *29*, 159–170.

Galper, R. E. (1970). Recognition of faces in photographic negative. *Psychonomic Science*, *19*, 154–158.

George, N., Jemel, B., Fiori, N., Chaby, L., & Renault, B. (2005). Electrophysiological correlates of facial decision: Insights from upright and upside-down Mooney-face perception. *Cognitive Brain Research*, *24*, 663–673.

Goren, C. C., Sarty, M., & Wu, P. Y. (1975). Visual following and pattern discrimination of face-like stimuli by newborn infants. *Pediatrics*, *56*(4), 544–549.

Haig, N. D. (1984). The effect of feature displacement on face recognition. *Perception*, *13*, 505–512.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Science*, *4*(6), 223–233.

Kanwisher, K., McDermott, J., & Chun, M. M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.

Kanwisher, K., Tong, F., & Nakayama, K. (1998). The effect of face inversion on the human fusiform face area. *Cognition*, *68*, B1–11.

Kemp, R., McManus, C., & Piggot, T. (1990). Sensitivity to the displacement of facial features in negative and inverted images. *Perception*, *19*(4), 531–543.

Latinus, M., & Taylor, M. J. (2006). Face processing stages: Impact of difficulty and the separation of effects. *Brain Research*, *1123*, 179–187.

Leo, I., & Simion, F. (2009). Newborns' Mooney-face perception. *Infancy*, *14*(6), 641–653.

Macchi Cassia, V., Turati, C., & Simion, F. (2004). Can a nonspecific bias toward top heavy patterns explain newborns' face preference? *Psychological Science*, *4*, 379–383.

Maurer, D., Mondloch, C. J., & Le Grand, R. (2002). The many faces of configural processing. *Trends in Cognitive Sciences*, *6*(6), 255–260.

McKone, E. (2004). Isolating the special component of face recognition: Peripheral identification and a Mooney face.

Journal of Experimental Psychology. Learning, Memory, and Cognition, *30*(1), 181–197.

Mondloch, C. J., Le Grand, R., & Maurer, D. (2002). Configural face processing develops more slowly than featural face processing. *Perception*, *31*, 553–566.

Mondloch, C. J., Le Grand, R., & Maurer, D. (2003). Early visual experience is necessary for the development of some – but not all – aspects of face processing. In O. Pascalis & A. Slater (Eds.), *The development of face processing in infancy and childhood* (pp. 99–117). New York, NY: Nova Science.

Mooney, C. M. (1957). Age in the development of closure ability in children. *Canadian Journal of Psychology*, *11*, 219–226.

Moore, C., & Cavanagh, P. (1998). Recovery of 3D volume from 2-tone images of novel objects. *Cognition*, *67*, 45–71.

Morton, J., & Johnston, M. H. (1991). CONSPEC and CONLERN: A two-process theory of infant face recognition. *Psychological Review*, *98*, 164–181.

Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience*, *9*, 555–604.

Parr, L. A., Dove, T., & Hopkins, W. D. (1998). Why faces may be special: Evidence for the inversion effect in chimpanzees (*Pan troglodytes*). *Journal of Cognitive Neuroscience*, *10*, 615–622.

Parr, L.A., Hecht, E., Barks, S. K., Preuss, T. M., & Votaw, J. R. (2009). Face processing in the chimpanzee brain. *Current Biology*, *19*, 1–4.

Rousselet, G. A., Mace, M. J., & Fabre-Thorpe, M. (2003). Is it an animal? Is it a human face? Fast processing in upright and inverted natural scenes. *Journal of Vision*, *3*, 440–455.

Taubert, J., & Parr, L. A. (2010). Geometric distortions affect face recognition in chimpanzees (*Pan troglodytes*) and monkeys (*Macaca mulatta*). *Animal Cognition*, *14*(1), 35–43.

Tsao, D. Y., & Livingstone, M. S. (2008). Mechanisms of face perception. *Annual Review of Neuroscience*, *31*, 411–437.

Weiner, K. S., & Grill-Spector, K. (2010). Sparsely-distributed organization of face and limb activations in human ventral temporal cortex. *NeuroImage*, *52*, 1559–1573.