



What's in a Face (Made of Foods)? Comparing Children's and Monkeys' Perception of Faces in Face-Like Images of Food

Michael J. Beran^{1*}, Bonnie M. Perdue², Andrew J. Kelly³, and Audrey E. Parrish⁴

¹Georgia State University, Atlanta, GA

²Agnes Scott College, Decatur, GA

³Georgia Gwinnett College, Lawrenceville, GA

⁴The Citadel, Charleston, SC

*Corresponding author (Email: mberan1@gsu.edu)

Citation – Beran, M. J., Perdue, B. M., Kelly, A. J., & Parrish, A. E. (2017). What's in a face (made of foods)? Comparing children's and monkey's perception of faces in face-like images of food. *Animal Behavior and Cognition*, 4(3), 324-339. <https://doi.org/10.26451/abc.04.03.10.2017>

Abstract - Arcimboldo images are pictorial stimuli composed of fruits, vegetables, and other objects arranged in a way to resemble human faces. These images were originally created by the artist Giuseppe Arcimboldo in the 16th century, but more recently have been used by psychologists and neuroscientists to explore perceptual processes among human adults. Past research has demonstrated that humans process these stimuli in a very similar manner to the processing of actual human faces. The present study investigated if children, rhesus monkeys, and capuchin monkeys also would holistically process these and similar-looking images as faces. After learning to classify training images as faces or foods, participants were presented probe trials of new food images, new face images, illusory images (i.e., Arcimboldo images and similar face-like images), and scattered images (i.e., those same images with critical pieces of the image rearranged to take away the sense of seeing a face), and they had to classify each image as a face or non-face. Three-and-a-half to five-year-old children reported seeing faces in the illusory stimuli significantly more than in the scattered images. Conversely, rhesus and capuchin monkeys were equally likely to classify the illusory stimuli and the scattered stimuli as faces. These results suggest that young children have a tendency to process stimuli more holistically when they resemble a face, whereas monkeys process these face-like images more locally.

Keywords – Perception, Faces, Arcimboldo images, Perceptual processing mode, Rhesus monkeys, Capuchin monkeys, Children

Humans see faces everywhere, even where they do not exist (a form of *pareidolia*). For example, people have seen the face of Jesus or the Virgin Mary on a piece of toast and many other places. They have seen a face on the surface of Mars where only a rock structure exists, and they have seen other similar “illusory” faces in ordinary objects like parking meters that contain face-like features resembling two eyes, a nose, and a mouth (e.g., Liu et al., 2014). Much research has been conducted on why this happens. One compelling finding is that the area of the brain that plays a large role in processing facial stimuli, called the fusiform gyrus or fusiform face area (Kanwisher, McDermott, & Chun, 1997; Weiner & Zilles, 2016), also activates in response to those non-face stimuli that evoke the sense that one is looking at a face (e.g., Hadjikhani, Kveraga, Naik, & Ahlfors, 2009; Summerfield, Egner, Mangels, & Hirsch, 2006). Thus, our

susceptibility as a species to seeing faces allows for manipulation of our perceptual experiences, often for the purposes of artistic expression. Giuseppe Arcimboldo (1527–1593) produced a series of fascinating paintings in the 16th century in which he arranged various fruits, vegetables and even fish in ways that, for adult humans, evoked a strong sense of looking at a human face. These images have attracted much attention from the public, and serve as a clear indicator that people can easily see faces in all manner of stimuli. They also serve as intriguing stimuli for comparative and developmental assessments of perception, but have rarely been used for such purposes.

With adult human participants, these stimuli have been used to study the facial inversion effect, in which perception and recognition of faces is impaired when those images are presented upside down (e.g., Barton, Radcliffe, Cherkasova, Edelman, & Intriligator, 2006; Haxby et al., 1999; Rakover & Teucher, 1997; Rossion, & Gauthier, 2002). For example, Bubic, Susac, and Palmovic (2014) reported that when participants were presented with Arcimboldo images, they tended to fixate more on the parts of the painting that looked like faces (the eyes and the mouth) when the paintings were upright compared to when they were inverted. Caharel et al. (2013) reported that adult humans showed a pattern of holistic face-like processing of Arcimboldo paintings in brain regions relevant to facial processing such as the right occipito-temporal cortex as measured through event-related potentials. Others also showed that Arcimboldo images produced highly similar brain responses to the viewing of actual faces (e.g., Jeffreys & Tukmachi, 1992; Rossion & Jacques, 2008). Thus, research that used Arcimboldo images converged on the idea that those stimuli are processed in a holistic, top-down manner by adult humans in much the same way that real faces are processed (Busigny, Joubert, Felician, Ceccaldi, & Rossion, 2010; Maurer, Le Grand, & Mondloch, 2002; Muth & Carbon, 2013). There is additional evidence that these stimuli are “special” in terms of how they are processed as both faces and images in the human brain. Moscovitch, Winocur, and Behrmann (1997) presented Arcimboldo images to object agnosics (individuals who struggle to identify visual objects), and they found that only faces were perceived, whereas the objects making up those faces were not, again suggesting that processing of the images occurred at a more holistic level akin to the processing of true faces.

Arcimboldo images also have been used in developmental research. For example, Kobayashi et al. (2012) used a preferential looking method with 5- to 8-month-old children and found that the 7- to 8- month-old children looked longer at upright Arcimboldo images compared to inverted images, suggesting that they preferred those face-like images. They then measured blood flow in the brain in 7- and 8-month-olds during viewing of inverted or upright Arcimboldo images or control images that consisted only of individual vegetables, and they found that the concentration of oxyhemoglobin increased in the left temporal area for the upright images compared to the baseline vegetable images, indicating that participants processed the Arcimboldo images holistically as faces.

To this point, processing of Arcimboldo images has not been examined in nonhuman species, despite great strides in documenting similarities and differences in perception of facial stimuli by humans and nonhuman animals. For example, research with nonhuman primates has shown that faces are “special” for monkeys and apes too. Facial processing includes individual recognition, an essential socio-cognitive specialization among complex group-living species (see Parr, 2011a, for a review). Researchers have documented that some species also show the inversion effect when viewing conspecific and sometimes heterospecific faces and non-face images (e.g., Parr, 2011b; Parr, Dove, & Hopkins, 1998; Tomonaga, 1999; Tomonaga, Itakura, & Matsuzawa, 1993), including the special case of the Thatcher effect with conspecific faces (Adachi, Chou, & Hampton, 2009; Dahl, Logothetis, Bülthoff, & Wallraven, 2010, but see Parron & Fagot, 2008, and Weldon, Taubert, Smith, & Parr, 2013, for alternative findings among baboons and rhesus monkeys). Research also suggests that recognition of facial stimuli by chimpanzees involves similar psychological mechanisms and brain areas to those activated in humans (e.g., Parr, Hecht, Barks, Preuss, & Votaw, 2009; Parr, Winslow, Hopkins, & de Waal, 2000).

However, we also know that monkey species tend to process non-facial visual stimuli differently than humans. When presented with multi-element arrays (e.g., a large letter *F* comprised of smaller letter *E*s), several monkey species perceive the individual items (i.e., the local features) prior to and sometimes more accurately than the global configuration, including rhesus macaques (Hopkins & Washburn, 2002),

baboons (Deruelle & Fagot, 1998; Fagot & Deruelle, 1997), capuchin monkeys (De Lillo, Spinozzi, Truppa, & Naylor, 2005; Spinozzi, De Lillo, & Salvi, 2006; Spinozzi, De Lillo, & Truppa, 2003; Spinozzi, De Lillo, Truppa, & Castorina, 2009), and cotton-top tamarins (Neiworth, Gleichman, Olinick, & Lamp, 2006). This local processing bias is contrasted with a hallmark global advantage in typically-developing humans who process visual stimuli at the global level first (e.g., Broadbent, 1977; Kimchi, 1992; Lamb & Robertson, 1988; Navon, 1977, 1981). A human-like global bias leads individuals to holistically perceive a stimulus as one cohesive unit prior to perceiving its individual parts. Interestingly, altering the spatial proximity of elements within an array impacts visual processing of these stimuli by primates. Decreasing inter-element distance eliminates the local advantage for capuchin monkeys (De Lillo et al., 2005; Spinozzi et al., 2003), baboons (Deruelle & Fagot, 1998; Fagot & Deruelle, 1997), and chimpanzees (Fagot & Tomonaga, 1999), and even reverses it to a global advantage for cottontop tamarins (Neiworth et al., 2006).

Perception of the Arcimboldo images as faces may require the holistic integration of features that resemble facial structures (eyes, nose, mouth) that are organized in the appropriate spatial pattern and orientation. Given the apparent differences in processing modes across primate species, it is an open question as to whether monkeys might see faces in images that are organized in such a way as readily as humans perceive faces in these images. Further complicating the story is the possibility that, although monkeys tend to exhibit a local advantage (i.e., processing the local elements prior to the global unit), they may be global processors when it comes to facial stimuli as evidenced in earlier work assessing facial recognition in primates (e.g., Taubert, Aagten-Murphy, & Parr, 2012). In addition, there is some evidence that nonhuman species may respond to the face-like properties of stimuli even when those stimuli are not actually faces. For example, macaque monkeys (*Macaca fuscata*) were trained to discriminate gaze direction in two-dimensional human faces as well as black and white face sketches and arrangements of shapes that mimicked facial arrangements (Nguyen et al., 2013). The key finding from that study was that some pulvinar nuclei, which have been proposed to be involved in processing facial stimuli, responded differentially to the face-like stimuli in a way that did not occur for the same images presented after being scrambled (so that facial configurations were no longer present). Other face-like stimuli elicited interesting responses from some animals. Newly born chicks, for example, appeared to show an innate bias for face-like stimuli compared to non-face-like stimuli (Rosa-Salva, Regolin, & Vallortigara, 2010). Thus, it may be that even species that show a local bias in visual processing of non-face stimuli still selectively process specific features of face-like patterns.

We presented rhesus monkeys (*Macaca mulatta*), capuchin monkeys (*Cebus apella*), and human children (*Homo sapiens*; 3 to 5 years of age) with a task in which visual stimuli were presented on a computer screen and then had to be classified as faces or non-faces. First, we trained individuals to make this classification with images of true faces and images of fruits, flowers, or vegetables that had no arrangements that would evoke the sense of a face being present in those stimuli. After reaching criterion on the training phase, the individuals then classified novel exemplars of true faces, true non-faces, a set of Arcimboldo and other similar images that, to adult humans, clearly appear to contain faces, and a set of scattered Arcimboldo images that rearranged the pieces of those images so that they no longer looked like faces but were otherwise identical. Arcimboldo and scattered stimuli were non-differentially reinforced so that monkeys and children could not learn how to classify those images through feedback. From these data, we could compare the performances of individuals and species. Because children of this age process stimuli more globally but monkeys tend to process stimuli more locally (e.g., De Lillo et al., 2005), we predicted that children would show a greater likelihood to report these probe images as being faces compared to the matched, scattered images, but monkeys would not show this difference between the two types of probe stimuli.

Method

Participants

We tested seven adult male rhesus monkeys (Chewie: age 15; Han: age 13; Hank: age 32; Lou: age 22; Luke: age 16; Murph: age 22; and Obi: age 12). Rhesus monkeys were housed individually at Georgia State University's Language Research Center (LRC). They had constant visual and auditory access to other nearby monkeys. They also spent at least one day per week with direct access to a compatible social partner in an indoor-outdoor enclosure. The monkeys had continuous access to water and were fed manufactured chow, fruits and vegetables each afternoon.

We tested 14 capuchin monkeys including seven males (Benny: age 12; Gabe: age 17; Griffin: age 18; Liam: age 12; Logan: age 10; Mason: age 18; and Nkima: age 8) and seven females (Bailey: age 16; Bias: age 28; Gambit: age 19; Gonzo: age 10; Lily: age 18; Widget: age 7; and Wren: age 13). Capuchin monkeys were group housed at the LRC, but they voluntarily shifted into individual enclosures for testing once per day. These monkeys also had continuous access to water and were fed manufactured chow and various fruits and vegetables daily as part of their maintenance diet.

These monkeys had participated previously in multiple psychological experiments involving the computerized test system used in this study (e.g., Beran, 2008; Beran, Evans, Klein, & Einstein, 2012; Beran & Parrish, 2012, 2013; Beran, Parrish, Futch, Evans, & Perdue, 2015; Beran & Smith, 2011; Evans & Beran, 2012, 2014; Evans, Perdue, Parrish, & Beran, 2014; Klein, Evans, Schultz, & Beran, 2013), including tests of visual illusions (e.g., Agrillo, Parrish, & Beran, 2014; Parrish, Brosnan, & Beran, 2015).

We tested 22 children ranging in age from 36 months to 59 months (11 females and 11 males) at a local preschool near Atlanta, Georgia. Children were tested during normal school hours. Experimenters brought children from their classrooms to the testing room where they worked on the task on a laptop computer and with the aid of an experimenter. Children were tested in pairs, seated across from one another at a table with their own experimenter. Children could not see each other's computer monitor during testing. Parents of the children consented to their participation in the study, and children chose if they wanted to work with the experimenters, and when they wanted to stop working during each session.

Apparatus and Materials

The nonhuman primates were tested using the Language Research Center's Computerized Test System (LRC-CTS), which consisted of a personal computer, digital joystick, color monitor, and pellet dispenser (Evans, Beran, Chan, Klein, & Menzel, 2008; Richardson, Washburn, Hopkins, Savage-Rumbaugh, & Rumbaugh, 1990). Primates manipulated the joystick with their hands to produce isomorphic movements of a small cursor on the computer screen. They were not restrained during testing. They viewed the monitor from a distance of approximately 30 cm to 40 cm. Contacting stimuli with the cursor sometimes resulted in the delivery of a food reward. Capuchin monkeys were rewarded with 45-mg banana-flavored chow pellets and rhesus monkeys were rewarded with 94-mg pellets (Bio-Serv, Frenchtown, NJ) via a pellet dispenser interfaced to the computer through a digital I/O board (PDISO8A; Keithley Instruments, Cleveland, OH).

Children performed the task on touchscreen laptop computers using the same computer program as the nonhuman primates. They viewed the monitor from a distance of approximately 40 cm to 50 cm. However, rather than responding with joystick manipulation, children could touch the stimuli onscreen or verbally announce their responses to the experimenter, who entered those responses with a key press or by touching the monitor. Also, rather than food rewards, children received visual and auditory feedback following correct/incorrect trials (i.e., happy/sad faces and melodic/buzz tones). Additionally, children received a sticker and/or small toy of their choice at the end of each test session as a reward for participating, regardless of how many trials they completed correctly or incorrectly.

Design and Procedure

All species completed a computerized task that was written using Visual Basic 6.0. At the start of each trial, participants contacted a rectangle in the top center of the screen to initiate a trial. Monkeys did this using the cursor onscreen that was controlled by their joystick movements. Children did this by touching the box with their finger, although in some cases, children asked the experimenter to begin the trials with a finger touch to the box.

Training phase. Each session began with a training phase. After contact with the initiation stimulus during trials in the training phase, participants then saw only images of human faces or collections of non-face items such as foods (see Figure 1 for examples). These images were presented as sketches or photographs, and all were in color. There were 10 of each of those classes of images (faces and non-faces), and, on each trial, one of these images was randomly chosen. Across 20 trials, each image was presented once, so that no image repeated until all images had been presented. These images were presented in the top center of the computer screen. The images were programmed to be 7.5 cm wide and 7.0 cm tall, although the screen resolution on the laptops used with children presented those images as slightly smaller relative to the lower-resolution monitors presented to the monkeys. Two response images, the words FACE or FOOD, appeared below and to the left and right of the images, and participants chose one of those response classes for the presented image. Monkeys did this using the joystick to move the cursor into contact with one of those images, and children did this through screen presses or by announcing the response so that the experimenter could make the keypress. When the response matched the category of the sample stimulus, positive feedback was given, whereas incorrect responses led to negative feedback. For monkey species, this feedback consisted of a melodic chime and the delivery of a single food pellet for correct responses, and a buzz tone and a 20 s timeout for incorrect responses during which the screen remained blank. For children, feedback consisted of a happy face presented onscreen and an excited shout for correct responses and a sad face presented onscreen and a sad sound for incorrect responses. These training trials continued to be presented until a child was correct on seven of the last eight trials presented, or until monkeys were correct on 34 of the last 40 trials. Then, the test phase began. Participants were required to meet training criterion at the start of each test session.

Test Phase. In the test phase, the same stimuli from the training phase continued to be presented on approximately 75% of the trials. On the remaining 25% of the trials, there were four types of probe trials presented. Two of these types presented transfer stimuli in which new, never trained images of face and non-face foods were shown, and participants received feedback depending on the correctness of their responses as described above. The other two probe trials involved the presentation of illusory stimuli that consisted of fruits, vegetables, and flowers in arrangements that appeared to constitute faces or scattered stimuli that were versions of the illusory stimuli but with the face-like features such as the eyes removed by scattering critical parts of the images (see Figure 1 for examples). Responses to these two types of probe trials generated non-differential feedback in which 50% of trials ended with positive feedback and 50% of the trials provided no feedback and immediately led to the presentation of the initiation rectangle to begin the next trial.

There was one critical difference in the methodology used with rhesus monkeys compared to capuchin monkeys and children. When rhesus monkeys contacted the trial initiation rectangle, the sample image remained visible onscreen until a monkey classified it as a face or food. However, for children and capuchin monkeys, the sample image was presented for only 500 ms before being removed. Data collection occurred first with children, using the speeded presentation of the sample. We then collected the monkey data, and we wanted to vary the duration of sample visibility to see if either condition (speeded or continuously available) would affect the likelihood of seeing faces in the illusory stimuli. Given the small number of available rhesus monkeys, we opted to assess this between species rather than within each species. We anticipated switching both species to the other presentation format if we found any evidence

of illusory perception of faces, but given that we did not find this (see below), we did not reverse these presentation formats for the nonhuman primate species.

In each session, participants generated as many or as few trials as they chose to complete. Children performed the computer task across multiple sessions that lasted 5 to 15 min so that we could attempt to collect at least 200 trials from each child. One child (the youngest child in the sample) had some difficulty classifying the images, and also showed poor generalization to new images in terms of classifying them as faces or foods. This child's data were removed from the analyses. All other children met the training criterion, and could verbalize the "face or food" rule. These children completed between 3 and 9 sessions ($M = 5.90$ session, $SD = 1.45$). The monkeys, in most cases, completed many more trials than children in a given session and showed more variability in the number of sessions required to meet the criterion for training at the beginning of the session. Table 1 provides the details for each monkey regarding the number of sessions and number of trials completed. One rhesus monkey and one capuchin monkey failed to meet the training criterion, and were not included in the analyses.

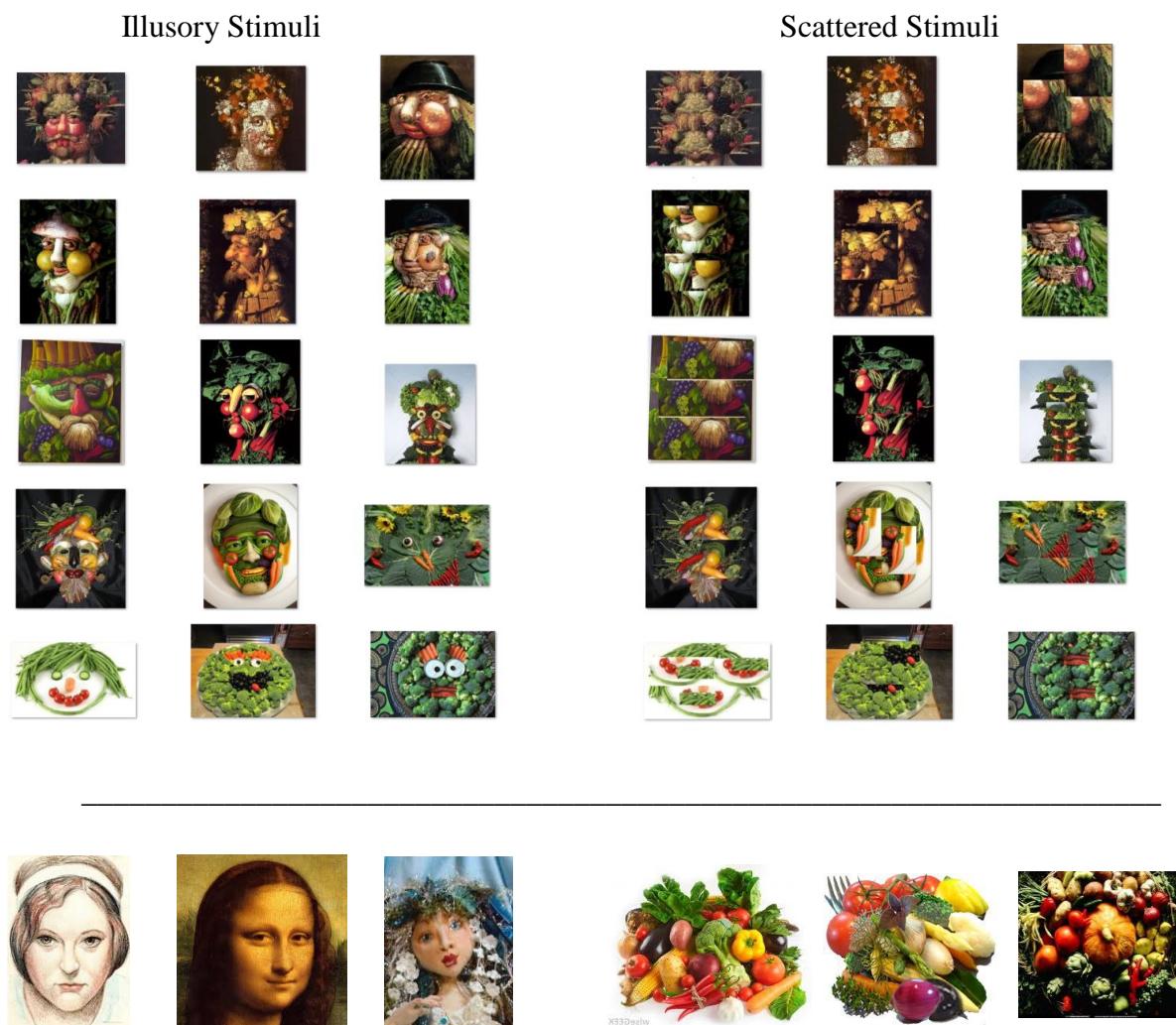


Figure 1. The probe illusory stimuli and scattered stimuli presented during the test phase. Each illusory stimulus at left has a matching scattered stimulus at right in the same location within the array. The bottom row of images shows some of the training stimuli used to teach participants to classify images as faces or foods.

Table 1

Session and Trial Counts for Each Monkey

Capuchin Monkeys	Sessions to Criterion	Total Sessions*	Total Trials	Rhesus Monkeys	Sessions to Criterion	Total Sessions*	Total Trials
Bailey	4	4	3,321	Chewie	1	1	815
Benny	1	1	1,461	Han	1	1	1,327
Bias	1	1	1,216	Hank	7	8	2,337
Gabe	Failed	6	1,574	Lou	1	1	1,584
Gambit	2	3	1,661	Luke	Failed	10	5,413
Gonzo	1	2	1,768	Murph	4	4	1,531
Griffin	1	1	678	Obi	2	3	2,688
Liam	3	3	2,358				
Lily	2	2	1,394				
Logan	1	1	700				
Mason	1	1	1,347				
Nkima	2	2	620				
Widget	1	1	931				
Wren	1	2	885				

Note. *Total sessions for some animals included one session beyond the session at which criterion was met. This occurred when a monkey met the criterion near the end of that session, and we wanted to collect more probe trial data. In all cases, those monkeys met the criterion in that next session and then provided more probe trial data.

Results

There were six trial types that could occur during the test phase, after the training criterion was met: training face stimuli, training food stimuli, probe face stimuli, probe food stimuli, illusory stimuli, and scattered stimuli. Analyses were carried out separately for each species at the level of individuals. First, we assessed performance against chance (50%) for training face stimuli, training food stimuli, probe face stimuli, and probe food stimuli using a two-tailed binomial test. Next, we compared performance on illusory stimuli and scattered stimuli with a Chi Square test to assess whether the proportion of trials classifying those stimuli as faces differed. If it did, we then assessed whether performance in classifying the illusory stimuli as faces exceeded the 50% chance level using a binomial test.

Figure 2A presents the percentage of trials correct for each rhesus monkey for the training face stimuli, training food stimuli, probe face stimuli, and probe food stimuli. In all cases except one (Hank, with probe face stimuli), performance was above chance level, all $p < 0.05$, binomial test. This indicated that rhesus monkeys continued to perform well with training stimuli, but also correctly classified the probe stimuli depicting true faces and foods. Figure 2B shows for each monkey the percentage of trials that the illusory stimuli were classified as faces and the percentage of trials the scattered stimuli were classified as faces. Only Obi showed a significantly higher proportion of Face classifications for the illusory stimuli compared to the scattered stimuli, $\chi^2(1, 282) = 4.63, p = 0.031$, but this proportion did not exceed chance levels, $p = 0.06$, binomial test.

Figure 3A presents the percentage of trials correct for each capuchin monkey for the training face stimuli, training food stimuli, probe face stimuli, and probe food stimuli. Capuchin monkeys struggled more with the probe stimuli compared to the training stimuli. Only 7 of 13 monkeys exceeded chance levels of responding with the probe face stimuli, and only 7 of 13 monkeys (with only some overlap with the first set of monkeys) exceeded chance levels with the probe food stimuli. Only two of the monkeys failed to exceed chance levels with both types, however, indicating that some capuchin monkeys could show transfer of classification of these stimuli. Figure 3B shows for each monkey the percentage of trials that the illusory stimuli were classified as faces and the percentage of trials that the scattered stimuli were classified as faces. None of the monkeys showed a significantly higher proportion of face classifications for the illusory stimuli compared to the scattered stimuli, all χ^2 tests $p > 0.10$.

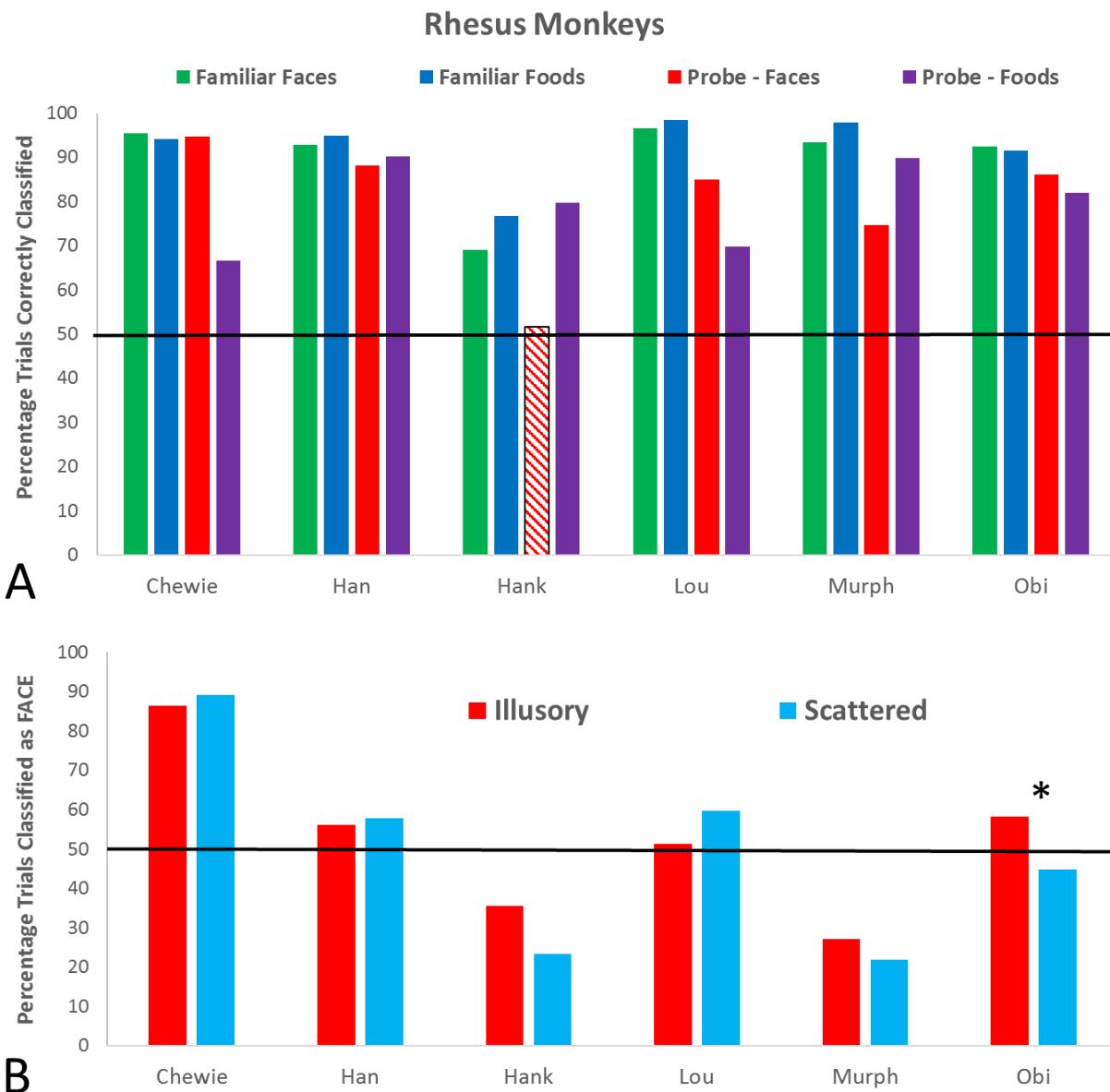


Figure 2. Rhesus monkey performance. (A) The percentage of trials in which stimuli were correctly classified for each of the four trial types. The horizontal line shows the chance level of performance. Solid bars indicate performance that exceeded chance levels. Hatched bars indicate performance that did not exceed chance levels. (B) The percentage of trials in which illusory and scattered images were classified as being faces. The horizontal line indicates the chance level of responding. Asterisks indicate the single monkey who classified the illusory stimuli as faces significantly more often than he classified the scattered images as faces.

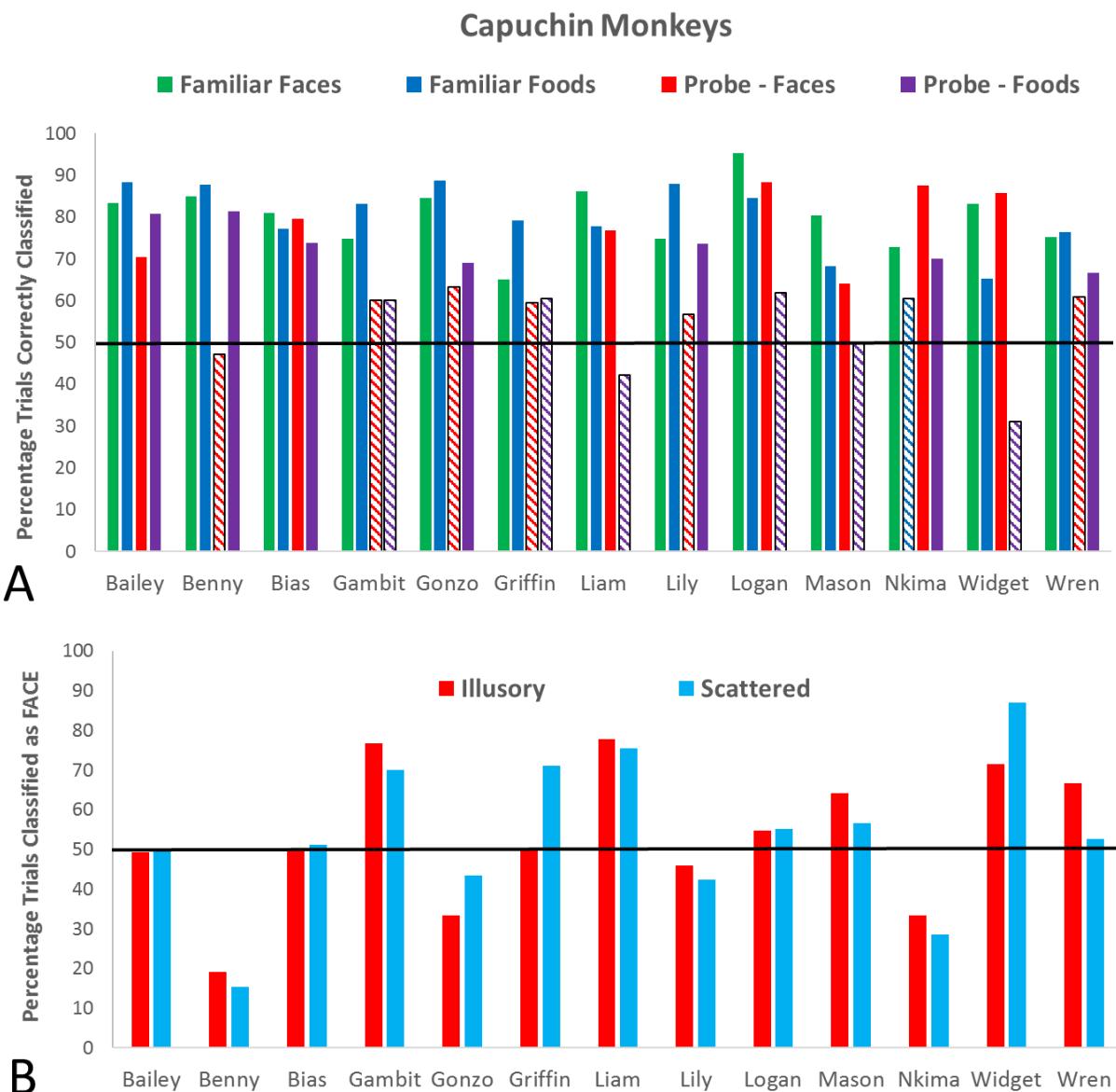


Figure 3. Capuchin monkey performance. (A) The percentage of trials in which stimuli were correctly classified for each of the four trial types. The horizontal line shows the chance level of performance. Solid bars indicate performance that exceeded chance levels. Hatched bars indicate performance that did not exceed chance levels. (B) The percentage of trials in which illusory and scattered images were classified as being faces. The horizontal line indicates the chance level of responding. None of the monkeys classified the illusory stimuli as faces significantly more often than they classified the scattered images as faces.

Figure 4 presents the data for the youngest 10 children and Figure 5 presents the data for the 11 oldest children. Figure 4A and Figure 5A show the percentage of trials correct for each of the children for the training face stimuli, training food stimuli, probe face stimuli, and probe food stimuli. In nearly all cases, performance exceeded chance levels. Children continued to perform well with training stimuli, but also correctly classified the probe stimuli from both categories. Figure 4B and Figure 5B show that 10 of the 21 children showed a significantly higher proportion of face classifications for the illusory stimuli compared to the scattered stimuli, all χ^2 tests $p < 0.05$. Of these 10 children, four called the illusory images faces significantly more often than expected by chance, all binomial tests $p < 0.05$, and two other children approached conventional levels of statistical significance, $p = 0.056$, binomial test.

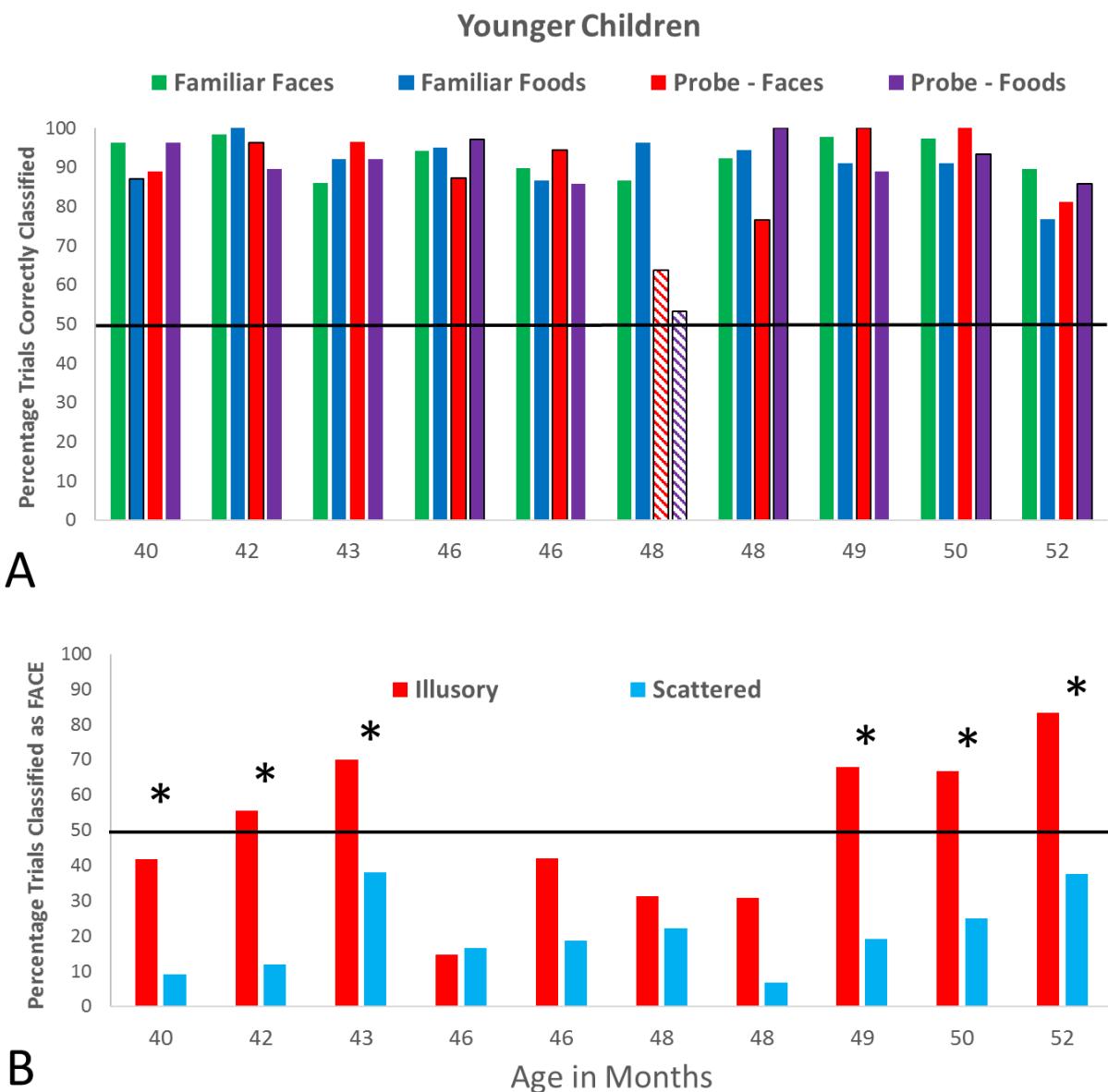


Figure 4. Performance of the 10 youngest children. (A) The percentage of trials in which stimuli were correctly classified for each of the four trial types. The horizontal line shows the chance level of performance. Solid bars indicate performance that exceeded chance levels. (B) The percentage of trials in which illusory and scattered images were classified as being faces by each participant. The horizontal line indicates the chance level of responding. Asterisks indicate participants who classified the illusory stimuli as faces significantly more often than they classified the scattered images as faces.

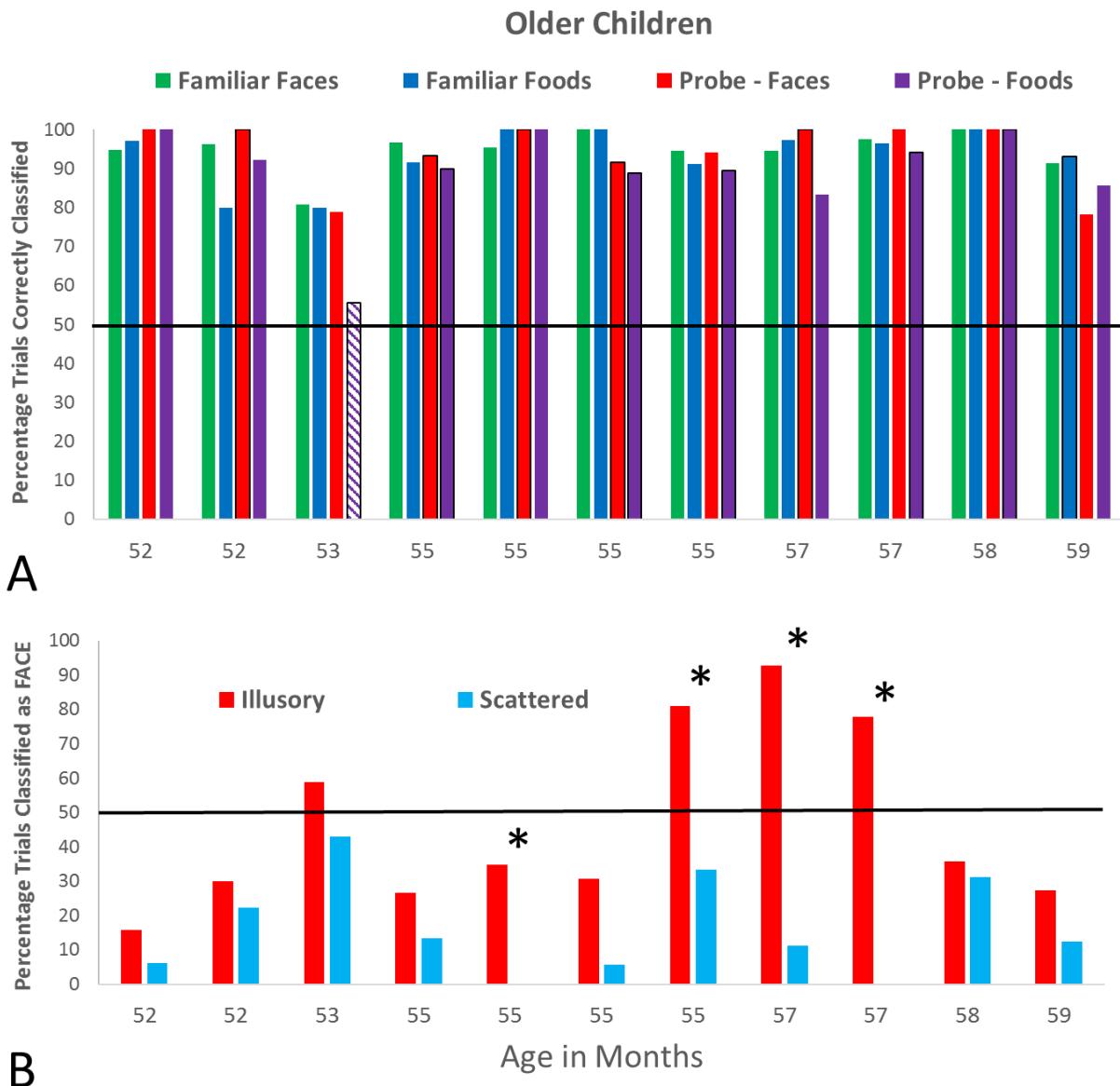


Figure 5. Performance of the 11 oldest children. (A) The percentage of trials in which stimuli were correctly classified for each of the four trial types. The horizontal line shows the chance level of performance. Solid bars indicate performance that exceeded chance levels. Hatched bars indicate performance that did not exceed chance levels. (B) The percentage of trials in which illusory and scattered images were classified as being faces by each participant. The horizontal line indicates the chance level of responding. Asterisks indicate participants who classified the illusory stimuli as faces significantly more often than they classified the scattered images as faces.

Discussion

Only children were significantly more likely to report that the illusory face-like stimuli looked like faces compared to the scattered stimuli that were otherwise identical to the illusory stimuli (i.e., same luminance, pixilation, size, etc.). Both monkey species showed no differences in how often they classified each of these stimulus types as being faces. However, monkeys did not respond randomly to all probe stimuli. Nearly all rhesus monkeys (like the children) were adept at classifying new faces and foods into the correct categories, and some capuchin monkeys also did this readily. One possibility for the difference

among the monkey species with the probe face and food stimuli could be the difference in number of trials completed (Table 1). However, the main point is that, whereas one can argue that all species transferred the “face or food” classification rule to new exemplars, only children differentially responded to the illusory stimuli more often as being faces compared to the scattered stimuli.

It is important to note that not all children overwhelmingly saw faces in the illusory stimuli. There were clear individual differences, and those differences do not appear to be age-related in the sample tested here, as shown in Figure 4 and Figure 5. Thus, it appears that, by 3 ½ years of age, some children are more likely to perceive faces in these kinds of stimuli than in matched stimuli without facial configurations. Of course, we presented the stimuli rapidly (500 ms) to children, and so with longer presentation times, children might report more face classifications or fewer such classifications, as presentation duration may be a critical factor. Similarly, a more robust Arcimboldo effect might emerge in children older than those tested in the current study as recent research has documented a more adult-like global processing bias around six years of age (as compared to four years of age; Dukette & Stiles, 1996). Future work that extends this developmental work through adolescence will be important to delineating age-related changes in responding to Arcimboldo and similar images.

That neither monkey species reported seeing faces more often in the Arcimboldo and similar stimuli as do humans is not surprising given the differences in perceptual processing modes across primate species. The monkey species tested here predominantly display a local advantage, in which they first focus on individual features comprising an array prior to the global or holistic grouping of those elements (e.g., *Cebus apella*: De Lillo et al., 2005; Spinozzi, et al., 2003, 2006; *Macaca mulatta*: Hopkins & Washburn, 2002, but see Tanaka & Fujita, 2000, and Tanaka, Onoe, Tsukada, & Fujita, 2001, for evidence of global processing in macaques). Perceiving faces in the Arcimboldo images requires global processing of these arrays, such that one rapidly and simultaneously assesses the individual parts comprising the image holistically, generating the phenomenon of face or face-like perception. A local advantage, as documented among capuchin monkeys and rhesus monkeys, would most likely delay or perhaps even prevent this facial processing. An interesting comparison species for the current work would be chimpanzees (and potentially other great apes and non-primate species) because they show stronger evidence of global processing more similar to humans than monkey species (e.g., Fagot & Tomonaga, 1999; Hopkins, 1997; Hopkins & Washburn, 2002; Matsuzawa, 1989).

An interesting point to consider is that if monkeys attended only to the elements of these probe stimuli as suggested by a local processing bias, they should have been significantly more likely to call the probe images foods than faces, as the elements of most of the stimuli were food items. That this did not occur suggests that, instead, the monkeys simply did not know how to classify these odd stimuli. Importantly, when real food or real faces were presented as probes, most monkeys could classify those items above chance levels as they had with the training stimuli. High performance with these true face transfer stimuli provides support for the hypothesis that faces are special for primates too, as evidenced in the extensive research assessing facial processing among monkeys and apes (see Parr, 2011a, for a review). It is clear that the monkeys learned the classification rule of foods and non-foods in this experiment, and successfully transferred those classifications to novel stimuli with true foods and faces. However, this mastery did not extend to the Arcimboldo and scattered images, which were treated as unique stimuli sets not belonging to either of the categories established in training.

Previous studies investigating the Thatcher effect with inverted faces have led to mixed results among rhesus monkeys. Studies employing looking time tasks among rhesus have reported positive evidence of the Thatcher effect in the same direction as human adults (Adachi et al., 2009; Dahl et al., 2010), but a recent study employing a matching-to-sample procedure found evidence for the Thatcher effect among chimpanzees but not rhesus monkeys (Weldon et al., 2013). In a series of follow up experiments in Weldon et al., rhesus monkeys appeared less sensitive to internal facial features and slight changes to these features (including inversion), instead of attending to external features of conspecific faces more readily than internal features. The current study shows that primate species with a local advantage (rhesus monkeys and capuchin monkeys) appear less sensitive to non-traditional face-like stimuli containing internal features

that are arranged such that they typically give rise to face or face-like perception among globally-advantaged populations (human adults and children).

Another consideration for the current work is that children and monkeys were presented with images of real or animated human faces in the present experiment, creating a conspecific perceptual judgment for children but a heterospecific judgment for the monkeys. Although the Arcimboldo images were not of true human faces, they are designed to resemble human-like facial features and face shape. Despite this difference in procedure for children and monkeys in the current study, capuchin and rhesus monkey successfully learned to classify human faces in training and test probe trials as faces at above chance levels. Thus, the assumption is that there should have been an equivalent sensitivity to Arcimboldo and similar images among monkeys and children. However, it is important to consider that monkeys may have shown more success in classifying the illusory stimuli as faces if they were arranged to be closer to conspecific monkey faces rather than human faces. Relatedly, previous work assessing inversion effects has shown that chimpanzees are sensitive to these facial manipulations exclusively among conspecifics, but that rhesus monkeys sometimes demonstrate inversion effects in response to conspecific, heterospecific, and nonface stimuli (e.g., Parr, 2011b; Parr et al., 1998; Tomonaga, 1999; Tomonaga et al., 1993). Future work presenting monkeys with Arcimboldo-like images that more closely resemble conspecific faces is an important extension to determine if perception of these images may be more sensitive to within-species manipulations. And, of course, it would be good to present these stimuli to a wider range of species, to help narrow down the possible factors that influence how these stimuli are perceived.

These findings add to the literature on perceptual precedence effects (local and global processing) with potential implications for lateralized processing across the primate species tested here. The popular notion of “left-brained” versus “right-brained” individuals is not supported by scientific research (Nielsen, Zielinski, Ferguson, Lainhart, & Anderson, 2013); however, there are some apparent differences in gross and cellular anatomy and function between the hemispheres of the brain (e.g., Geschwind & Galaburda, 1985; Toga & Thompson, 2003). This lateralization of function is studied using a variety of techniques ranging from surgical division of the hemispheres (e.g., split-brain patients) to measuring differences in activity via functional imaging during various types of cognitive tasks. The right hemisphere appears to be somewhat dominant for global processing as well as face processing in humans (e.g., Gazzaniga, 2000; Martinez et al., 1997; Rossion et al., 2000). It is highly speculative, but perhaps the inconsistent evidence of lateralization for face processing in normal and split-brain monkeys (e.g., De Winter et al., 2015; Hamilton & Vermeire, 1983; Perrett et al., 1988; Vermeire & Hamilton, 1998) and the inconsistent use of holistic modes of processing for faces (e.g., Taubert et al., 2012) and other stimuli (e.g., Hopkins & Washburn, 2002; Neiworth et al., 2006; Spinozzi et al., 2006) may underlie the present findings.

Acknowledgements

This research was supported by Grant HD060563 from the National Institutes of Health. The authors thank the animal care staff at the Language Research Center of Georgia State University, the administrators and teachers at Suburban Nursery School and Pre-K in Atlanta, GA, and the parents of the children for their assistance and support for this research project.

Ethics statement. This experiment with the nonhuman primates was carried out in accordance with the protocols approved by the Georgia State University Institutional Animal Care and Use Committee and met the requirements of the National Institutes of Health guide for the care and use of Laboratory animals. Georgia State University is an AAALAC accredited institution. The experiment with children was carried out in accordance with the protocol approved by the Georgia State University Institutional Review Board.

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