

eScholarship

International Journal of Comparative Psychology

Title

A Free Choice Task Evaluating Chimpanzees' Preference for Photographic Images of Sex Swellings: Effects of Color, Size, and Symmetry

Permalink

<https://escholarship.org/uc/item/86h5r1m3>

Journal

International Journal of Comparative Psychology, 25(2)

ISSN

0889-3675

Authors

Breaux, Sarah D.
Watson, Sheree L.
Fontenot, M. Babette

Publication Date

2012

DOI

10.46867/ijcp.2012.25.02.03

Copyright Information

Copyright 2012 by the author(s). This work is made available under the terms of a Creative Commons Attribution License, available at <https://creativecommons.org/licenses/by/4.0/>

Peer reviewed

A Free Choice Task Evaluating Chimpanzees' Preference for Photographic Images of Sex Swellings: Effects of Color, Size, and Symmetry

Sarah D. Breaux

University of Louisiana at Lafayette-New Iberia Research Center, U.S.A.

Sheree L. Watson

University of Southern Mississippi, U.S.A.

M. Babette Fontenot

University of Louisiana at Lafayette-New Iberia Research Center, U.S.A.

Exaggerated sex swellings characterized by increased size of skin surrounding the anogenital region occur in female chimpanzees in response to ovarian hormone fluctuations and are associated with increased likelihood of ovulation and female receptivity. The swellings generate heightened sexual interest from males and evoke increased male competitive behavior. To determine potential attractiveness of specific visual characteristics of these signals to males, a free choice task using push-button methodology that allowed subjects to choose one stimulus in a pair by pressing a button corresponding to the stimulus choice was developed. Initially, preferences for specific food items were first determined based on animals' selection of actual items, followed by selection of same items from photographs and subsequently selection of preferred food utilizing push-button responses to photographs. We found that when allowed to choose between photographs of sex swellings, novel objects, and other body parts, male chimpanzees preferred images of both sex swellings and other body parts over images of objects, and showed a significant preference for sex swellings over other body parts. However, chimpanzees showed no preference in sex swelling color or symmetry. Only one subject displayed a preference for normal sized swellings rather than enlarged swellings. Overall these results suggest that when considered individually, visual characteristics alone are not sufficient to provoke preference responding.

Sex swellings are hormonally regulated reddening and/or tumescence of the anogenital region occurring in approximately 10% of nonhuman primates (i.e., cercopithecines and *Pan* species) that have evolved as a cue to advertise female fertility and receptivity to males (Dixson, 1998). In chimpanzees, tumescence of the sex swelling is linked to ovulation (Deschner, Heistermann, Hodges, & Boesch, 2003; Emery & Whitten, 2003; Thompson, 2005). During the follicular phase, an increase in estrogen causes gradual reddening and swelling of the anogenital tissue. Once ovulation occurs during the luteal phase, progesterone causes a sudden decrease in the swelling and the skin returns to normal color (Deschner et al., 2003; Emery & Whitten, 2003; Thompson, 2005). The presence of the swelling triggers increased competition between males for access. Further, dominant chimpanzees concentrate their mating efforts to periods of maximum

This work includes dissertation research of the first author and was funded in part through the National Institutes of Health National Center for Research Resources grants RR015087, RR014491, RR016483. Correspondence concerning this article should be addressed to Sarah D. Breaux, Division of Behavioral Sciences, UL Lafayette-NIRC, PO Box 13610, New Iberia, LA 70562-3610. (sarahdbreaux@gmail.com)

tumescence (Deschner, Heistermann, Hodges, & Boesch, 2004; Thompson & Wrangham, 2008).

In nonhuman primate species such as macaques and baboons, coloration of the sex skin plays an important role in attracting mates (Bergman, Ho, & Beehner, 2009; Bielert, Girolami, & Jowell, 1989; Waitt, Gerald, Little, & Kraiselburd, 2006). Waitt et al. (2006) presented male rhesus macaques (*Macaca mulatta*) with video-captured images of red female rhesus hindquarters and non-red female rhesus hindquarters, and found that they gazed significantly longer at the reddened anogenital skin than non-reddened anogenital skin (Waitt et al., 2006). In a separate study, Bielert et al. (1989) compared masturbatory responses of male chacma baboons (*Papio ursinus*) when presented with the same ovariectomized female in each of three conditions. First, experimenters measured baseline masturbatory response of nine male baboons when an ovariectomized female was placed in full view. Then experimenters measured masturbatory response when males were presented with the same female treated with estradiol benzoate to induce a fully swollen anogenital region. Finally, experimenters presented the males with the same ovariectomized female baboon fitted with a prosthetic sex swelling in one of each of the following colors: white, red, orange, yellow, green, blue, purple, or black. Not only did the red prosthetic elicit the same level of masturbatory response as the estradiol induced swelling, but the red prosthetic also elicited significantly greater male masturbatory response than all other colors (Bielert et al., 1989). Together, these studies suggest that the color of female sex skin plays a substantial role in stimulation of male sexual behavior and sexual interest.

The exaggerated size of the sex skin also serves as an attractant in some primate species. Bielert and Anderson (1985) noted individual differences in the size of sex swellings among female chacma baboons and demonstrated that males were more aroused by extremely large swellings regardless of undifferentiated female proceptive behavior. The male chacma baboons exhibited more masturbatory behavior toward females with larger swellings leading Bielert and Anderson (1985) to suggest that larger swellings served as a supernormal stimulus (i.e., similar to naturally occurring stimuli except more extreme in the relevant dimension) eliciting a more exaggerated response. Similarly, at least one study has demonstrated that male chimpanzees prefer mating with the female whose swelling is largest intraindividually (Deschner et al., 2004).

The influence of symmetry on sexual attractiveness has been most widely investigated in humans. Both human males and human females perceive individuals with more symmetric faces, body shape, and breasts as more attractive than individuals who are less symmetric in these features (Langlois et al., 2000; Perrett et al., 1999; Singh, 1995; Singh & Young, 1995; Thornhill & Gangestad, 1999). At least one study has investigated nonhuman primate preference for facial symmetry. Waitt and Little (2006) employed a looking time paradigm to present rhesus monkeys with images of symmetric and asymmetric versions of opposite-sexed conspecific faces. While monkeys gazed significantly longer at symmetric faces, it remains unknown whether in other primates symmetry in a fluctuating feature such as a sex swelling would be important.

In a number of species, visual characteristics including color, size, or symmetry of specific morphological traits (e.g., faces, breasts, sex skin) may serve as reliable indicators of an individual's health and quality (for review see Maynard-Smith & Harper, 2004). For example, changes in health during growth and development increase fluctuating asymmetry, bilateral symmetry reflects an individual's ability to generate the same phenotype under differential environmental conditions. Among nonhuman animals, individuals with more symmetric secondary sexual characteristics tend to have greater reproductive success than individuals with less symmetric characteristics (for review see Moller & Thornhill, 1998). Similarly, characteristics such as color and size can also be affected by diseases or parasitism, such that individuals would be less likely to achieve maximum size or as bright coloration when in poor health (Hamilton & Zuk, 1982). It has yet to be demonstrated experimentally whether chimpanzees attend to any of these visual features in a manner similar to that shown in other species.

In the following series of experiments we first examined the ability of male chimpanzees to preferentially choose between food items using a push-button methodology which was validated by comparing responses to previously established preferences. Then we evaluated whether males preferred sex swellings to other body parts (excluding faces) and novel inanimate objects. Finally male preference for color, size, and symmetry of sex swellings was evaluated. We hypothesized that the subjects would choose reddened swellings over non-reddened swellings, larger swellings over smaller swellings, and more symmetric swellings over less symmetric swellings.

Method

Subjects

The subjects (A and B) were two adult male captive born, nursery-reared chimpanzees, aged 17 and 15 years, respectively, housed in a multi-male social group at the University of Louisiana at Lafayette-New Iberia Research Center (UL Lafayette-NIRC). Both subjects were previously housed with females for several years prior to these experiments and were sexually experienced individuals. Subjects were fed a commercially available primate chow supplemented with fresh fruits and vegetables daily in accordance with UL Lafayette-NIRC Standard Operating Procedures. Water was provided *ad libitum*. Subjects were housed in a 385 square foot indoor enclosure with an outdoor 23 ft diameter, 34 ft high geodesic dome (Primadome[®]) attached. Each subject was tested individually in a section of the indoor portion of his home cage between 1000 and 1230 and participated voluntarily in all testing procedures without food or water restrictions. All procedures were approved by UL Lafayette-NIRC Institutional Animal Care and Use Committee. The UL Lafayette-NIRC is fully accredited by AAALAC, International.

Apparatus

The free choice task used a push-button procedure in which subjects selected a button corresponding to preferred photographic stimuli. The experimental apparatus was comprised of a 17 in color monitor and CPU as well as a pair of red 33 mm push-buttons. An opaque barrier occluded all computer equipment from the subjects' view except the screen of the monitor. The push-buttons were mounted to the home cage just below the screen; the monitor was situated directly behind the button mount. The height of the cart and buttons allowed subjects to view both the monitor and the buttons comfortably from a seated position so that the buttons would not obstruct visual access to the stimuli presented on screen. Each button corresponded to a stimulus on its analogous side of the

screen. For each trial, the subject was presented with two stimuli, one on the left half and one on the right half of the screen. Subjects were allowed 10 s per trial to respond by pressing a button. When a button was pressed, the corresponding image enlarged to full screen and remained visible for 5 s. Each trial was followed by a 1.5 s inter-trial interval. Stimuli were presented for each experimental session using E-Prime 1.1 (Psychology Software Tools, USA) and response data were collected by E-Prime for later analysis.

Food Preference Testing

To ascertain individual food preferences, each subject was presented with all pairwise combinations of four food items (i.e., grape, celery, peanut, and broccoli). The six pairs were presented 10 times each in random order. Food pairs were counterbalanced for side of presentation to control for a possible side bias. Each 60 trial session was repeated over five days for a total of 300 total trials (i.e., 50 trials per food item pair per subject). During each trial the pair of food items was presented in small amounts of relatively similar volume to control for a preference for a greater amount of food. The food items were simultaneously presented to the subjects in the palms of the experimenter's hands at a distance of two feet apart. The subject was allowed to consume the food item initially selected and the alternative item was taken away.

Based on the subjects' food item choices across pairs, it was possible to determine which food item was most preferred and which food was least preferred. Subject A demonstrated an affinity for grapes and celery, and Subject B demonstrated an affinity for grapes. While Subject A disliked broccoli, Subject B disliked celery. The subjects' pairwise food item selections are detailed in Table 1. To simplify the push-button food preference procedure, grape was chosen as a high preference food for both subjects while celery was chosen as Subject B's low preference food item and broccoli was chosen as Subject A's low preference food item. Chi square analysis indicated that both subjects chose grape significantly more often than their low preference food item in the food preference testing (Subject A, broccoli vs. grape: $\chi^2(1, N = 50) = 20.48, p < 0.001$; Subject B, celery vs. grape: $\chi^2(1, N = 50) = 50.0, p < 0.001$).

After first assessing the subjects' food preferences, we utilized the push-button methodology to compare performance on a computerized dichotomous free choice task to established food preferences. This validation procedure was conducted to ensure that the subjects were able to comprehend the task, indicating preference by pressing a button which corresponded to the favored photographic stimulus.

Table 1
Contingency matrix of food preferences

Subject A	Broccoli	Celery	Grape	Peanut
Broccoli	-	78	82	48
Celery	22	-	28	12
Grape	18	72	-	10
Peanut	52	88	90	-
Subject B	Broccoli	Celery	Grape	Peanut
Broccoli	-	2	80	58
Celery	98	-	100	90
Grape	20	0	-	8
Peanut	42	10	92	-

Data reflects the percentage of each column item chosen over row item for each subject.

Initial Training

As neither subject had been used in behavioral or cognitive research prior to this series of experiments, both subjects were desensitized to and trained to operate the push-button apparatus using positive reinforcement technique with juice or cola administered via squirt bottle as the reinforcement. After initial desensitization to the apparatus, subjects were trained three to five times per week for approximately 30 mins per training session. In order to train subjects to associate an image on either the left side of the monitor or the right side of the monitor with its respective button, the subjects were presented with single-stimulus training trials which randomly displayed images on either the left or right side of the screen. Once subjects reached criterion by selecting the correct button corresponding to the image on screen with 80% accuracy for three consecutive training days or 90% accuracy for one training day, subjects began push-button preference testing. Training time to criterion was approximately six months for both subjects.

Validation of Preference Testing: Food Choice Task with Photographs

Once high and low preference foods were ascertained for each subject, we examined whether subjects would reliably use the push-button procedure to choose preferred items when presented with photographs of the high and low preference foods rather than the actual food item. Low preference food items were paired with either high preference foods or the squirt bottle used to administer cola reinforcement during training.

Each pair of photographs was presented in random order and balanced for side of presentation during each session. Once the pair of photos was presented and the subject selected a food item by pressing its corresponding button, the subject was rewarded with his selected food item or squirt of cola. Each push-button food preference testing session consisted of 80 trials: 40 high-low preference food item pairs and 40 squirt bottle-low preference food item pairs. Sessions were repeated over 5 testing days for a total of 200 high-low preference trials and 200 squirt bottle-low preference trials per subject.

Experiment One: Preference for Sex Swelling over Body Parts and Inanimate Objects

Procedure

To assess the subjects' level of interest in sex swelling, a series of photographs of maximally tumescent sex swellings were presented simultaneously with photographs of either a novel inanimate object (i.e., rubber mallet, roll of gray tape, remote control, bowl) or a body part from an unfamiliar chimpanzee (i.e., hand, foot, back of head, arm). The presentation of the novel inanimate object was intended to control for stimulus novelty in that photographs of objects and swellings were unfamiliar. The presentation of chimpanzee body parts was presented to control for a preference for sexual stimuli over nonsexual stimuli. Faces were purposefully not used in this study to simplify interpretation of results as numerous studies have investigated visual processing of faces and facial features and have identified a strong preference for faces in chimpanzees (Hirata, Fuwa, Sugama, Kusunoki, & Fujita, 2010; Kano & Tomonaga, 2009; Parr, Heintz, & Akamagwuna, 2006; Parr, Waller, & Heintz, 2008).

Experiment One was conducted in four phases. Each possible pair of stimuli (each of four objects vs. each of four swellings; each of four body parts vs. each of four swellings; each of four body parts vs. each of four objects) was presented in phases A through C. Phase A consisted of sex swelling-object pairs and compared the number of times the sex swelling photo was selected to the number times the novel object photo was selected. Phase B consisted of sex swelling-body part pairs and compared the number of times the sex swelling photo was chosen to the number of times the photo of another body part was chosen. Phase C consisted of body part-object stimuli pairs and compared the number of times a body part photo was chosen to the number of times an object photo was chosen. A fourth phase, phase D, consisted of all three stimuli pair types. For each phase, experimental trials were interspersed with food preference trials throughout each session to ensure that the subjects' responses were based on preference.

Within each of the four phases, both experimental trials and food trials were randomized and counterbalanced for side of presentation. Trials were randomized so that each swelling versus object (or body part) or object versus body part trial, where applicable, was not presented one after

another nor were any pair type (e.g., swelling/foot, or swelling/arm pair) presented more than twice in a row. No single stimulus type was shown more than twice in a row on the same side of the screen. Food trials and experimental trials were randomized separately, and then the two types of trials were randomized such that for every 12 trials presented, four were sex swelling trials. This procedure was followed to ensure that experimental trials were evenly dispersed throughout each 96 trial session.

Each phase was completed in succession. Each 96 trial session (32 experimental trials and 64 food preference trials) was repeated over five days for each phase. Preference for a given stimulus item was indicated by number of times the subject pressed the button corresponding to that “half” of the paired stimuli choices. On food preference trials, subjects were rewarded with a small piece of the food item chosen, while on all experimental trials subjects were rewarded with a small squirt of cola regardless of stimulus choice.

Stimuli

All sex swelling photographs were obtained from female chimpanzees aged 12 to 26 years housed at UL Lafayette-NIRC. The photographs were obtained from females that were unfamiliar to either of the subjects. Each female’s anogenital region was photographed both from directly behind and from the side on a daily basis for a period of three months to obtain a representative sample of each female’s maximally tumescent sex swelling. Each swelling was also rated daily by the first author with a relative swelling size from 0 to 4, with 0 being maximally detumescent and 4 being maximally tumescent. This ensured that photos used for experiments were of maximally tumescent swellings from each female. Only photos from directly behind with hips and at least a portion of the female’s legs visible were used as stimuli.

Images were standardized to approximately 480x620 pixels maintaining the height and width ratio of the original photo. For sex swelling stimuli and object stimuli, the swelling or object comprised at least 75% of the image. For chimpanzee body part stimuli, body parts comprised the majority of the image but were scaled so that the body parts (such as hands and feet) would not appear larger than the sex swellings, as found in nature. See Figure 1 for sample stimuli from Experiment One.

All stimuli were photographed using the same equipment, a JVC Everio, to ensure consistent photo quality. All stimuli were presented on a neutral white background and all photographs were black and white in Experiment One to control for the possibility of the color of the objects or swellings affecting preference. All stimulus manipulations were completed in Adobe Photoshop®.

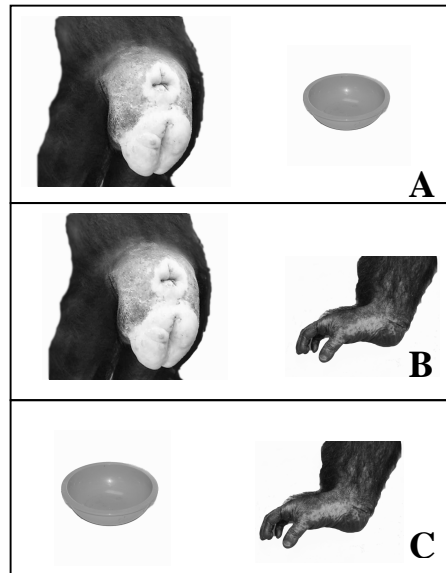


Figure 1. Experiment One sample stimuli. Sample stimulus pairs for **A**) Phase A: swelling vs. object, **B**) Phase B: swelling vs. body part, and **C**) Phase C: body part vs. object.

Experiment Two: Color Effects on Sex Swelling Preference

Procedure

Experiment Two evaluated the effects of sex swelling color on preference by comparing naturally colored swellings to color manipulated swellings. A series of maximally tumescent sex swellings in their natural color were presented alongside either a darkened (i.e., reddened) version or a lightened version of the swelling. Stimulus pairs consisting of darkened and lightened versions of sex swellings were also presented. Subjects were presented with pairs of all possible color combinations for each of 8 sex swellings. Each session consisted of 96 trials: 48 experimental trials (16 trials of each pair type per session: each pair of color combinations for all 8 swellings was presented twice and counterbalanced) and 48 food preference trials. As in Experiment One, food preference trials were interspersed equally throughout each session. All trial types were randomized and each stimulus was counterbalanced for side of presentation. Each session was repeated over 5 testing days for approximately 240 total trials, 80 trials per stimulus pair for each subject.

Stimuli

All sex swelling stimuli were color calibrated using RGB color calibration methods (Gerald, Bernstein, Hinkson, & Fosbury, 2001). Two color variations of each sex swelling stimulus were created once the stimuli were color calibrated. Manipulated to increase the redness of the sex swelling, darkened versions were created by increasing the red saturation by 50%. Similarly, lightened stimuli were created by decreasing red saturation by 50%. See Figure 2 for sample stimuli from Experiment Two.

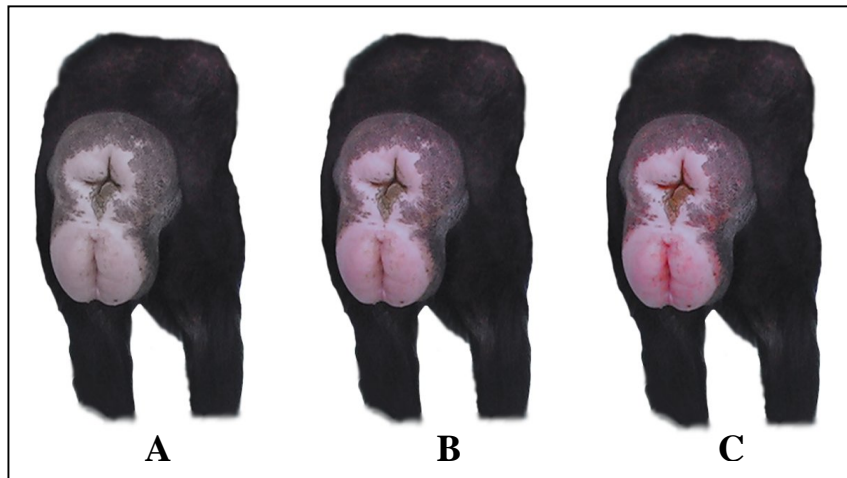


Figure 2. Example of color manipulations on sex swelling stimulus for Experiment Two: **A)** lightened color sex swelling, **B)** natural color sex swelling, and **C)** reddened (darkened) color sex swelling. Stimuli were presented in light/natural, dark/natural, and light/dark pairs.

Experiment Three: Size Effects on Sex Swelling Preference

Procedure

Experiment Three evaluated preference in swelling size by comparing naturally sized swellings to size manipulated swellings. A series of maximally tumescent swellings were presented simultaneously with either an enlarged version of the swelling or a reduced version of the swelling. Reduced and enlarged versions of the sex swelling were also presented as stimulus pairs. Subjects were presented with pairs of all possible size combinations for each of 8 sex swellings used as stimuli. Each 96 trial session consisted of 48 experimental trials (16 trials each pair type: each pair of size combinations for all 8 swellings was presented twice and counterbalanced) and 48 food

preference trials which were interspersed equally throughout each session. All trial types were randomized and each stimulus was counterbalanced for side of presentation. Sessions were repeated over 5 testing days for approximately 240 total trials: 80 trials per stimulus pair per subject.

Stimuli

Two size variations of each stimulus were created from the naturally sized swelling stimuli by first standardizing the image size. An enlarged swelling stimulus was created by increasing the area of the sex swelling size by 40-50%, maintaining the height-to-width ratio. The swelling in the original image was replaced by the enlarged size swelling. Similarly, the reduced swelling stimulus was created by decreasing the area of the sex swelling size by 40-50%, maintaining the height-to-width ratio. Then, the swelling in the original image was replaced by overlaying the reduced size swelling. Minor adjustments to the enlargement were made so that the entire enlarged swelling would be visible in the original image. For the reduced stimuli, portions of legs or hips were also included so that the reduced portion of the image would fully cover the original swelling image. Sex swelling color remained constant for each stimulus pair to control for any color effects on subject preferences. Figure 3 illustrates a sample sex swelling with size manipulations.

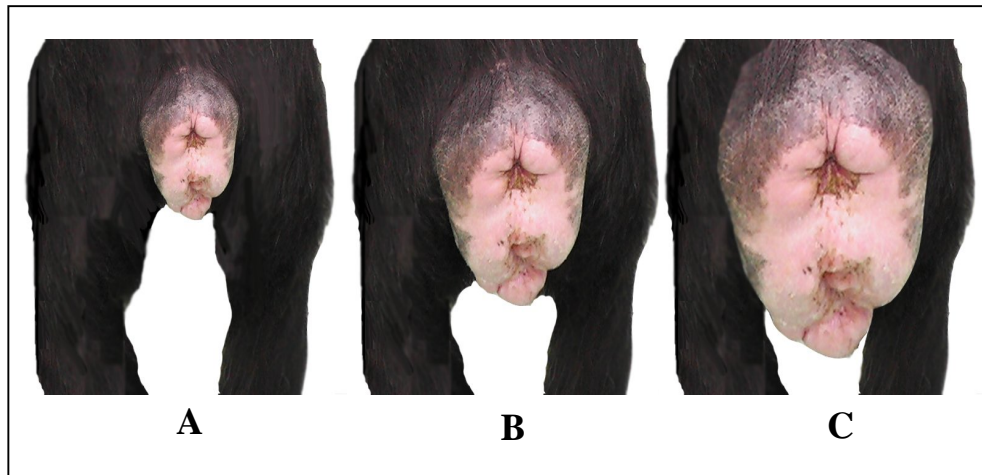


Figure 3. Example of size manipulations on sex swelling stimulus for Experiment Three: **A)** reduced size sex swelling, **B)** normal size sex swelling, and **C)** enlarged size sex swelling. Stimuli were presented in normal/enlarged, normal/reduced, and enlarged/reduced pairs.

Experiment Four: Effect of Symmetry on Sex Swelling Preference

Procedure

To evaluate the effect of symmetry on preference for sex swellings, a skewed version and a symmetric version of the sex swelling stimuli were created. Eight sex swellings were each presented with one of two shape variations of the same swelling, a symmetric version, which was manipulated to increase symmetry and a skewed version, which was manipulated to decrease symmetry. Additionally, symmetric and skewed versions were used as stimulus pairs (e.g., normal vs. symmetric; normal vs. skewed; symmetric vs. skewed). Subjects were presented with pairs of all possible shape combinations for each of 8 sex swellings used as stimuli. Each 96 trial session contained 48 experimental trials (16 trials each pair type: each pair of symmetry combinations for all 8 swellings was presented twice and counterbalanced) and 48 food preference trials, interspersed equally throughout session. All trial types were randomized and each stimulus was counterbalanced for side of presentation. Sessions were repeated over 5 testing days for approximately 240 total trials, 80 trials per stimulus pair per subject.

Stimuli

Sex swelling stimuli were from the same bank of swelling photos obtained for the previous experiments. Symmetric stimuli were created using mirror image technique by bisecting the sex swelling and replacing one half of the swelling with the other so that the resultant image contained two copies of the same half. Skewed stimuli were created by exaggerating perceived asymmetries in the original swelling. Using the Warp tool, bulbous protrusions of swellings were enlarged; small sections of labia were pinched to make them smaller. Resultant images were notably and substantially asymmetric sex swellings. As in Experiment Three, swelling color remained constant for each stimulus pair. See Figure 4 for sample symmetry manipulations.

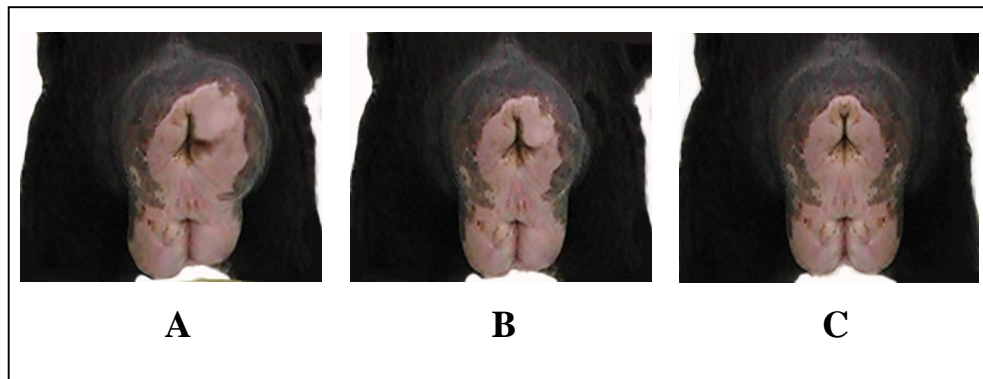


Figure 4. Example of sex swelling stimulus and its symmetry manipulations for Experiment Four. **A)** Skewed shape sex swelling, **B)** normal shape sex swelling, and **C)** symmetric shape sex swelling. Stimuli were presented in normal/symmetric, normal/skewed, and symmetric/skewed pairs.

Data Analysis

The frequency of selections of each stimulus by pair was compared for the preference testing validation procedure as well as each of the experiments using chi square analysis.

Results

Validation of Preference Testing

Results of chi square analysis indicated that both subjects chose their high preference food item photo significantly more often than their low preference food item photo (Subject A, broccoli vs. grape: $\chi^2(1, N = 194) = 81.83, p < 0.001$; Subject B, celery vs. grape: $\chi^2(1, N = 187) = 24.59, p < 0.001$). The performance of both Subject A and Subject B on the push-button food preference testing reflected their established food preferences. Thus we extended the food preference procedure to include experimental photographic pairs in the following experiments to allow the chimpanzees to make a choice selection based on preference. Figure 5 reflects both subjects' stimulus selections on the push-button food preference testing.

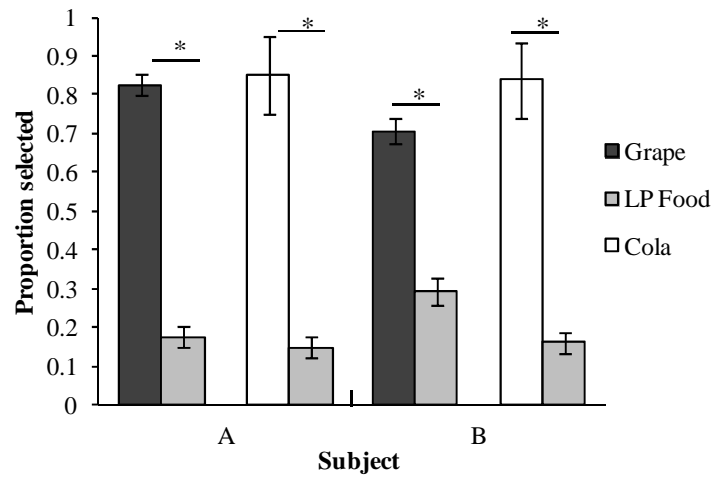


Figure 5. The proportion (\pm SE) of each food item selected for each subject during push-button food preference testing. Low preference food items (LP Food) were broccoli for Subject A and celery for Subject B.

* $p < 0.001$

Experiment One: Swellings, Body Parts and Objects

A difference between proportions test investigated significant differences in pressing behavior between Phases A, B, and C and their respective trial types in Phase D for either subject. Since there were no reversals in preference between phases (e.g., a subject pressed preferentially for swellings over objects in Phase A and then pressed preferentially for objects over swellings in Phase D), data from all four phases were combined for analysis.

As depicted in Figure 6, both Subject A and Subject B chose sex swelling stimuli preferentially over objects (Subject A: $\chi^2(1, N = 197) = 17.67, p < 0.0001$; Subject B: $\chi^2(1, N = 198) = 11.64, p < 0.001$) but not more frequently than body parts (Subject A: $\chi^2(1, N = 198) = 1.64, p = 0.20$; Subject B: $\chi^2(1, N = 170) = 1.15, p = 0.28$). However, when data from the two subjects are combined, there is a significant preference for sex swellings over other body parts ($\chi^2(1, N = 362) = 3.99, p = 0.05$). Subject A chose body parts significantly more often than objects ($\chi^2(1, N = 262) = 8.08, p < 0.001$), while Subject B did not choose preferentially between objects and body parts ($\chi^2(1, N = 211) = 0.12, p = 0.73$).

Additionally, both subjects chose their high preference food items significantly more often than their low preference food items (Subject A: $\chi^2(1, N = 1227) = 552.02, p < 0.001$; Subject B: $\chi^2(1, N = 1232) = 129.87, p < 0.001$).

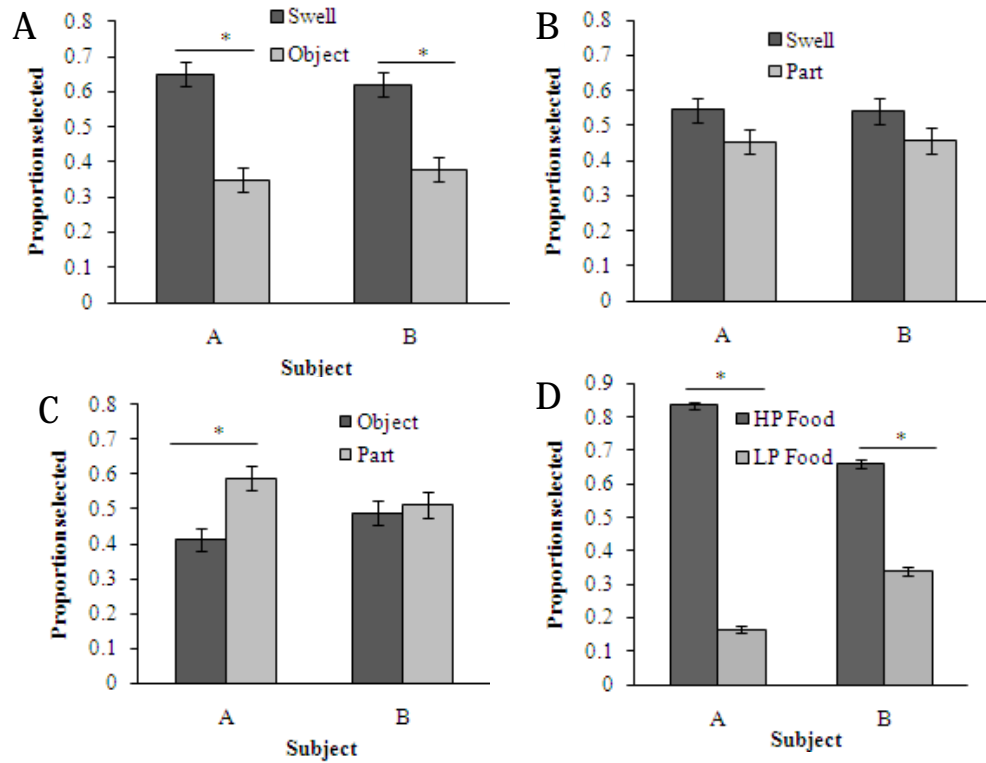


Figure 6. Proportion (\pm SE) of item selections by each subject for each stimulus pair type for Experiment One: **A)** swelling vs. object trials, **B)** swelling vs. body part trials, **C)** body part vs. object trials, and **D)** food preference trials. High preference food items (HP Food) items were grape and cola for both subjects. Low preference food items (LP Food) were broccoli for Subject A and celery for Subject B.

* $p < 0.001$

Experiment Two: Color

As depicted in Figure 7, chi square analysis revealed that Subject A did not press preferentially between naturally colored swellings and lightened swellings ($\chi^2(1, N = 73) = 0.12, p = 0.73$), between naturally colored and darkened swellings ($\chi^2(1, N = 75) = 0.12, p = 0.73$), or between lightened and darkened swellings ($\chi^2(1, N = 75) = 0.01, p = 0.91$). Subject B's performance reflected similar results for all three trial types: natural vs. lightened, $\chi^2(1, N = 78) = 0.21, p = 0.65$; natural vs. darkened, $\chi^2(1, N = 80) = 0.05, p = 0.82$; lightened vs. darkened, $\chi^2(1, N = 79) = 0.32, p = 0.57$. When the subjects' choices were combined, results reflected the same pattern (natural vs. lightened, $\chi^2(1, N = 151) = 0.01, p = 0.94$; natural vs. darkened, $\chi^2(1, N = 154) = 0.10, p = 0.75$; lightened vs. darkened, $\chi^2(1, N = 155) = 0.16, p = 0.69$).

Results from these analyses did not support the hypotheses that the chimpanzees would prefer naturally colored swellings over pale swellings and would prefer slightly reddened sex swellings over pale or naturally colored sex swellings.

Although neither subject chose preferentially between sexual stimuli, both subjects chose preferentially between food stimuli (Subject A: $\chi^2(1, N = 225) = 165.55, p < 0.001$; Subject B: $\chi^2(1, N = 259) = 105.12, p < 0.001$).

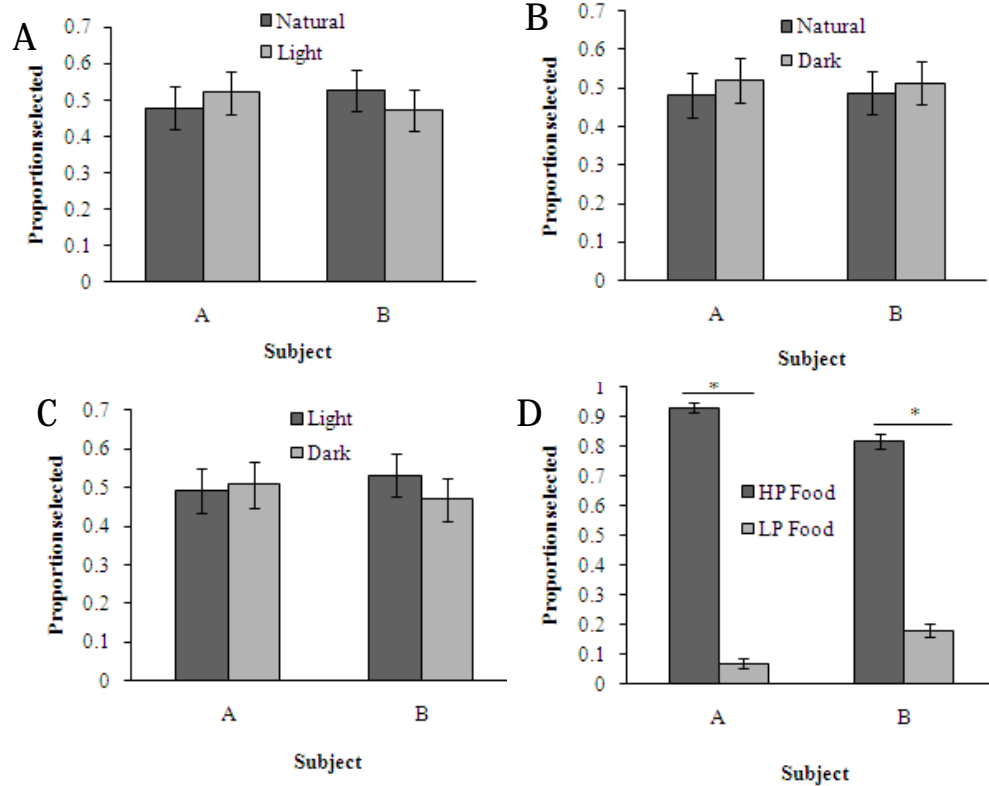


Figure 7. Proportion (\pm SE) of item selections by each subject for each stimulus pair type for Experiment Two: **A)** natural vs. light colored swelling trials, **B)** natural vs. dark colored swelling trials, **C)** light vs. dark colored swelling trials, and **D)** food preference trials. HP Food items were grape and cola for both subjects. LP Food items were broccoli for Subject A and celery for Subject B. * $p < 0.001$

Experiment Three: Size

As presented in Figure 8, neither subject chose the enlarged swelling more frequently than normal sized or reduced swellings. Chi square analysis revealed that Subject A pressed preferentially between normally sized swellings and enlarged swellings ($\chi^2(1, N = 87) = 6.08, p = 0.01$), though not in the direction expected. Rather, Subject A chose normally sized swellings more frequently than enlarged sized swellings. Subject A did not choose preferentially between normally sized and reduced swellings ($\chi^2(1, N = 87) = 0.93, p = 0.33$), or between reduced and enlarged swellings ($\chi^2(1, N = 90) = 1.60, p = 0.21$).

Unlike Subject A, Subject B did not press preferentially between normal sized and enlarged swellings, $\chi^2(1, N = 90) = 0.71, p = 0.40$. While Subject B did choose normally sized swellings more often than reduced swellings ($\chi^2(1, N = 89)$

= 4.96, $p = 0.02$), he did not choose preferentially between reduced and enlarged swellings ($\chi^2(1, N = 90) = 0.44, p = 0.83$).

Analysis revealed that these subjects together displayed a preference for normal over enlarged swellings ($\chi^2(1, N = 177) = 5.43, p = 0.02$), but displayed no preference for either normal over reduced ($\chi^2(1, N = 176) = 0.82, p = 0.37$) or reduced over enlarged swellings, $\chi^2(1, N = 180) = 0.56, p = 0.46$.

Both subjects continued to choose preferentially among food preference trials (Subject A: $\chi^2(1, N = 267) = 192.99, p < 0.001$; Subject B: $\chi^2(1, N = 267) = 70.30, p < 0.001$).

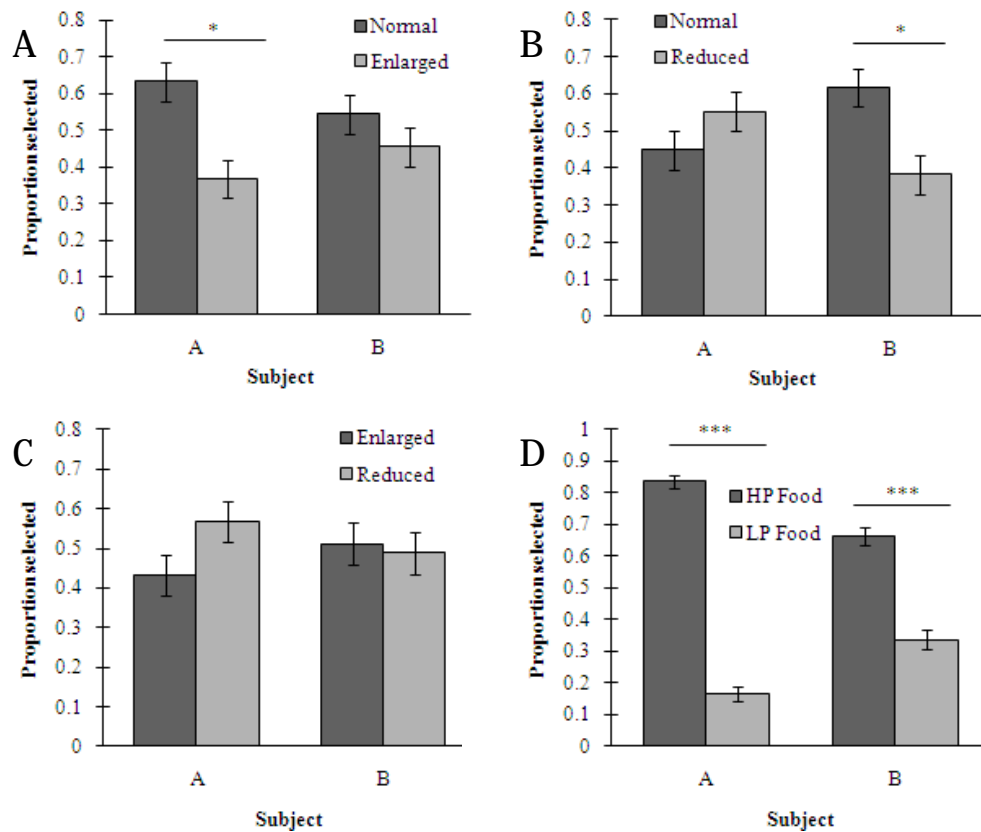


Figure 8. Proportion (\pm SE) of item selections by each subject for each stimulus pair type for Experiment Three: **A)** normal vs. enlarged size swelling trials, **B)** normal vs. reduced size swelling trials, **C)** enlarged vs. reduced size swelling trials, and **D)** food preference trials. HP Food items were grape and cola for both subjects. LP Food items were broccoli for Subject A and celery for Subject B. * $p < 0.05$

*** $p < 0.001$

Experiment Four: Symmetry

There was no strong preference for any symmetry variation by either subject within any stimulus pair, as depicted in Figure 9. Analysis of Subject A's choices revealed he displayed no preference between normal and symmetric

swellings, $\chi^2(1, N = 73) = 0.12, p = 0.73$, between normal and skewed swellings, $\chi^2(1, N = 73) = 0.01, p = 0.91$, or between symmetric and skewed swellings, $\chi^2(1, N = 74) = 0.22, p = 0.64$. Similarly, Subject B's choices reflected no preferences between normal and symmetric swellings, $\chi^2(1, N = 83) = 0.30, p = 0.58$, between normal and skewed swellings, $\chi^2(1, N = 85) = 0.11, p = 0.74$, or between symmetric and skewed swellings, $\chi^2(1, N = 81) = 0.01, p = 0.91$.

Further analysis revealed that the lack of preference for any symmetry variation remained when subjects' responses were combined (normal and symmetric swellings, $\chi^2(1, N = 156) = 0.41, p = 0.52$; normal and skewed swellings, $\chi^2(1, N = 158) = 0.03, p = 0.87$; symmetric and skewed swellings, $\chi^2(1, N = 155) = 0.06, p = 0.81$).

As in previous experiments, subjects preferentially chose high preference food items (Subject A: $\chi^2(1, N = 225) = 165.55, p < 0.001$; Subject B: $\chi^2(1, N = 257) = 111.13, p < 0.001$).

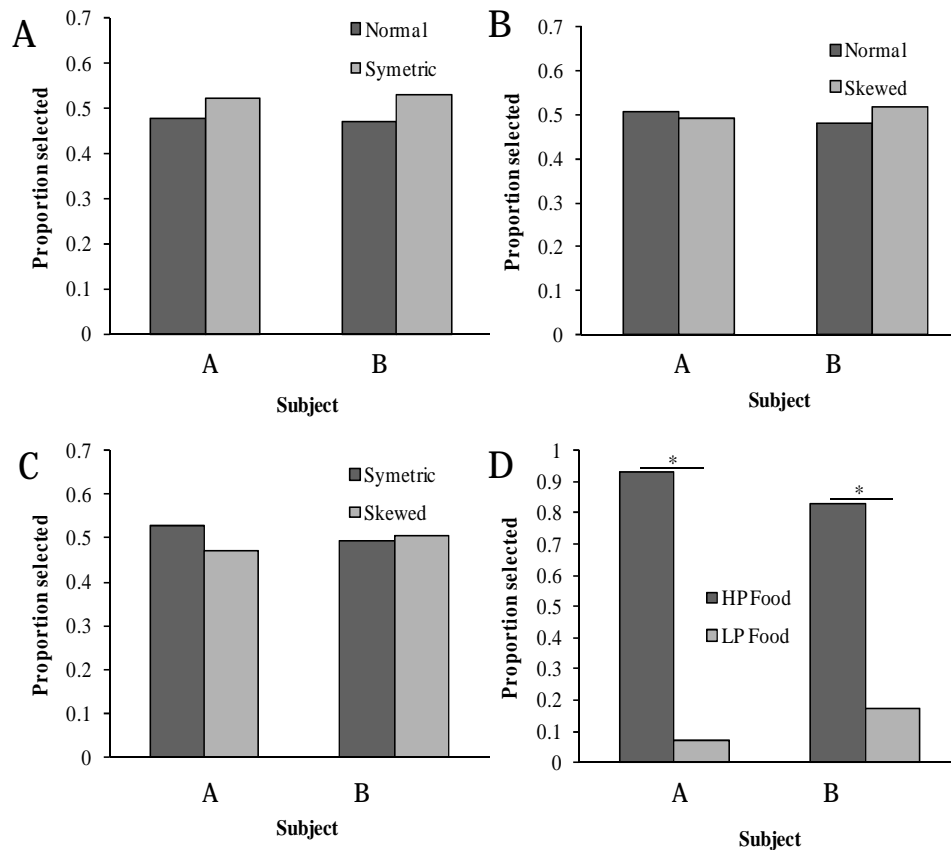


Figure 9. Proportion (\pm SE) of item selections by each subject for each stimulus pair type for Experiment Four: **A)** normal vs. symmetric shape swelling trials, **B)** normal vs. skewed shape swelling trials, **C)** symmetric vs. skewed shape swelling trials, and **D)** food preference trials. HP Food items were grape and cola for both subjects. LP Food items were broccoli for Subject A and celery for Subject B.

* $p < 0.001$

Discussion

The purpose of the present experiments was to evaluate chimpanzees' preferences for visual characteristics of sex swellings using a methodology validated for determining preferences of food items. We determined that male chimpanzees preferentially choose sex swellings and body parts over inanimate objects, but did not demonstrate a significant preference for swellings over other body parts although they did display a trend toward choosing swellings more often. The fact that the subjects continued to consistently choose their favored food item supports our conclusion that the animals are selecting their choices based on actual preferences.

Although the importance of color of secondary sex characteristics has been demonstrated in other species including rhesus macaques, chacma baboons, and gelada baboons (Bergman et al., 2009; Bielert et al., 1989; Waitt et al., 2006), our results do not indicate that the color of sex swellings, independent of other features, affects preference responding in our subjects. There does not appear to be a strong preference for any swelling color by either Subject A or Subject B. This unexpected finding may be explained by the possibility that the color manipulations created a stimulus which was unnatural in appearance and, thereby, unattractive to the males. However, this explanation should have resulted in the subjects' preference for normal colored swellings, which was not found. In humans, facial color is indicative of an individual's health (Stephen, Coetzee, Smith, & Perrett, 2009) and in other nonhuman primates, coloration of secondary sex characteristics indicates individual health, fertility, and in some cases social status (Bergman et al., 2009; Bielert et al., 1989; Waitt et al., 2006). Our results suggest, however, that among chimpanzees color may not serve the same functions. The pink swelling color in contrast to dark body hair and skin coloration may simply serve to attract the attention of male chimpanzees by color contrast and allow the males to identify individual females, an ability suggested from previous research (de Waal & Pokorny, 2008).

Contrary to research suggesting male chimpanzees prefer females with larger swellings (Deschner et al., 2004) and that supersized sex swellings are more attractive in other species (e.g., baboons, Bielert & Anderson, 1985), in our study, we did not find that chimpanzees preferred photographs of enlarged sex swellings. Similarly, while symmetrical morphological features play a role in sexual attractiveness in other species including humans (Moller & Thornhill, 1998; Perrett et al., 1999; Singh & Young, 1995; Thornhill & Gangestad, 1999; Waitt & Little, 2006) our study did not determine that chimpanzees prefer photographs of symmetrical sex swellings. The subjects' lack of preference for symmetrical stimuli may be a reflection on the method used in creating the stimuli which could have resulted in unnatural looking and unattractive sex swellings. Were this the case we would expect a preference for normal shaped swellings, but, as in the color experiment, subjects did not display such a preference.

Since neither color, size nor symmetry manipulations of photographs of sex swellings elicited preferential responding from the male chimpanzees in this study, we can not assume that these visual characteristics, when varied independently, were salient to the preference for sex swellings in general, as

demonstrated in Experiment One. It may be that the more relevant features of the sex swelling involve olfactory, tactile and/or behavioral cues, specifically female receptivity. For example, it is known that male chimpanzees concentrate mating efforts during the period of maximum tumescence when female chimpanzees are more receptive to male solicitation of sex and ovulation is likely (Deschner et al., 2004). Additionally, male chimpanzees often engage in tactile or olfactory investigation of female anogenital regions both in the context of sexual solicitation as well as nonsexual contexts. While previous research suggests that symmetrical faces and even facial skin tone are important components of sexual attractiveness in humans (Krupp, 2008; Little, Jones, DeBruine, & Feinberg, 2008; Miller & Todd, 1998; Perrett et al., 1999; Scheib, Gangestad, & Thornhill, 1999; Stephen et al., 2009), other studies suggest that in heterosexual human males short term mating strategies (Buss & Schmitt, 1993; Gangestad & Thornhill, 1997; Schmitt, 2005) for casual sex are based on female willingness rather than on facial symmetry, breast size or waist-to-hip ratio (Greer & Buss, 1994; Regan, Levin, Sprecher, Christopher, & Cate, 2000; Schmitt & Buss, 2001). Finally, motivational factors may have affected the subjects' responses in our study in that during food trials subjects were rewarded with the food selected where as subjects were not able to interact with a maximally tumescent female.

While many studies have investigated categorization or discrimination of visual stimuli in nonhuman primates (Bovet & Vauclair, 2000; Koba & Izumi, 2008; Spinozzi, Lubrano, & Truppa, 2004; Tanaka, 2001; Tomasello & Call, 1998; Vogels, 1999), few studies have investigated chimpanzee preference for visual stimuli. When visual preference has been investigated, methodology has recorded responses to images presented one by one or responses to arrays of multiple images. One study (Fujita & Matsuzawa, 1986) determined preference for photographs (i.e., Japanese scenery with or without humans) by comparing duration of push-button presses for individual images, while two other investigations (Tanaka, 2003, 2007) determined preference for photographs by recording how often an image was chosen first among an array of several images. No studies to date have investigated visual preference in a dichotomous free choice task. More importantly, no other research has verified preference assessment methodology by comparing previously ascertained preferences to performance on a computerized task. Our study is unique in that we first established food preferences to ensure that choices of the computerized stimuli actually reflected the individual chimpanzee's food preferences. The addition of experimental photographs of sexual stimuli to the established food preference procedure encouraged the chimpanzees to choose other photographic stimuli based on preference.

Although the current set of experiments was unable to definitively determine whether or not these two subjects discriminate between females on the basis of sex swelling color, size or symmetry, it is plausible that more naturalistic experimental methods conducted with a larger subject pool would elicit preferential choosing between females. Given equal willingness and readiness of females and equal health and fertility of females, males might then defer to assessments of attractiveness to choose between females.

Future research will focus on categorization of hormonal characteristics of intra-and interindividual variations in sex swellings characteristics. We will seek to determine whether males' preferences are related to hormonal characteristics that determine receptivity of individual females. In addition, we will test whether sex swellings of known versus unfamiliar females affects males' preference responding as well as behavior.

References

- Bergman, T., Ho, L., & Beehner, J. (2009). Chest color and social status in male geladas (*Theropithecus gelada*). *International Journal of Primatology*, *30*, 791-806.
- Bielert, C., & Anderson, C. M. (1985). Baboon sexual swellings and male response: A possible operational mammalian supernormal stimulus and response interaction. *International Journal of Primatology*, *6*, 377-393.
- Bielert, C., Girolami, L., & Jowell, S. (1989). An experimental examination of the colour component in visually mediated sexual arousal of the male chacma baboon (*Papio ursinus*). *Journal of Zoology*, *219*, 569-579.
- Bovet, D., & Vauclair, J. (2000). Picture recognition in animals and humans. *Behavioural Brain Research*, *109*, 143-165.
- Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, *100*, 204.
- Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2003). Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour*, *66*, 551-560.
- Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2004). Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. *Hormones and Behavior*, *46*, 204-215.
- de Waal, F., & Pokorny, J. (2008). Faces and behinds: Chimpanzee sex perception. *Advanced Science Letters*, *1*, 99-103.
- Dixson, A. (1998). *Primate sexuality: Comparative studies of the prosimians, monkeys, apes, and human beings*. Oxford: Oxford University Press.
- Emery, M. A., & Whitten, P. L. (2003). Size of sexual swellings reflects ovarian function in chimpanzees (*Pan troglodytes*). *Behavioral Ecology and Sociobiology*, *54*, 340-351.
- Fujita, K., & Matsuzawa, T. (1986). A new procedure to study the perceptual world of animals with sensory reinforcement: Recognition of humans by a chimpanzee. *Primates*, *27*, 283-291.
- Gangestad, S. W., & Thornhill, R. (1997). The evolutionary psychology of extrapair sex: The role of fluctuating asymmetry. *Evolution and Human Behavior*, *18*, 69-88.
- Gerald, M. S., Bernstein, J., Hinkson, R., & Fosbury, R. A. E. (2001). Formal method for objective assessment of primate color. *American Journal of Primatology*, *53*, 79-85.
- Greer, A. E., & Buss, D. M. (1994). Tactics for promoting sexual encounters. *Journal of Sex Research*, *31*, 185-201.
- Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science*, *218*, 384-387.
- Hirata, S., Fuwa, K., Sugama, K., Kusunoki, K., & Fujita, S. (2010). Facial perception of conspecifics: Chimpanzees (*Pan troglodytes*) preferentially attend to proper orientation and open eyes. *Animal Cognition*, *13*, 679-688.
- Kano, F., & Tomonaga, M. (2009). How chimpanzees look at pictures: A comparative eye-tracking study. *Proceedings of the Royal Society B*, *276*, 1949-1955.

- Koba, R., & Izumi, A. (2008). Japanese monkeys (*Macaca fuscata*) discriminate between pictures of conspecific males and females without specific training. *Behavioural Processes*, 79, 70-73.
- Krupp, D. B. (2008). Through evolution's eyes: Extracting mate preferences by linking visual attention to adaptive design. *Archives of Sexual Behavior*, 37, 57-63.
- Langlois, J. H., Kalakanis, L., Rubenstein, A. J., Larson, A., Hallam, M., & Smoot, M. (2000). Maxims or myths of beauty? A meta-analytic and theoretical review. *Psychological Bulletin*, 126, 390-423.
- Little, A. C., Jones, B. C., DeBruine, L. M., & Feinberg, D. R. (2008). Symmetry and sexual dimorphism in human faces: Interrelated preferences suggest both signal quality. *Behavioral Ecology*, 19, 902-908.
- Maynard-Smith, J., & Harper, D. (2004) *Animal signals*. Oxford: Oxford University Press.
- Miller, G. F., & Todd, P. M. (1998). Mate choice turns cognitive. *Trends in Cognitive Science*, 2, 190-198.
- Moller, A. P., & Thornhill, R. (1998). Bilateral symmetry and sexual selection: A meta-analysis. *American Naturalist*, 151, 174-192.
- Parr, L. A., Heintz, M., & Akamagwuna, U. (2006). Three studies on configural face processing by chimpanzees. *Brain and Cognition*, 62, 30-42.
- Parr, L. A., Waller, B., & Heintz, M. (2008). Facial expression categorization by chimpanzees using standardized stimuli. *Emotion*, 8, 216-231.
- Perrett, D. I., Burt, D. M., Penton-Voak, I. S., Lee, K. J., Rowland, D. A., & Edwards, R. (1999). Symmetry and human facial attractiveness. *Evolution and Human Behavior*, 20, 295-307.
- Regan, P. C., Levin, L., Sprecher, S., Christopher, F. S., & Cate, R. (2000). Partner preferences: What characteristics do men and women desire in their short-term sexual and long-term romantic partners? *Journal of Psychology & Human Sexuality*, 12, 1-21.
- Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceedings of the Royal Society B*, 266, 1913-1917.
- Schmitt, D. P. (2005). Fundamentals of human mating strategies. In D. M. Buss (Ed.), *The evolutionary psychology handbook* (pp. 258-291). New York: Wiley.
- Schmitt, D. P., & Buss, D. M. (2001). Human mate poaching: Tactics and temptations for infiltrating existing mateships. *Journal of Personality & Social Psychology*, 80, 894-917.
- Singh, D. (1995). Female judgment of male attractiveness and desirability for relationships: Role of waist-to-hip ratio and financial status. *Journal of Personality and Social Psychology*, 69, 1089-1101.
- Singh, D., & Young, R. K. (1995). Body weight, waist-to-hip ratio, breasts, and hips: Role in judgments of female attractiveness and desirability for relationships. *Ethology & Sociobiology*, 16, 483-507.
- Spinozzi, G., Lubrano, G., & Truppa, V. (2004). Categorization of above and below spatial relations by tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 118, 403-412.
- Stephen, I. D., Coetzee, V., Smith, M. L., & Perrett, D. I. (2009). Skin blood perfusion and oxygenation colour affect perceived human health. *PLoS ONE* 4, e5083. doi:10.1371/journal.pone.0005083
- Tanaka, M. (2001). Discrimination and categorization of photographs of natural objects by chimpanzees (*Pan troglodytes*). *Animal Cognition*, 4, 201-211.
- Tanaka, M. (2003). Visual preference by chimpanzees (*Pan troglodytes*) for photos of primates measured by a free choice-order task: Implication for influence of social experience. *Primates*, 44, 157-165.

- Tanaka, M. (2007). Development of the visual preference of chimpanzees (*Pan troglodytes*) for photographs of primates: Effect of social experience. *Primates*, 48, 303-309.
- Thompson, M. E. (2005). Reproductive endocrinology of wild female chimpanzees (*Pan troglodytes schweinfurthii*): Methodological considerations and the role of hormones in sex and conception. *American Journal of Primatology*, 67, 137-158.
- Thompson, M. E., & Wrangham, R. W. (2008). Male mating interest varies with female fecundity in *Pan troglodytes schweinfurthii* of Kanyawara, Kibale National Park. *International Journal of Primatology*, 29, 885-905.
- Thornhill, R., & Gangestad, S. W. (1999). Facial attractiveness. *Trends in Cognitive Sciences*, 3, 452-460.
- Tomasello, M., & Call, J. (1998) *Primate cognition*. Oxford: Oxford University Press.
- Vogels, R. (1999). Categorization of complex visual images by rhesus monkeys. Part 2: single-cell study. *European Journal of Neuroscience*, 11, 1239-1255.
- Waitt, C., Gerald, M. S., Little, A. C., & Kraiselburd, E. (2006). Selective attention toward female secondary sexual color in male rhesus macaques. *American Journal of Primatology*, 68, 738-744.
- Waitt, C., & Little, A. C. (2006). Preferences for symmetry in conspecific facial shape among *Macaca mulatta*. *International Journal of Primatology*, 27, 133-145.