A Zoo-housed Chimpanzee's (*Pan troglodytes*) Responses to Potentially Arousing Stimuli

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In Experiment 1, we wished to determine whether a singly-housed adult male captive chimpanzee could discriminate the behavioral categories of sex and aggression. He was reinforced for selecting sexual rather than aggressive images on a touch-screen computer in a two-choice discrimination paradigm. He showed no discrimination after 24 sessions with non-human photos, but immediately selected human sexual images at above-chance levels. To explore whether this differential discrimination was due to a preference for human sexual images, he was presented with images of humans versus non-humans under non-differential reinforcement in Experiment 2. He preferred human photos if the images depicted sex, but not if the images depicted aggression. To further explore these preferences in Experiment 3 the chimpanzee was presented with images of genitalia of non-humans versus humans, genitalia versus eyes, and finally female versus male genitalia of both non-humans and humans, using non-differential reinforcement. The chimpanzee preferred human to non-human genitalia, and eyes to genitalia, but did not prefer female to male genitalia. This chimpanzee's unusual social environment may have interfered with species-typical social preferences.

When primates are raised in captivity they may fail to show species-specific behaviors (Cross & Harlow, 1965; Harlow & Harlow, 1962; 1971; Harlow & Suomi, 1971). Even non-isolate monkeys raised in captivity may show atypical behaviors relative to their wild born counterparts. For example, nursery-reared monkeys showed deficiencies in the form and conduct of sexual behavior such as grooming each other less, frequent fights, and unusual postures never displayed by wild-born monkeys (Mason, 2008). Human-reared versus mother-reared captive chimpanzees exhibit more failed initiations of social behavior and less grooming bouts (Martin, 2005). More severe disruptions in behavior may be found in those raised in isolation. Individuals who are raised in social isolation, or in close contact with humans rather than conspecifics, can exhibit pronounced difficulties acquiring species-typical social behaviors and preferences (Cross & Harlow, 1965; Harlow & Harlow, 1971; Mallapur, Waran, Seaman, & Sinha, 2006; Tinklepaugh, 1928; Turner, Davenport, & Rogers, 1969). Socially isolated primates can be incompetent in social and sexual behavior relative to socially housed age-mates. For instance, infant and adolescent rhesus macaques that had been isolated from birth showed failures initiating and reciprocating the play and grooming behaviors of peers. As adults, they consistently exhibited abnormal sexual, aggressive and maternal behaviors. Total isolation for at least the first six months of life has been shown to damage or even destroy the subsequent development of typical social and sexual behavior (Harlow & Suomi, 1971). Some have even found deficits in cognitive ability following isolation compared to social rearing (Sánchez, Hearn, Do, Rilling, & Herndon, 1998). Even brief periods of social isolation (i.e., solitary confinement) have been shown to be enough to disrupt normal cognitive performance in rhesus macaques (Washburn & Rumbaugh, 1991). However Harlow and Schiltz (1967) reported that rhesus macaques showed deficits in social but not cognitive behavior. Thus, reported deficits in cognition are more

equivocal than deficits in social behavior. It is important to note however, as indicated in a more recent review (Saltzman & Maestripieri, 2011), that many decades of research ignored the important contributions of hormonal and biological influences, which can be affected by external stressors, such as the physical conditions of captive environments. Going forward, we must consider whether differences in primates that were mother-reared or human-reared are due to differences in opportunities for social learning or differences due to the effects of early biological and psychological stress.

Others have shown that maternal separation from six months to two years may not interfere with the development of normal sexual behaviors, at least in gibbons. However, the gibbons in this study developed more typical behavior if allowed to interact with young individuals close to their own age within 19 months of the separation (Mootnick & Nadler, 1997). Just one year of social-rearing may be enough to interrupt the disruption of normal maternal behavior in rhesus macaques (Schapiro, Bloomsmith, Suarez, & Porter, 1995). In addition, some have found that isolates are capable of normal reproductive behaviors (Meier, 1965). Maki, Fritz, and England (1993) found no differences in atypical social behaviors shown by captive chimpanzees reared either by their mothers or by human caregivers, but did find that, if the chimpanzees were sent away to another institution before the age of three, they exhibited more abnormal behaviors. Such findings support the idea that stress may be more critical than the absence of a natural mother or playmates. Martin (2005) also found few detrimental effects when comparing mother-reared to human-reared chimpanzees at five different zoos, with specific attention to initiation and maintenance of play and grooming. However, in an earlier study conducted at six zoos, socially deprived individuals demonstrated more atypical behaviors and a generally lower activity level (Martin, 2002). Rogers and Davenport (1969) found that isolate chimpanzees, unlike rhesus macaques, successfully mated with experienced partners later in life. They suggested that the involvement of humans may have more deleterious effects on chimpanzee sexual development as compared to social isolation. Thus, substituting a close bond with a human caregiver may do more harm than good if the chimpanzee cannot be raised by its own mother.

The majority of the research indicating deleterious effects of human-rearing or social isolation on primate development has been based on findings from rhesus macaques and chimpanzees. However, Sackett, Holm, and Ruppenthal (1976) demonstrated many years ago that there may be species differences in resilience to early social isolation, questioning the generalization of findings from rhesus macaques to even other closely related primates. Such research indicates the need for further work with a more diverse range of species. Importantly, Harlow's groundbreaking work in monkeys has been extended to the study of human behavior. Social isolation has been identified as an important factor in the development of abnormal social behavior in humans, as well as non-human primates (Blum, 2002).

Aside from the negative impact on social and reproductive behavior, studies have shown that human-rearing may influence non-human primates' spontaneous choice of photos under non-differential reinforcement. In these studies, captive chimpanzees and gibbons prefer photos of humans over members of their own species (Tanaka, 2003, 2007; Tanaka & Uchikoshi, 2010). Some species of macaque may also prefer images of the species they were foster-reared with, rather than members of their own species, again indicating how unique rearing experiences can alter typical preferences for two-dimensional images of conspecifics (Fujita, 1987b, 1993; Fujita & Watanabe, 1995; Fujita, Watanabe, Widarto, & Suryobroto,1997). In another study, mother-reared infant chimpanzees preferred faces of their own mother to that of another chimpanzee, but showed no preference for familiar over unfamiliar humans (Myowa-Yamakoshi, Yamaguchi,

Tomonaga, Tanaka, & Matsuzawa, 2005). Thus the preferences for humans may arise over time, and may be demonstrated only in chimpanzees not raised by their own mothers.

Experiments have shown that chimpanzees can visually discriminate humans as well as members from their own group (Martinez & Matsuzawa, 2009). Those with greater exposure to humans may be better at discriminating human than chimpanzee photos (Martin-Malivel & Okada, 2007). They may even show differential physiological responses to humans with whom they've had close contact, in that the pattern of heart rate response differs when exposed to photographs of human caregivers versus other familiar individuals or strangers (Boysen & Berntson, 1986). This study also revealed that apes showed a preference for viewing animals that they have a close social bond with when they were given an opportunity for direct visual access to conspecifics. Those that do not grow up with the opportunity for close social bonds would not show these typical preferences, and, in addition, fail to show typical behavior when presented with social situations. Macaques raised in social isolation may also be hindered in the ability to recognize different facial expressions in their peers (Geen, 1992), which would certainly lead to difficulties expressing appropriate behaviors in response to peers.

The chimpanzee subject in the current study, Joe, had an abnormal social rearing. In addition, he did not have a typical reaction to sexual stimuli. Even when briefly housed with a female chimpanzee he did not show typical arousal behavior. For instance, he did not attempt to mount or mate with a female when present, and did not show typical masturbatory behavior. However, he would show excitement and sexual arousal in the presence of familiar female human caretakers and researchers. Mootnick and Baker (1994) also observed that gibbons raised by humans and isolated from conspecifics early on were more likely to masturbate in the presence of humans. We wondered whether Joe may have bonded to humans rather than to chimpanzees, given that he was raised by humans and housed in captivity without access to other chimpanzees for years (Davis & Balfour, 1992). Although typically not demonstrated with primates, a variety of species will imprint on the first individual that they see after birth, rather than on members of their own species (Lorenz, 1935). In primates, including humans, individuals may demonstrate sexual imprinting, in which they are attracted to individuals similar to early close associates, such as parents (Bateson, 1979; Lorenz, 1965; Salzen, 1967). Fujita (2001) has argued that visual preferences are likely to reflect mating preferences. The goal of this study was to determine how a solitary, zoo-housed chimpanzee would respond to arousing stimuli of both humans and other apes. We examined preferences for human versus chimpanzee images in both sexual and non-sexual contexts.

It was predicted that Joe's behavior to arousing stimuli may reveal interesting patterns indicative of his abnormal rearing. For instance, he may show sexual arousal to provocative images of humans rather than non-humans, and fail to show aggressive responses to stimuli of non-humans engaged in aggressive behaviors. Others have found that rhesus macaques raised in social isolation may display more aggression and less sex (Mitchell, Raymond, Ruppenthal, & Harlow, 1966), suggesting reasons to suspect differences in both sexual and aggressive tendencies in isolated chimpanzees as well. However, Sackett (1966) suggested that responses to threat stimuli were innate in rhesus macaques, and were found equally disturbing by isolates and non-isolates, indicating that responses to aggressive stimuli may be less disrupted than responses to sexual stimuli. Kano, Tanaka, and Tomonaga (2008) showed that young chimpanzees raised by their mothers in social groups in captivity were more likely to remember images of chimpanzees depicting aggressive rather than neutral moods, again indicating that aggressive stimuli are highly salient to captive chimpanzees. Here, we exposed a singly-housed captive chimpanzee to sexual and aggressive images of both humans and non-human primates and measured his preference for

selecting different images under various comparisons. We used a forced choice procedure similar to that developed by Breaux, Watson, and Fontenot (2012), who demonstrated that choices for images in such a procedure reflect actual choices for real objects, such as food.

Experiment 1

In this experiment, the chimpanzee was presented with pairs of images on a touch-screen computer and reinforced for choosing an image that was sexual in nature and not reinforced for selecting stimuli that depicted aggression. In this manner, we could determine whether he discriminated these two types of photographs. In addition, we could determine whether learning was affected by whether the images were of humans or non-human apes.

Method

Subject

A zoo-housed adult male chimpanzee (*Pan troglodytes*), Joe, approximately 17 years of age participated in this study. Joe was singly-housed at the Mobile Zoo in Wilmer Alabama with access to an indoor and outside living area. Water was provided *ad libitum*. He was fed primate chow twice daily with fresh fruit and vegetables. No food adjustment procedures were used throughout testing. Joe came to the zoo from the entertainment industry where he had interacted with other chimpanzees but was not housed in a social group. His exact rearing history is unfortunately unknown. That is, it is unknown whether he was mother-reared or hand-reared, although, given that he worked in entertainment as a juvenile it is likely that he was hand-reared. He had lived alone for at least a decade, except for a two-year period where attempts were made to introduce him to an older female chimpanzee and her son, who were housed in an adjacent cage. Prior to this time, he had never mated with a female chimpanzee. Joe was housed first with the female, and then with the younger male for a period of several months. He was never observed to mate with the female during this time. Although we cannot know for certain whether any mating occurred – the female, who was in her thirties, was also never observed to display a full estrous swelling while in the care of the Mobile Zoo. She did occasionally however exhibit partial swelling. Joe had never lived in a typical chimpanzee social group. Joe had already participated in several other experiments using the touch-screen computer, including a study of natural category discrimination (Vonk, Jett, Mosteller, & Galvan, 2013), a study of social concepts (Vonk, in review) and a study of memory (Vonk & Mosteller, in press). Joe had also been trained on match-to-sample tasks, including a test of relational reasoning (unpublished data). Joe had been participating in the research program for approximately four years when this study began. Joe had been previously rewarded for selecting images of various primates, including both chimpanzees and humans, but had not previously viewed stimuli of a sexual nature. Thus, prior experience was not expected to affect current results. All procedures were in accordance with the University of Southern Mississippi IACUC and USDA regulations for animal care.

Testing Environment

Several objects were available for Joe's enrichment in his outdoor enclosure, such as a barrel, a bench to sit on, toys, and blankets. From Joe's outdoor enclosure he could view other primate enclosures and the zoo parking lot. The public could view Joe only from the outside enclosure. His indoor enclosure opened into a barn, in which he was housed opposite a Himalayan black bear and various other animals on a temporary basis. It was in this indoor area that the experiments were conducted. The touch-screen was raised and presented against the open bars of Joe's enclosure where he could sit on a bench during testing. Joe was free to move within and between the indoor and outdoor area during testing.

Materials

The subject's food rewards consisted of dried fruits. A variety of color images downloaded from the internet and cropped to 400 x 600 pixels were presented via a Panasonic Toughbook computer CF18 on a 21" capacitive touch screen that was mounted in a hydraulic lift cart. Images were presented in a two-choice discrimination procedure that was programmed using Real Basic software. The images varied between experiments. In Experiment 1, 80 photographs were selected from the broad categories of aggression ($N = 40$) and sex ($N = 40$). Within the category of aggression,

there were two sub-categories; fighting ($N = 20$) and displaying ($N = 20$). Within the category of sex, there were two sub-categories of mating ($N = 20$) and estrus ($N = 20$). Within each of these subcategories, half of the photographs were of humans and half were of non-human primates, primarily chimpanzees, but also some bonobos, gorillas and orangutans. This was due to the greater difficulty obtaining adequate high resolution images of chimpanzees that had not been presented to the subject previously (Vonk et al., 2013). Thus, there were eight sub-categories of ten photos each, totaling 80 photographs, generally grouped into four categories of 20 photos each; human aggression (fighting and displaying), human sex (mating and presenting in a provocative way), non-human aggression (fighting and displaying), non-human sex (mating and images of estrus female or erect males). Although the photographs were not standardized in terms of background, contrast, brightness etc., this variability is more in line with real life experiences where objects encountered appear in varying conditions and within various contexts. Furthermore, Breaux et al. (2011) have shown that chimpanzees' preference for images of sexual swellings is not affected by size, symmetry, or color despite the fact that they generally preferred images of sexual swellings. Sample images from Experiments 1-3 are depicted in Figure 1.
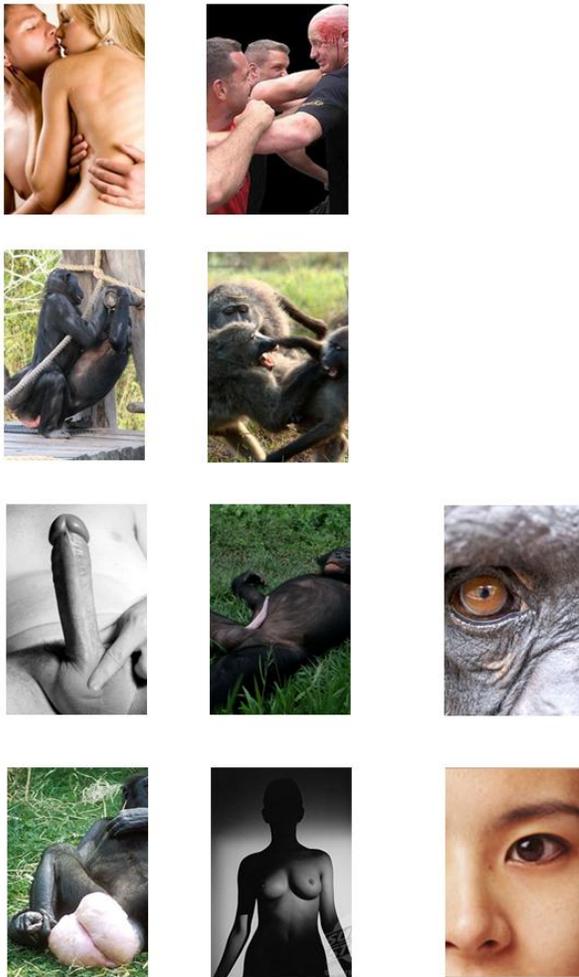
Figure 1. Sample images used in Experiments 1-3. From top to bottom (left to right), human sex versus aggression, non-human sex versus aggression, human versus non-human male genitalia versus eyes/face, nonhuman versus human female genitalia body parts versus eyes/face. Images in the two top rows were used in both Experiments 1 and 2. Images in the two bottom rows were used in Experiment 3.

Procedure

These experiments utilized the two-choice discrimination used previously by Vonk and MacDonald (2002, 2004) and Vonk et al. (2013), and similar to the push button forced choice procedure of Breaux et al. (2011). The chimpanzee had already been trained on the procedure in previous experiments. Each session consisted of twenty trials in which the chimpanzee was presented with pairs of photographs; one member of each pair representing one of two different categories. On each trial, a photo from each category was presented, randomly paired and randomly ordered with side presentation of each category counterbalanced within the session. On each trial the subject selected by touching one of the images and was rewarded with a pleasant tone and a food reward for touching an image from the S+ category. He received an unpleasant buzz sound and no reward if he touched a photo from the S- category. The experimenter viewed the subject's responses on a laptop placed behind the touch screen monitor and stepped forward to hand the chimpanzee food rewards immediately following his response. However, the experimenter could not see the subject making the response and thus did not cue or prompt his responses.

Each session consisted of twenty trials in which selecting/touching images of sex/estrus were reinforced and touching images of aggression (fighting and displaying) were not reinforced. Twenty images each of non-human sex, mating ($n = 10$) and estrus ($n = 10$), were randomly paired with twenty images each of non-humans aggression, fighting ($n = 10$) and displaying ($n = 10$), such that, on each trial, one sex photo and one aggression photo was presented, with side counterbalanced. After 24 sessions with the non-human stimuli, Joe was still performing at chance levels, so it was decided to present him with the human stimuli (20 images each of human sex, mating ($n = 10$) and presenting provocatively ($n = 10$), versus twenty images each of human aggression, fighting ($n = 10$) and displaying ($n = 10$) to ascertain whether his choices would differ with human stimuli, regardless of not having "learned" the discrimination with non-human stimuli. All statistical tests were two-tailed.

Results

After 24 sessions Joe did not learn to select sex versus aggression images with non-human stimuli, but, when given human photos, he was above chance immediately (on first session, 85% correct, binomial test, $p = 0.003$). He required only eight sessions to meet criterion of an average of 80% within a block of four sessions. Thus, Joe immediately learned to touch the human sex versus aggression photos but demonstrated no such learning with non-human sex versus aggression photos (Figure 2). A binomial test revealed chance performance for non-human pictures across all trials, ($N = 480$ trials, $p = 0.96$, $M = 46.04$, $SD = 0.09$), while he was above chance selecting sex images with human pictures ($N = 160$ trials, $p < 0.001$, $M = 79.38$, $SD = 0.08$). A paired t-test confirmed that performance on the two tasks was not equivalent, ($t (7) = 5.88$, $p = 0.001$, CI: -8.59 - 3.66).

Because we included both chimpanzee and non-chimpanzee images in all categories of images, we were concerned that Joe's difficulty discriminating the non-primate photos might have been due in part to the use of non-chimpanzee images. Thus, we calculated the likelihood that he selected images of both chimpanzees and non-chimpanzees in each of the four categories of non-human images. We include that information in the Appendix that contains information about all images used in the study. One can see that Joe was not more likely to select chimpanzee images, either when those images belonged to the reinforced category of sexual images, or the non-reinforced image of aggressive images. Just to be sure, we conducted paired t-tests to compare Joe's selections of chimpanzee versus non-chimpanzee images in both the sex and aggression categories broadly and found both tests non-significant (both t's < 1.1, both p's > 0.34).
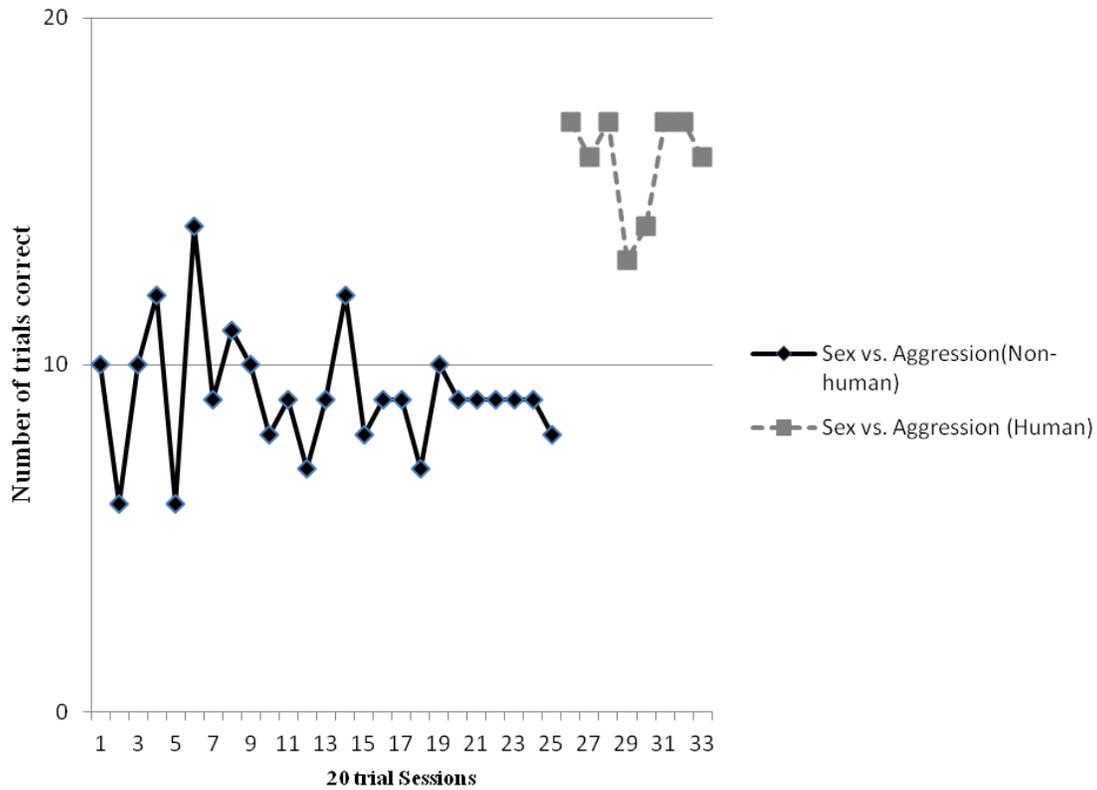
Figure 2. Number of correct trials across sessions when reinforced for choosing images of a sexual rather than aggressive nature, first with non-human (primarily chimpanzee) photos – then with photos of humans (Exp. 1). The solid line indicates chance performance.

Discussion

Because Joe had not previously shown expected arousal to the presence of a female chimpanzee, but had shown arousal in the presence of familiar humans and during aggressive threat displays, we were curious about his ability to differentiate between threatening/aggressive and sexual stimuli. Therefore, in Experiment 1, Joe was reinforced for choosing an image that was sexual in nature but not reinforced for choosing aggressive stimuli. He demonstrated an immediate bias to select human sexual photos, as indicated by immediate above chance levels of selection for sexual stimuli on the first session, despite not having learned to choose sex images with non-human images. This finding supported our anecdotal observations that Joe was not interested in female chimpanzees, even in estrus, and made us wonder whether Joe was more attracted to or interested in humans than other chimpanzees. However, we also wondered if Joe did not show a distinction between sex and aggression photos with non-humans because aggressive stimuli of non-humans might be more salient than aggressive stimuli of humans. Chimpanzees may find aggression photos more arousing or salient than sex photos, but only when they depict members of their own or closely related species.

Experiment 2

We hypothesized that Joe's bias to select human sexual over aggression images and the lack of such a bias with non-human images might be due to the fact that non-human aggression images were particularly salient, whereas human aggression images may not be. Thus, in Experiment 2, we directly paired human versus non-human aggression images. In addition, in order to more directly test Joe's preference for human versus non-human sexual images, we paired these two sets of images in a separate discrimination task.

Method

This experiment followed the same basic procedure as Experiment 1, with the same subject.

Materials

The same images as those that were used in Experiment 1 were presented again here except that all of the human sex photos were paired with all of the non-human sex images, and all of the human aggression images were paired with the non-human aggression images to create two discriminations; one in which Joe discriminated between human and non-human sexual images, and one in which he discriminated between human and non-human aggressive images.

Procedure

The procedure was identical to Experiment 1, except that non-differential reinforcement was used such that Joe was given a reward regardless of which photo he selected on each trial, as in Breaux et al. (2011) and Tanaka (2003, 2007). In addition, no criterion was applied. Joe was presented with only four sessions with both the sexual and the aggression discriminations to ascertain his spontaneous preferences. We calculated his choices of humans with the sex images, and of non-humans with the aggression photos.

Results

Follow-up tests revealed that performance in Experiment 1 was not due to a greater interest in non-human (relative to human) aggression photos, as pairing these two sets of images resulted in chance performance (50% on the first session, binomial test, $p = 1.0$ and 42.5% across four sessions, $p = 0.22$). However, pairing the human and non-human sex photos still resulted in a preference for the human sex photos (80% on the first session, binomial test, $p = 0.01$, and 81.25% across four sessions, $p < 0.001$). See Figure 3. Because side location of each type of stimulus was counterbalanced, it is clear that Joe did not simply adopt a position bias. Examination of the data confirms this. Choices were randomly distributed between left and right side options across sessions. A paired t-test confirmed that performance on the two tasks was not equivalent, ($t (3) = 7.52, p = 0.005, CI: 4.47 – 11.03$).
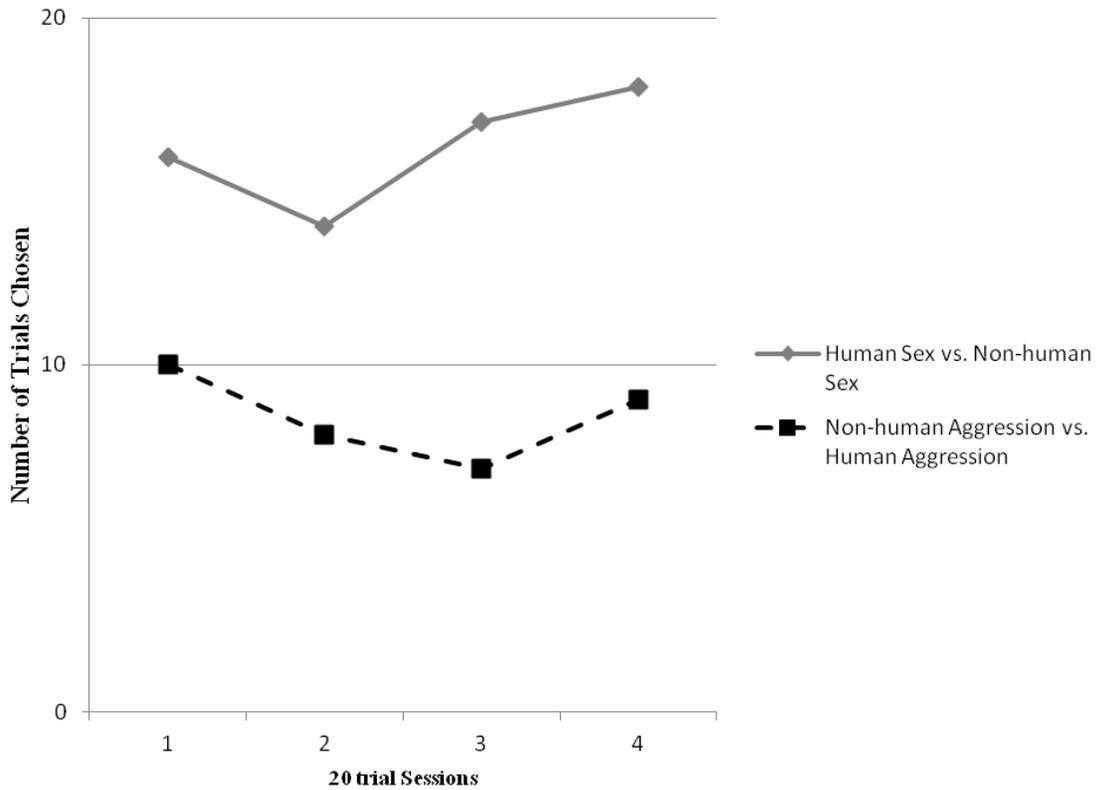
Figure 3. Number of trials on which human images were chosen when presented with human versus chimpanzee photos depicting sex and number of trials on which chimpanzee images were chosen when presented with human versus chimpanzee photos depicting aggression, using non-differential reinforcement (Exp. 2).

Discussion

Joe's differential performance with sexual and aggressive images depicting different species in Experiment 1 cannot be attributed to greater salience or interest in aggression images when these images involved members of his own species and other non-human primates, because he showed no preference for these photos when they were paired with human aggression photos. Yet, he preferred the human sexual photos over the non-human sexual photos when given the chance to choose between them. These findings cannot be due to the prior reinforcement of sex photos in Experiment 1 because selection of both human and non-human sex photos was reinforced in that experiment. This finding was consistent with his random choices when non-human sex images were paired with non-human aggression images, and his above-chance selection of human sex photos in Experiment 1. Other captive primates have shown similar preferences for photos of humans (Tanaka, 2003; 2007; Tanaka & Uchikoshi, 2010), but in those experiments the photos were not specifically of a sexual or aggressive nature. Of course it will be necessary to compare these responses to those of chimpanzees raised in more species-typical chimpanzee social groups in order to draw firm conclusions regarding the possible basis for such preferences, but these results, along with the prior findings reported here, are suggestive with regard to potentially damaging effects of long-term social isolation on the development of species typical preferences.

Experiment 3

Joe's choices on the previous discriminations left us with a number of questions concerning which area of the images he had focused on to determine his choices. We were curious as to whether Joe would prefer images of humans to chimpanzees when the images focused on areas of the body relevant to sexual behavior (such as genitalia) versus if the images simply showed the eyes – a very salient part of the face. Thus, the preference for human photos may not indicate a sexual preference specifically. We were also curious as to whether he was generally interested in the sexual part of the body, regardless of whether it was male or female, as sexual arousal as indicated by a male's erect penis could also be an important signal for male chimpanzees to attend to, or whether he preferred images of female genitalia. These discriminations would allow us to determine the extent to which Joe's choices might simply reflect general arousal rather than sexual preferences per se. Along with Breaux et al.'s (2011) finding that forced choices match real life choices, Fujita (2001) indicated that preferences for photographs might reflect behavioral sex preferences as well. Thus, there is a precedent for using forced choice procedures depicting images to infer an organism's preference for those real life objects.

Method

Subject

The same chimpanzee who participated in Experiments 1 and 2 participated in the current experiment.

Materials

For this experiment, novel images were downloaded and cropped to 600 X 400 mp. The first discrimination involved pairing 20 images of chimpanzee body parts with 20 images of human body parts. The photos depicted genitalia, breasts and rumps of both species. We calculated how often Joe chose the chimpanzee images. For the second discrimination, ten of the images of human body parts and ten of the images of chimpanzee body parts were included together into one set of images of body parts and twenty images of human and chimpanzee eye regions were combined together into a set of eye images. We calculated how often Joe selected the body part images. For the third discrimination, we selected some of the best images of male and female body parts from the previous sets, but also included more novel images including chest, rump and genital regions to create two sets of images; one of male chimpanzee and human body parts and one of female chimpanzee and human body-parts. We calculated how often Joe selected female over male body parts. Joe completed eight sessions of each discrimination under non-differential reinforcement before he began the next one.

Procedure

This experiment followed the same procedure as Experiment 2, except that Joe was presented with eight sessions of three different discriminations; chimpanzee versus human genitalia, breasts and rumps, genitalia versus eyes (both human and non-human), and female versus male genitalia of both humans and chimpanzees.

Results

On the first session of the first two discriminations (non-human versus human body parts and body parts versus eyes) Joe's selections of non-human and human body parts was at chance, 35%, $p = 0.26$. He also chose randomly on the first session of the third discrimination between female and male body parts, 50%, $p = 1.0$. Across all eight sessions of discriminating non-human versus human body parts, Joe chose the non-human images at below chance levels ($M = 40.56\%$,

$p = 0.01$, $N = 180$) indicating an above chance preference for images of human genitals. However, when images of genitalia were contrasted with images of eyes (using a mixture of both human and non-human images), Joe also chose the images of genitalia at below-chance levels ($M = 41.88\%$, $p = 0.05$, $N = 160$) indicating that he preferred to choose the images of the eyes. Lastly, when he was presented with images of female versus male genitalia of both humans and non-humans, he revealed no preference for female genitalia ($M = 46.25\%$, $p = 0.39$, $N = 160$). See Figure 4.
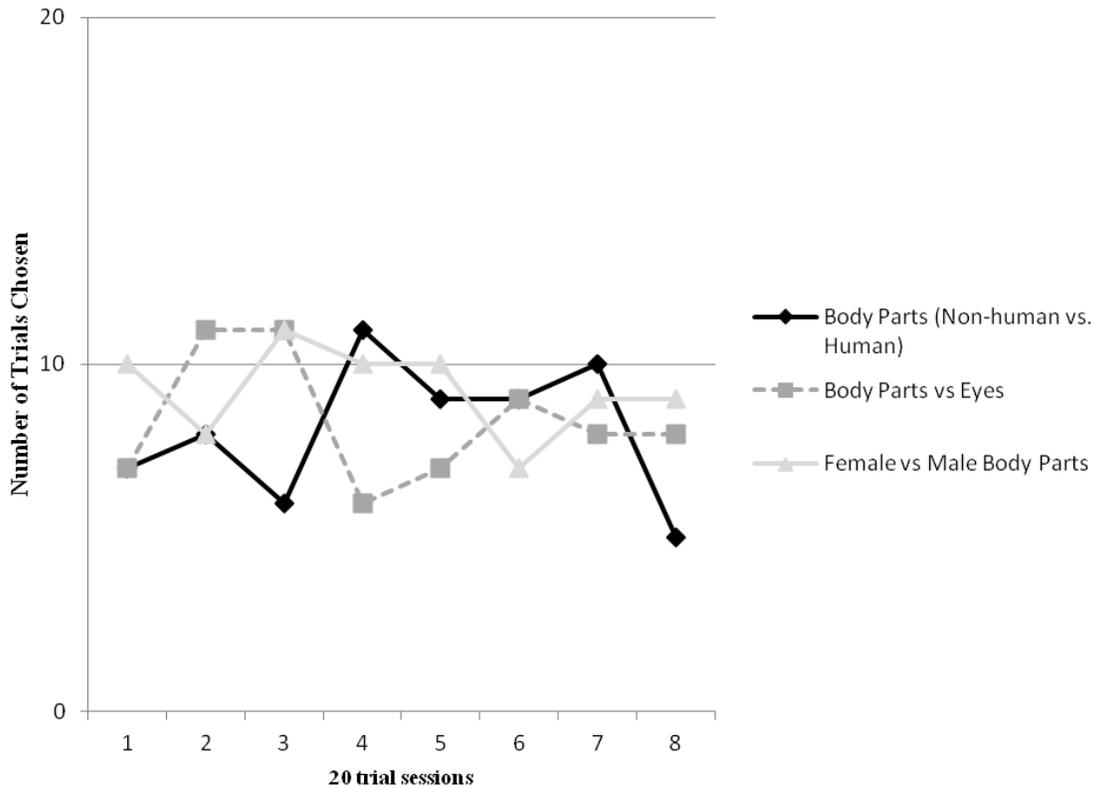
Figure 4. Number of trials on which images of chimpanzee genitalia were selected when presented with human genitalia, when images of genitalia were selected when presented with images of faces, and number of trials on which images of female versus male genitalia were selected, using non-differential reinforcement (Exp. 3).

Discussion

Joe had initially preferred photos of humans to non-humans when the individuals in the photographs were engaged in sexual behavior (Exp. 2). He continued to prefer images of humans even when only genital areas and parts of the chest and rump were shown. However, it appears that he had a slight preference for images of the facial region, namely the eyes, rather than for images of genitalia, breasts, and rumps. In addition, he did not show a preference for selecting images of females over males, when images of both species were presented. However, we cannot conclude that Joe simply had a general preference for photos of humans, over those of non-humans, regardless of context, because this same preference was not demonstrated when aggressive photos only were paired (Experiment 2). However, those photos depicted largely males, so it is possible his preference was for human females, regardless of whether they were

shown in provocative poses or not. Thus, we can conclude only regarding Joe's general preference for images of human females over non-humans and cannot suggest that this preference is specific to sex preferences. This is an important finding as it contradicts that of Breaux et al. (2011) who found that socially housed male chimpanzees preferred images of sexual swellings to other parts of the body. Because these chimpanzees were nursery-reared but later housed in social groups, the findings, taken together, suggest that adult socialization and sexual experience may be more critical to the development of species and sexual preferences than early rearing environment.

General Discussion

Despite prior research emphasizing the salience of aggressive stimuli to both rhesus macaques (Sackett, 1966) and chimpanzees (Kano et al., 2008), Joe preferred images of a sexual nature to those depicting aggression, but only if the images were of humans. This preference was not due to the fact that aggressive images were more salient if they depicted non-humans rather than humans, as Joe showed no preference for aggressive photos of non-humans over humans. He did continue to prefer photos of humans versus other primates when the photos were sexual in nature, or explicitly focused on the genital region, breasts and rump area. It appears that Joe preferred to touch photos of human females, although he did not prefer female over male genitalia when those images were comprised of both human and chimpanzee images. The preference did not appear to be specific to sexual images, as Joe generally preferred photos of eyes to photos of genitalia. Joe's preference for human over non-human images is consistent with data from other chimpanzees (Tanaka, 2003, 2007) and a gibbon (Tanaka & Uchikoshi, 2010) raised in captivity. It is likely that captive rearing, especially human-rearing, or being housed in isolation, disrupts normal species-specific preferences for images of members of one's own species (Fujita, 1987, 1993b; Fujita & Watanabe, 1995; Fujita et al.,1997).

Tanaka (2007) showed that adult, but not young chimpanzees preferred images of humans to other primates regardless of whether they were born in the wild or captivity. Regardless of origin, all adults had been primarily raised by humans, while the younger chimpanzees were mother-reared. Tanaka concluded that the human preference may depend on socialization, rather than being innate or the result of imprinting. Comparisons between our subject's preference and that of the socially housed males in Breaux et al. (2011) support that conclusion. It is possible that the preference for humans depends on the quality and not quantity of human relationships. Fujita (1987, 1990) found that rhesus macaques, but not Japanese macaques, preferred members of their own species. He suggested that, because of their geographical isolation, the mechanism of psychological isolation leading to conspecific preference wasn't necessary in order to ensure that Japanese macaques mated with only members of their own species. Because chimpanzees are geographically isolated from their closest relatives, the bonobos, it is possible there is no innate conspecific preference in chimpanzees either (see also Tanaka, 2007). Most studies investigating species preferences have focused on captive individuals with close relationships with humans. Control individuals are needed to determine the role of human relationships in driving the preference for humans.

Given that only a single subject with an atypical yet partially unknown rearing history was tested in these experiments, and there is no equivalent data from a socially-housed mother-reared chimpanzee with which to compare Joe's results, it would be premature to draw conclusions regarding the effects of abnormal rearing on chimpanzee preferences in general. However, in this study we expanded upon prior research to investigate whether apparent

preferences for human over non-human images are limited to sexual contexts, or more general. In addition, we explored whether Joe preferred selecting images of genitalia to images of the eye region, further specifying whether the preferences reflected mate preferences, or general preferences. Given that Joe preferred human to non-human images in a sexual but not an aggressive context and preferred human to non-human genitalia, but generally preferred images of eyes to images of genitalia and did not prefer images of female to male genitalia, we cannot speculate regarding the extent to which his preferences for these two dimensional images translate to his sexual preferences. We think this data is important, although preliminary, to demonstrate how this methodology can be utilized to gauge chimpanzees' (and other primates') interests and preferences, and to explore those preferences further. It will also be important to examine whether non-human primates' choices with two-dimensional pictorial stimuli really do translate to mating preferences, as noted by Fujita (2001). The present results indicate in more detail the nature of a chimpanzee's preference for human photos, in specific contexts such as sex and aggression and further investigated whether the chimpanzee distinguished between sex-related body parts and facial features, or between images of animals of different sexes. These results can indicate further whether the preference is related to mating preferences or is instead a general species preference. We hope that these studies will inspire others with access to more diverse populations to further explore these questions, as more data is needed with more individuals of diverse rearing backgrounds to better understand the effects of atypical rearing and housing practices on species preferences.

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Appendix

Table 1

Detailed description of image features

Exp.	Set	Image	Reinforced	Species/Race	Times Selected	Clothing Present	Body/Face	New
1	1	Non-human mating	+	Chimpanzee	1	N	Body	Y
	1		+	Macaque	19	N	Body	Y
	1		+	Chimpanzee	16	N	Body	Y
	1		+	Macaque	12	N	Body	Y
	1		+	Chimpanzee	6	N	Body	Y
	1		+	Chimpanzee	16	N	Body	Y
	1		+	Chimpanzee	13	N	Body	Y
	1		+	Bonobo	18	N	Body	Y
	1		+	Macaque	18	N	Body	Y
	1		+	Macaque	7	N	Body	Y
	1	Non-human estrus	+	Macaque	20	N	Body	Y
	1		+	Chimpanzee	1	N	Rump	Y
	1		+	Chimpanzee	19	N	Body	Y
	1		+	Chimpanzee	9	N	Vulva	Y
	1		+	Chimpanzee	11	N	Body	Y
	1		+	Macaque	6	N	Body	Y
	1		+	Chimpanzee	4	N	Vulva	Y
	1		+	Chimpanzee	5	N	Body	Y
	1		+	Macaque	1	N	Lower body	Y
	1		+	Chimpanzee	17	N	Body	Y
	1	Non-human display	-	Chimpanzee	12	N	Face	Y
	1		-	Bonobo	12	N	Body	Y
	1		-	Chimpanzee	14	N	Body	Y
	1		-	Orangutan	18	N	Body	Y
	1		-	Chimpanzee	12	N	Face	Y
	1		-	Chimpanzee	7	N	Face	Y
	1		-	Gorilla	14	N	Face	Y
	1		-	Orangutan	10	N	Body	Y
	1		-	Baboon	15	N	Body	Y
	1		-	Gorilla	18	N	Upper body	Y
	1	Non-human fighting	-	Chimpanzee	9	N	Body	Y
	1		-	Baboon	9	N	Upper body	Y
	1		-	Macaque	10	N	Body	Y
	1		-	Chimpanzee	12	N	Body	Y
	1		-	Gelada Baboon	16	N	Upper body	Y
	1		-	Macaque	3	N	Upper body	Y
	1		-	Gorilla	18	N	Body	Y

	1		-	Macaque	13	N	Upper body	Y
	1		-	Macaque	15	N	Upper body	Y
	1		-	Chimpanzee	17	N	Body	Y
	2	Human mating	+	White		Y	Upper Body	Y
	2		+	White		Y	Body	Y
	2		+	White		Y	Upper Body	Y
	2		+	White		Y	Upper Body	Y
	2		+	White		N	Upper Body	Y
	2		+	White		N	Upper Body	Y
	2		+	White		N	Body	Y
	2		+	Latino		Y	Upper Body	Y
	2		+	White		Y	Upper Body	Y
	2		+	White		N	Upper Body	Y
	2	Human estrus	+	White		N	Upper Body	Y
	2		+	White		Y	Upper Body	Y
	2		+	White		Y	Upper Body	Y
	2		+	White		N	Face	Y
	2		+	White		N	Face	Y
	2		+	White		N	Face	Y
	2		+	White		N	Upper Body	Y
	2		+	Latino		Y	Upper Body	Y
	2		+	White		N	Face	Y
	2		+	white		Y	Body	Y
	2	Human display	-	White		Y	Body	Y
	2		-	White		Y	Body	Y
	2		-	White		Y	Body	Y
	2		-	Black		Y	Body	Y
	2		-	Black		Y	Body	Y
	2		-	White		Y	Body	Y
	2		-	Black		N	Body	Y
	2		-	White		N	Body	Y
	2		-	White		N	Upper Body	Y
	2		-	White		Y	Body	Y
	2	Human fighting	-	White		Y	Upper Body	Y
	2		-	White		N	Body	Y
	2		-	White		Y	Upper Body	Y
	2		-	White		Y	Body	Y
	2		-	White		Y	Body	Y
	2		-	White		Y	Body	Y
	2		-	White		Y	Body	Y
	2		-	White		N	Upper Body	Y
	2		-	White		Y	Body	Y
	2		-	White		Y	Body	Y
2	1	Human sex	Non-differential	Same as above		Same as above	Same as above	N
		Non-human sex	Non-differential	Same as above		Same as above	Same as above	N

	2	Human aggression	Non-differential	Same as above	Same as above	Same as above	N
		Non-human aggression	Non-differential	Same as above	Same as above	Same as above	N
3	1	Chimp body	Non-differential	Chimp	No	Body	Y
			Non-differential	Chimp	No	Body	Y
			Non-differential	Chimp	No	Body	Y
			Non-differential	Chimp	No	Upper body	Y
			Non-differential	Chimp	No	Face	Y
			Non-differential	Chimp	No	Face	Y
			Non-differential	Chimp	No	Face	Y
			Non-differential	Chimp	No	Face	Y
			Non-differential	Chimp	No	Face	Y
			Non-differential	Chimp	No	Penis only	Y
			Non-differential	Chimp	No	Body	Y
			Non-differential	Chimp	No	Penis only	Y
			Non-differential	Chimp	No	Body	Y
			Non-differential	Chimp pale	No	Penis only	Y
			Non-differential	Chimp	No	Body	Y
			Non-differential	Chimp	No	Lower body	Y
			Non-differential	Chimp	No	Lower body	Y
			Non-differential	Chimp	No	Lower body	Y
			Non-differential	Chimp	No	Lower body	Y
			Non-differential	Chimp	No	Lower body	Y
			Non-differential	Chimp	No	Lower body	Y
		Human body	Non-differential	White	N	Breast only	Y
			Non-differential	B&W dark	N	Body	Y
			Non-differential	White	Y	Upper body	Y
			Non-differential	White	Y	Upper body	Y
			Non-differential	White	N	Face	Y
			Non-differential	White	N	Face	Y
			Non-differential	White	N	Face	Y
			Non-differential	White	N	Face	Y
			Non-differential	Asian	N	Face	Y
			Non-differential	white	N	Face	Y
			Non-differential	White	N	Penis only	Y
			Non-differential	Black	N	Penis only	Y
			Non-differential	White	Y	Penis only	Y
			Non-differential	White	N	Penis only	Y
			Non-differential	White	N	Penis only	Y
			Non-differential	White	N	Vulva only	Y
			Non-differential	B&W	N	Vulva only	Y
			Non-differential	White	N	Vulva only	Y
			Non-differential	White	N	Body	Y
			Non-differential	White	N	Buttocks	Y
	2	Human Genitals	Non-differential	White	N	Penis only	N
			Non-differential	Black	N	Penis only	N

		Non-differential	White	Y	Penis only	N
		Non-differential	White	N	Penis only	N
		Non-differential	White	N	Penis only	N
		Non-differential	White	N	Vulva only	N
		Non-differential	B&W	N	Vulva only	N
		Non-differential	White	N	Vulva only	N
	Chimp Genitals	Non-differential	Chimp	No	Penis only	N
		Non-differential	Chimp	No	Body	N
		Non-differential	Chimp	No	Penis only	N
		Non-differential	Chimp	No	Body	N
		Non-differential	Chimp pale	No	Penis only	N
		Non-differential	Chimp	No	Body	N
		Non-differential	Chimp	No	Lower body	N
		Non-differential	Chimp	No	Lower body	N
		Non-differential	Chimp	No	Lower body	N
		Non-differential	Chimp	No	Lower body	N
		Non-differential	Chimp	No	Lower body	N
		Non-differential	Chimp	No	Lower body	N
2	Chimp Eyes	Non-differential	Chimp	No	Face	Y
		Non-differential	Chimp	No	Face	Y
		Non-differential	Chimp	No	Face	Y
		Non-differential	Chimp	No	Face	Y
		Non-differential	Chimp	No	Face	Y
		Non-differential	Chimp	No	Face	Y
		Non-differential	Chimp	No	Face	Y
		Non-differential	Chimp	No	Face	Y
		Non-differential	Chimp	No	Face	Y
		Non-differential	Chimp	No	Face	Y
		Non-differential	Chimp	No	Face	Y
	Human eyes	Non-differential	White	N	Face	N
		Non-differential	White	N	Face	N
		Non-differential	White	N	Face	N
		Non-differential	White	N	Face	N
		Non-differential	Asian	N	Face	N
		Non-differential	White	N	Face	N
		Non-differential	White	N	Face	Y
		Non-differential	White	Y	Face	Y
		Non-differential	Indian	N	Face	Y
3	Female Genitals	Non-differential	White	N	Vulva only	N
		Non-differential	B&W	N	Vulva only	N
		Non-differential	White	N	Vulva only	N
		Non-differential	Chimp	N	Lower body	N
		Non-differential	Chimp	N	Lower body	N
		Non-differential	Chimp	N	Lower body	N
		Non-differential	Chimp	N	Lower body	N

	Non-differential	Chimp	N	Lower body	N
	Non-differential	Chimp	N	Lower body	N
	Non-differential	Chimp	N	Body	N
	Non-differential	Chimp	N	Body	N
	Non-differential	Chimp	N	Body	N
	Non-differential	Chimp	N	Upper body	N
	Non-differential	White	N	Breast only	N
	Non-differential	B&W dark	N	Body	N
	Non-differential	White	Y	Upper body	N
	Non-differential	White	Y	Upper body	N
	Non-differential	White	N	Body	N
	Non-differential	White	N	Buttocks	N
	Non-differential	White	Y	Face	N
Male Genitals	Non-differential	White	N	Penis only	N
	Non-differential	Black	N	Penis only	N
	Non-differential	White	Y	Penis only	N
	Non-differential	White	N	Penis only	N
	Non-differential	White	N	Penis only	N
	Non-differential	Chimp	N	Penis only	N
	Non-differential	Chimp	N	Body	N
	Non-differential	Chimp	N	Penis only	N
	Non-differential	Chimp	N	Body	N
	Non-differential	Chimp pale	N	Penis only	N
	Non-differential	Chimp	N	Body	N
	Non-differential	White male	N	Upper body	Y
	Non-differential	B&W	N	Penis only	Y
	Non-differential	White	N	Body	Y
	Non-differential	White male	N	Face	N
	Non-differential	White	Y	Body	N
	Non-differential	White	N	Upper Body	N
	Non-differential	White	Y	Body	N
	Non-differential	White	Y	Body	N
	Non-differential	Black	N	Body	N