Individually Identifiable Body Odors Are Produced by the Gorilla and Discriminated by Humans

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Accepted January 23, 2010

Abstract

Many species produce odor cues that enable them to be identified individually, as well as providing other socially relevant information. Study of the role of odor cues in the social behavior of great apes is noticeable by its absence. Olfaction has been viewed as having little role in guiding behavior in these species. This study examined whether Western lowland gorillas produce an individually identifiable odor. Odor samples were obtained by placing cloths in the gorilla's den. A delayed matching to sample task was used with human participants (n = 100) to see if they were able to correctly match a target odor sample to a choice of either: 2 odors (the target sample and another, Experiment 1) and 6 odors (the target sample and 5 others, Experiment 2). Participants were correctly able to identify the target odor when given either 2 or 6 matches. Subjects made fewest errors when matching the odor of the silverback, whereas matching the odors of the young gorillas produced most errors. The results indicate that gorillas do produce individually identifiable body odors and introduce the possibility that odor cues may play a role in gorilla social behavior.

Key words: great ape, human, individual recognition, odor, social behavior

Introduction

For many species olfactory information plays a central role in guiding their behavior (Stoddart 1980; Wyatt 2003). Odor may influence feeding, reproductive, territorial, predatory and predator avoidant, navigatory, and many aspects of social behavior. Odor cues in the social context may provide information on group and family membership, relatedness, dominance, reproductive status, and individuality. The ability to recognize the individual identity of others is important for the social behavior of most species (Halpin 1986; Thom and Hurst 2004; Johnston 2008). Given the importance of odor for many species, covering all the major vertebrate groups, it is perhaps not surprising to find that they produce individual odor cues and have the ability to discriminate and recognize individuals from these cues (e.g., Halpin 1986).

One group where there has been little investigation of olfactory abilities is that of the great apes (Hepper et al. 2008). Olfaction is considered to play a very secondary role in guiding behavior in these species compared with the role played by vision and audition (Heymann 2006; Hepper et al. 2008). As a consequence, very little attention has been given to any possible role for olfactory cues in great ape behavior. It is not in question that some great apes are able to recognize members of their species individually using other sensory modalities. Chimpanzees and gibbons possess individually distinctive calls (e.g., Haimoff and Gittins 1985; Mitani et al. 1996). Further chimpanzees are able to recognize other individuals through the use of auditory and visual cues (e.g., Bauer and Philip 1983; Parr et al. 2000; Kojima et al. 2003). Research has also suggested that great apes may also have the ability to recognize self (Swartz et al. 1999).

Humans, closely related to great apes, were similarly viewed as having poor olfactory abilities. However, studies have demonstrated that humans possess acute olfactory abilities (Schaal and Porter 1991). Humans are able to discriminate and recognize odors of individuality and relatedness (e.g., Hold and Schleidt 1977; Wallace 1977; Porter 1999; Weisfeld et al. 2003; Lenochova and Havlicek 2008), even able to match the odor of twins (Roberts et al. 2005). This ability is present soon after birth: newborn infants have the ability to recognize their mother using olfactory cues (e.g., Schaal et al. 1980).

Additionally, other primate species have been shown to recognize individuals through use of odors, for example: lemurs (Mertl 1975; Palagi and Dapporto 2006), marmosets (Smith 2006), tamarins (Epple 1974), and galagos (Clark 1982).

Given the ability of great apes to recognize members of their species by individual cues in auditory and visual modalities, the "cognitive" processing requirements to discriminate and recognize individuals by odors should present little problem, providing individuals produce individually distinctive odors. Study of the skin of the great apes has revealed a similarity with that of the human, in particular the presence of apocrine sweat glands and eccrine glands from the axillary organ system (Ellis and Montagna 1962; Montagna and Yun 1963). Thus, there is the potential for the production of body odor in great apes that could be individually identifiable.

In this study, we wished to determine if a great ape, the Western lowland gorilla (*Gorilla gorilla gorilla*), produced an individually distinctive odor that could be discriminated from other individuals of the same species. Previous studies have shown that human participants are able to detect very minor differences in the odor signatures of other species, for example, mice (Gilbert et al. 1986), dogs (Wells and Hepper 2000), and thus we used human "smellers" to determine if the gorilla produced an individually identifiable odor.

Experiment 1

Materials and methods

Participants

Subjects were recruited from the student population at Queen's University Belfast in response to a request for individuals to participate in a study on olfactory discrimination. Subjects were excluded if they smoked, had a cold or other temporary problem with their ability to smell, or had a known medical condition that affected their sense of smell.

Recruitment continued until 100 participants had completed the study. In total, 108 people were recruited; 8 (5 females and 3 males) failed to complete the study due to the onset of a cold during the testing. Their data are not included. Data are reported for 100 subjects (61 females and 39 males) aged between 18 and 45 years (mean age: 21 years 6 months). There was no difference in the results between the sexes, and their data were pooled for this analysis.

Odor donors

Individual odors were obtained from the colony of Western lowland gorillas housed at Belfast Zoological Gardens, Co. Antrim, Northern Ireland. The group comprised an adult male silverback (aged 15 years, AM), a castrated male (aged 11 years, CM), 2 adult females (aged 36 and 13 years, AF1 and AF2), a young male (aged 5 years, YM), and a young female (aged 4 years, YF). All gorillas were unrelated to one another.

Odors were obtained by placing clean beige cotton flannel towels (100×150 cm) in the individual sleeping quarters of the gorillas in the late afternoon. Individual dens were 3-m long, 2-m wide, and 3-m high. All had individual entrances, approximately 3-4 m apart. The doors to the 2 dens in which the young gorillas slept were fixed half open to prevent the adults entering. Observations of the animals indicated that they used their individual dens to sleep in with little mixing between them. Towels were machine washed twice in plain water (40 °C), with no detergent and then dried prior to their use. The animal's dens were cleaned before use and fresh straw placed within each. The towels, individually marked with a small permanent ink mark to enable identification, were placed on the straw. Observations indicated that the gorillas lay on, or wrapped the towels around them, while in the individual cages. Towels were collected the next morning. Towels contaminated by faecal matter were discarded.

Upon collection, towels were handled by wearing plastic gloves and each cut into 32 pieces, 15 cm square (swatches). The outer 15 cm of the towels was not used. Each swatch was placed individually into plastic "Ziploc" bags, sealed, and stored in a freezer (-28 °C) until use. Approximately 120 min passed from collection of towels in the morning to their deposit in the freezer. All bags were carefully labeled with the name of the donor before storage. Prior to their use in the study, bags were removed from the freezer and left at room temperature (18–20 °C) for 4 h. In total, 7–8 towels were collected from each gorilla and all were treated identically as above. Swatches were used between 7–10 days after collection.

Apparatus

Participants were presented with the odors, via the swatches, in 350-mL clear plastic cups with a domed clear plastic cap. The cap contained a 2.5-cm hole through which the participants could smell the swatch inside the cup. This was sealed with an opaque plastic bung when not in use. The swatch was removed from its plastic bag and placed in the cup, sealed, for 60 min prior to its use. Containers were numbered by the experimenters to keep a record of the identity of the odor donor. Containers were only used for one swatch, and for 1 day, they were then discarded after use.

Procedure

The study employed a delayed matching to sample task. On each trial, participants were initially presented with 1 of the 6 gorilla's odors, referred to as the "target sample," and asked to smell it for 15 s. Sixty seconds later they were then presented with 2 further samples. One was a match to the odor of the gorilla they had been presented with as the target sample and the other, an odor belonging to one of the other

Each participant received all possible combinations of odor pairings, that is, the odor of Gorilla a as the target sample on 5 occasions and paired once with the odor of Gorilla b, c, d, e, and f as the matches. Similarly for Gorilla b and so on. Participants were not tested with 2 identical matches, that is, Gorilla a as the target sample and Gorilla a as both matches. In total, subjects received 30 trials. Trials were spread over a 5-day period with 6 trials per day, each trial separated by at least 5 min. The order of target sample presentation was randomized across all participants to prevent any order effects. Furthermore, when presented with the matches, for 50% of the trials, the match was presented first, and for the other 50% of trials, the nonmatch sample was presented first. Within any day, subjects received a maximum of 2 trials using the same target sample odor, that is, on a maximum of 2 occasions, for example, Gorilla a's odor was used as the target sample.

Containers were only used for one swatch, and for 1 day, they were then discarded after use. Each swatch was only used on 1 day and discarded after use. On that day, each swatch was used a maximum of 5 times as the target sample and 5 times as a match. The same swatch was not used as the target sample odor and the match odor on the same trial.

Whether the participant correctly identified the match was recorded on each trial. The number of times the correct match was made for each pair was calculated and a 2-tailed binomial test performed to determine if the participants were correctly able to make the match.

Results

The results, presented in Table 1, indicate that all odors were correctly identified at a significance level of greater than 0.05 (for a 2-choice test with n = 100 and an expected value of 0.5,

Table 1The number of correct responses made by 100 participants whenasked to identify a sample of gorilla odor from 1 of 2 options, the same ordifferent gorilla odor, for each match

Sample	Match								
	AM	СМ	AF1	AF2	YM	YF			
AM	×	82	83	88	87	92			
СМ	85	×	72	73	79	80			
AF1	84	71	×	74	77	81			
AF2	82	75	76	×	73	79			
YM	89	81	82	83	×	71			
YF	91	85	83	83	69	×			

Target samples appear in the left-hand column and the unfamiliar match in the 6 right-hand columns. Thus, when asked to match target sample AM against AM or CM, 82 participants correctly matched the sample.

when the number of correct matches = 61, this results in a 2-tailed significance of 0.032, whereas when the number of correct matches = 60, P = 0.052, nonsignificant).

The results thus indicate that participants were able to match the sample odor to the target odor. Based on the number of correct matches, the adult male's was the easiest odor to identify, especially when paired against the young gorillas. The most difficult identification was when the 2 young gorillas were paired together.

Experiment 2

The initial study indicated that participants could accurately match a target odor to 1 of 2 possible samples. Although this provides some support for the notion individuals could identify the target from among the 2 odors provided, it is possible that a correct match could be achieved by identifying the unfamiliar novel odor. That is, participants detected the unfamiliar odor and by default determined the correct match must then be the other odor. Although subjects reported that they positively identified the match, the possibility remains they achieved this, in part, through recognition of a novel odor. This demonstrates a level of recognition and odor identification but perhaps not explicitly individual identification. To address this, a second study was undertaken in which instead of providing 2 choices as samples, participants were given all 6 odors as samples and asked to identify the one that matched the target sample odor. Subjects now had to choose between 6 odors making a simple identification of the "unfamiliar" odor more difficult and biasing the task to one of positive recognition of the target odor.

Materials and methods

Participants

Thirty undergraduate students were used, 20 females and 10 males, aged between 19 and 37 years (mean age 20 years 7 months). None had previously taken part in this study. All were free from colds or other conditions affecting their ability to smell and none smoked.

Procedure

The procedure was identical to that reported above with the exception that following exposure to the sample target odor, participants were given a random choice of all 6 odors including that of the target sample. Participants were asked to identify which of the 6 sample odors was the same as the target odor. Participants were given each odor once as the sample and given a maximum of 2 trials per day. Each participant thus took part in 6 trials, and each target sample was matched 30 times (once by all participants).

Results

The results were analyzed by a 2-tailed binomial test (for a 6choice test with n = 30 and an expected value of 0.167, when the correct number of matches = 10, this results in a 2-tailed significance of 0.017, whereas when the correct number of matches = 9, P = 0.065, nonsignificant). All odors were correctly identified at a significance level of greater than 0.05.

The results indicated that human smellers correctly identified the target odors when given a choice of 6 possible sample odors and that some of the matches appeared easier than others (see Table 2). In particular, the adult male silverback was identified with no errors, whereas both the young gorillas were exclusively confused with one another, although still identified correctly at a level above chance.

Discussion

The results indicate that gorillas produce an odor that is individually distinctive and can be discriminated by human smellers.

A major issue when considering individual identification is whether this is actually achieved through use of individual cues (Thom and Hurst 2004). Other cues may be present that may also enable the identification, such as familiarity, sex, etc. There were obvious differences between the status of animals used in this study, for example, the silverback compared with the young female—dominance, sex, age, and these may have contributed to the identification of the odors.

The odor of the adult male, a full silverback, was identified with no mistakes when given a choice of 5 other odors (Study 2). In this study, participants reported a more intense sensation when smelling the odor of the silverback. Other than the silverback odor, no other odors were reported as being of different intensity, participants simply reported they were "different." This suggests that, although intensity may have been factor in the identification of the silverback odor, it did not play a role in other discriminations. This intensity may

Table 2The number of times respondents correctly identified the odor ofthe target sample when given a choice of 6 alternatives and where errorswere made what the errors were

Sample	Number of times	Match Number of times this gorilla identified incorrectly as the match						
	correctly matched							
		AM	СМ	AF1	AF2	YM	YF	
AM	30	×						
СМ	23		×	2	2	3		
AF1	21			×	8	1		
AF2	22			6	×	1	1	
YM	17					×	13	
YF	19					11	×	

have been related to dominance. Observations of gorillas in the wild have concluded that the silverback, at least, produces a marked, distinctive, pungent odor (Schaller 1963; Cousins 1990), which Fossey (1983) observed remained noticeable for sometime after they had passed. It must be noted that the silverback odor differed from other gorilla odors used in the study along other dimensions as well: age, sex, and reproductive status. However, this does not necessarily mean that the adult male was not identified by individual cues rather caution must be exercised in this interpretation. Of course, in this group, there was only one silverback so the odors of "dominance" and "reproductive status" would have individually identified this gorilla.

The husbandry practices for all the animals were identical, thus it is unlikely that differences in odor arose through differing husbandry practices between the gorillas. The group, as a whole, was fed the same food reducing a possible impact of transient dietary factors influencing odor production differentially.

Evidence that individual cues were used in the task emerges from the examination of the matching to sample trials involving 1) the 2 young gorilla's and 2) the 2 adult females. In both cases, when paired in the task, the odors were discriminated from one another. With regard to the young infant gorillas, although they were of different sexes neither had entered puberty and so reproductive status/condition/ sex was unlikely to influence odor. They were similarly aged and of equal dominance. The results suggested a similarity of odor between the 2 young gorillas. Study 2 found when errors were made in the matching of young gorilla odors, these were exclusively focused on the other young gorilla odor. This suggests that these odors although easily discriminated from adult gorillas were less easily discriminated from each other. However, despite this suggested similarity, human smellers correctly discriminated and identified the odors of each young gorilla. It is likely that this identification in this case is based on individual cues as opposed to a class difference, for example, age.

The discrimination of the adult female gorilla odors similarly lends strength to the argument that the odors were identified on individual grounds. Here, the odor donors were both reproductively mature females of equal dominance whose odors were discriminable from one another. There was a difference in age. Study 2 reveals that errors of identification of the 2 adult females were largely made by incorrectly matching one female to the other. If age were a factor, it might be expected that more errors would be made between similarly aged gorillas, although individuals of similar age also differed on other factors. We are unaware of any evidence that indicates age influences individual odor production in adults in the absence of other factors. It is likely that the odors here were individually distinctive.

It might be argued that the only true comparison of individuality is presented by the 2 adult females. Hence, when completing this discrimination in Study 2 the odors of the other 4 gorillas are excluded by the smellers on grounds of sex, status, and possibly other factors, leaving a choice of only 2 odors. However, even assuming this and adopting a chance level of 0.5, both adult females were correctly discriminated from the other choices available greater than chance (P < 0.05).

With noted caution, we suggest that the odors used in this experiment did represent odors of individuality rather than the odors of a particular class (e.g., male:female, dominant: submissive). Of course, in this group, there was only one silverback so the odors of dominance and reproductive status would have individually identified this gorilla. Further work is underway to examine this in more detail.

Odor collection was identical across all donors. The collection of odors is extremely problematic in great apes. Unlike humans, wearing of t-shirts or use of armpit pads to collect odors is not a possibility. The use of towels, an absorbent material, provided a solution to collect the odor of the gorilla. The gorillas did lie on and wrap the towels around them and thus it can be assumed that odors were absorbed onto the towels from the gorilla's body. It is not possible to say whether a particular area, for example, armpit, contributed to the odor more than others. However, it is reasonable to accept that the towels represented the whole body odor of the gorillas and that this odor was individually identifiable by human smellers.

One other possible confounder may have been the transfer of odor between individuals onto the towels. Of particular note is the fact that adult females and young have been reported to sleep together in the wild (Anderson 2000). If this occurred, there may be contamination of an individual's odor with that of potential sleeping partners. This could reduce the discriminability of the towels and indeed make certain discriminations more difficult, for example, female young, as reported here. A number of factors suggest this is unlikely. First, observations of the animals, on occasions throughout the night, indicated that they remained in their individual dens. Although this was not a continuous sampling procedure, it is suggestive of the fact that the animals remained in their dens. Second, the doors to the young gorilla's dens were fixed half open preventing the adults from entering. Thus, while the young could leave the den, the adults could not enter. Of course the young could enter each other's den but see above. Finally, the towels when collected from the dens in the morning were found in the same den as they were placed the preceding day. Although admittedly wholly anthropomorphic, the gorillas, especially the young, appeared to "like" the towels, wrapping themselves in them, and carrying them about their den. It is likely that if they moved dens, the towels would have been taken with them and potentially left or swapped with the towels were they subsequently slept. This was not found. Thus, although it is possible that there was some cross-contamination it is unlikely.

Recent studies suggest that the freezing of odors collected from humans and their use after freezing, and indeed even refreezing and reuse (although not used here), did not affect the subjective perception of the odors (Roberts et al. 2008; Lenochova et al. 2009). It is thus unlikely that the technique used to collect and store the odors influenced qualitative aspects of their sensation and perception.

Human smellers identified, in a matching to sample task, the odors of individual gorillas. The extent and limits of gorilla olfaction are largely unknown. We have previously demonstrated that gorillas can detect and discriminate between odorants of artificial origin, almond, and perfume (Hepper et al. 2008) indicating some functionality of their sense of smell. Examination of functional olfactory receptor genes (Gilad et al. 2004) indicates that old-world primates have approximately twice as many functional genes as humans (700 and 350, respectively). It might be argued that the gorilla's sense of smell would at least be comparable with that of humans if not better. Thus, the odors were individually identifiable by human smellers in this study may also be identifiable by the gorilla and used in their social behavior.

Observations of gorillas in their natural environment, and indeed great apes in general, do not report many obvious olfactory behaviors. Chimpanzees and orangutans have been reported to touch objects with their fingers and then smell their fingers (Blackman 1947; Rijksen 1978). Indeed orangutans have been observed to touch each others hands upon contact and then smell their hands (Rijksen 1978). Adult male gorillas may sniff the genital region of females prior to mating (Dixson 1981). However, given the general assumption of the primacy of auditory and visual systems on behaviors in these animals, attention may not have been paid to olfactory behaviors.

In conclusion, the skin of gorillas contains functioning apocrine glands and axillary organs (Ellis and Montagna 1962), organs involved in odor production. They have a functioning olfactory sense (Hepper et al. 2008). This study, for the first time in any great ape, indicates that gorillas produce individually distinctive odors, odors that are important in guiding social behavior in other species. Thus, odors although overlooked in the gorilla, and great ape, behavior, may be more important than previously thought in influencing behavior.

Funding

This work was supported by Project SOAP (Scent and Olfaction in Apes).

Acknowledgements

We thank Belfast Zoo and its Director Mark Challis for allowing us to work with the animals and all participants who gave their time for the study.

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