Sex attractants in primates

ERIC BARRINGTON KEVERNE*

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Synopsis—The importance of Olfactory communication in sexual attraction among primates is clear from our previous studies, which led to the term 'pheromone' being used to describe these olfactorily acting attractants. It is perhaps debatable whether such a term, originally defined to explain insect behaviour, can now be applied to the complex behaviour of a higher primate or man, where responses are not stereotyped. Such olfactory stimulants in these primates can produce mounting, masturbation and ejaculation, increase grooming behaviour and reduce aggression. Moreover, the ingredients in the composition of the stimulant may be added to, and produce improvements in the responsiveness of certain males. Since both the nature of the stimulants and the type of response produced can be varied, this clearly illustrates the complexity of defining an olfactory response in these higher primates.

Among the primates, communication of female sexual attractiveness appears to involve olfactory mechanisms, and a number of field and laboratory studies have observed sniffing of the female's genital region prior to copulatory behaviour. This is particularly true of the macaques where Carpenter (4) first observed that the vaginal overflow of the rhesus monkey possessed a characteristic odour which he thought might provide additional stimuli attracting males to females. Jay (7) perceived a strong smelling vaginal discharge in toque macaques, Macaca sinica, and observed males to examine the genitalia of females in the group each day. Bonnet macaques, Macaca radiata, have rarely been seen to present for copulation unless solicited by the male (14). This involved flipping the tail aside, olfactory examination of the genitalia, and on occasions, insertion of the

* Department of Anatomy, University of Cambridge.
finger into the vagina followed by smelling and tasting of the secretion (13). In the pigtail macaque, *Macaca nemestrina*, the male displayed the Flehmen posture following olfactory inspection of the female’s genitalia (6). In the stumptail macaque, *Macaca arctoides*, sniffing, fingering and licking of the perineal region occurs following female presentation (2) and prior to copulation (3). Although olfactory cues from the urine of receptive females are not ruled out, it would appear from these observations that in the macaques, communication of sexual status is by way of vaginal secretions.

To test this proposition use was made of operant conditioning techniques, in which male rhesus monkeys were required to press a lever in order to raise a partition which physically separated them from a female partner, but through which they could both see and smell the partner. Males had to work with some dedication, pressing the lever 250 times to gain access to the female. They regularly responded for ovariectomized partners treated with oestrogen, but rarely performed when faced with untreated ovariectomized females (9). Temporarily depriving these males of their sense of smell did not markedly affect either their pressing for or behaviour with the oestrogen-treated females; these females were presumably remembered as being attractive because of previously rewarding sexual experiences with them. However, the temporarily anosmic male failed to respond for unfamiliar ovariectomized females after these females were administered oestrogen, and shown to be sexually stimulating to normal males.

When the olfactorily deprived males had their sense of smell restored they readily began pressing for access to these females. That is to say, anosmia did not impair males’ sexual arousal and sexual activity with familiar oestrogenized females, but anosmic males were not able to detect the onset of attractiveness which oestrogen promoted in their unfamiliar partners. These results were consistent with the hypothesis that oestrogenized female rhesus monkeys produced substances which stimulated the sexual interest of their partners via the olfactory sense.

The preoccupation of males with the female’s genital region suggested this might be an obvious place at which to start looking for male sex attractants. We therefore studied the effects on male behaviour of transferring vaginal secretions from oestrogenized ‘donor’ monkeys to ovariectomized, unattractive ‘recipient’ partners. Application of vaginal secretions to the sexual skin area of recipients, which were themselves quite unresponsive to males, nevertheless resulted in a marked stimulation of the male partner’s sexual activity (10). Oestrogen-primed vaginal secretions have
now been applied to the sexual skin area of ovariectomized recipient rhesus monkeys on 249 separate occasions, and a 1 h behaviour test observed on each occasion in an acoustically isolated testing booth housed behind a one-way screen. These tests involved 11 pairs of animals and the secretions significantly increased the male partners' sexual behaviour above pre-treatment periods when only control substances were applied (Fig. 1). In

![Figure 1. Effects of applying vaginal secretions from oestrogenized 'donor' females to the sexual skin area of ovariectomized 'recipient' on the sexual stimulation of males. Data for 11 pairs involving five males, five females and five donors.](image)

the pre-treatment period eight ejaculations were recorded in 200 tests and these increased to 139 during 249 tests when vaginal secretions were smeared on the sexual skin of unreceptive recipients ($C^2 = 96.04, P \simeq 0.001$). Of even greater significance was the increase in male mounting attempts from 174 during the pre-treatment period to 2292 during applications to the same female partners. This high number of mounting attempts with few ejaculations was an indication of the unreceptive condition of the ovariectomized recipients, and clearly demonstrates the males' increased sexual interest in these pheromone treated females.

To determine the chemical nature of the substances in vaginal secretions responsible for these powerful behavioural effects, extraction and fractionation procedures were used in conjunction with behavioural assay methods.
The early stages of this procedure involved the use of ether extracts of secretions, collected by lavage with water from oestrogen-treated donor females (8). Ovariectomized rhesus monkeys were again the recipients for these extracts and the very low levels of sexual activity during the pre-treatment period was in marked contrast to the high levels seen during the applications of ether extracts. A gas chromatographic comparison of ether extracts of the vaginal secretion from ovariectomized untreated females indicated that the amounts of volatile components were absent or low, while oestrogen treatment stimulated production of volatile components and improved the sex attractant properties of vaginal secretions (11). Identification of these volatile components was obtained by preparative gas chromatography and mass spectrometry (5). The resultant mass spectra were compared with authentic samples, and established the identification of the first five peaks as acetic, proprionic, isobutyric, butyric and isovaleric acids. A mixture of authentic acids was made up to match their concentration in a pool of vaginal washings, and a small sample of this mixture when tested for behavioural activity was demonstrated to possess sex attractant properties (Fig. 2).

The effectiveness of these pheromones in stimulating sexual behaviour in the rhesus monkey does, however, vary according to social conditions: with some partners and in certain tests no sexual stimulation occurs. As more males are tested it is becoming evident that the response to pheromones varies between individuals and is also dependent in part upon the female partner with which they are paired. When the behavioural effects of fresh vaginal secretions and a synthetic mixture of their acid content were compared in the same nine pairs of animals, vaginal secretions appeared to be more effective in stimulating the male's sexual behaviour (Fig. 3). Although both vaginal secretions and the synthetic pheromone complex stimulated male sexual activity at significantly higher levels than in the pre-treatment tests, vaginal secretions were effective in 59% of applications compared with only 35% effectiveness of the synthetic acid mixture. Moreover, vaginal secretions stimulated 452 male mounting attempts compared with only 257 during application of synthetic pheromone to the same female partners (t = 2.39; P <0.02).

This lower proportion of effective tests during applications of the synthetic pheromone is due to its failure to stimulate mounting behaviour in certain pairs (Fig. 4). The relative effectiveness of untreated vaginal secretions and the synthetic acid mixture varied with the male partners from 100% in the case of male 113 to 45% success with male 68. With males 113
and 41, acids and vaginal secretions were equally effective and this was also the case with females 71, 78 and 74, although with female 74 they were equally ineffective (Fig. 4). With male 67 and 68, the synthetic acid mixture was approximately half as effective as the fresh secretion. This was due to these males being paired for some of their tests with female 76 where, although secretions have stimulated sexual activity in 52% of tests, the acid mixture has always been ineffective.

Thus it can be seen that the male's response to olfactory attractants varies between individuals and is also, in part, dependent on the female partner with which they are paired. Whereas some females readily evoke a sexual response from the male, others when treated in the same manner fail to do so. Hence, the response to pheromones in these highly-evolved social primates is not stereotyped. Furthermore, it can be seen that for certain pairs, the synthetic acid mixture is not as effective in stimulating the
males' sexual activity as the original vaginal secretions. This could mean there is a component in untreated secretions that is lacking in the synthetic mixture.

Phenylpropanoic (PPA) and parahydroxyphenylpropanoic acids (HPPA) are both odorous compounds identified in the rhesus monkey's vaginal secretion, but are quite ineffective in stimulating male sexual activity when applied alone to the sexual skin area of an ovariectomized female partner. By addition of PPA and HPPA to the synthetic acid mixture an enhancement of the effectiveness of synthetic pheromone has been obtained (Fig. 5). Sexual interactions were shown by the male in more tests (65%) than when just synthetic mixture of acids alone were applied (37% of tests). The mixture containing enhancers was almost as effective as the untreated vaginal secretions (70% of tests), although the amount of sexual behaviour stimulated was not so high. Untreated vaginal secretions when applied to the sexual skin of ovariectomized females in this test series stimulated 252
Figure 4. Variability in the response of different males to vaginal and synthetic pheromones and their relative effectiveness when applied to different female partners.

Figure 5. Improvement in the effectiveness of synthetic pheromones when phenylpropanoic and parahydroxyphenylpropanoic acids are added.
male mounting attempts and 15 ejaculations compared with 123 mounting attempts \( (t=1.6, P \text{ ns}) \) and 9 ejaculations \( (z^2=0.82; P \text{ ns}) \) during 20 tests when the synthetic mixture plus enhancers was applied.

From these results there is an indication that these phenolic components have an enhancing effect on the sexual stimulating properties of the synthetic pheromones. Nevertheless, it remains true that in some pairs the simple acid mixture appears to be completely effective. It is my opinion that the odour of the oestrus vaginal secretion is the true attractant and the acid mixture, mimicking the most odorous of the components, can in certain cases act as sufficient stimulus for some males. Others require additional volatile components such as PPA and HPPA, while still others require the whole untreated oestrous vaginal secretion. Hence, the odour cue is in itself complex.

Moreover, the source of the odour cue does not appear to be either glandular or an exudate through the vaginal wall, but microbial action plays an important part in producing the odours in the vaginal secretions, since aliphatic acid concentrations increase during incubation of the vaginal lavage, while autoclaving or the addition of penicillin prevents production of these fatty acids (12). It seems probable, therefore, that the production of these acidic pheromones depends upon the bacteria of the vagina, and that the ovarian hormones exert their influence on acid production in the intact animal by determining the availability of nutrients in the form of cornified cells and mucus.

An additional complication is to be found in the plasticity in the behavioural response of the male to the odour cue. It has already been shown that this can be modified by a partner preference, but perhaps of even more interest is the different behaviours which these odour cues can stimulate. The variability of the male's behavioural response to the same odour cue with different female partners is shown in Fig. 6. With the pairs 67, 76; 41, 71; and 68, 71, oestrogen primed vaginal secretions markedly stimulated male sexual activity. With the pairs 67, 78; 41, 79; 68, 78, an increase was produced in the social responsiveness of the male and he was prepared to groom his female partner for longer, although no stimulation of sexual activity occurred. With the pairs 67, 74; 41, 79; 68, 78, no stimulation of sexual activity occurred during the treatment with pheromone, but a marked reduction was observed in each male's aggressive behaviour towards his partner. It could be argued that we are dealing with more than one odour cue, and the vaginal secretion contains a grooming stimulant, and an aggression reducing pheromone, in addition to the sex attractant. My own feeling is that the coding for the behavioural response is not restricted to
Figure 6. Increases in sexual behaviour or grooming behaviour or the reduction of aggression by applications of pheromone but depending on the female partner. Those pairs marked with an asterisk had ether extracts of vaginal secretions applied.
the olfactory cue, but is integrated in higher areas of the neocortex. This opinion is reinforced by the variability in the male's response both to ether extracts of secretions (Fig. 6, those pairs marked with an asterisk), and in some cases to the synthetic acid mixture itself, which clearly rules out different odour cues.

It is most important that this lack of a stereotyped response is emphasized in this highly evolved social primate, particularly if consideration is to be given to the human situation and a search for human pheromones started. These aliphatic acids are present in human vaginal secretions (12) and the human male can distinguish variance in these odours between the phases of the menstrual cycle of the rhesus monkey. This does not, however, imply any causal relationship between these odour cues and the sexual behaviour of the human male. If we are to consider the complexity and plasticity in the response of the male rhesus monkey, then the further social and cultural evolution of man may make the search for an olfactory aphrodisiac with sexual releasing properties a fruitless task. Indeed, it may be argued that stimulation or provocation by female odours could be disruptive to our social order, and perhaps this is why we take such pains to disguise our body odours. This is not to say that these odours play no part in human sexual behaviour, but to give them significance at the level of sex attractants underestimates the complexity of human behaviour. What then might be the effect of these odour cues in human behaviour? Fig. 7 shows data which has been extracted from a number of experiments which I feel has some bearing on the kind of level these odour cues might be seen to act on the human. Following withdrawal of the sex attractant from the female partner, males usually lose sexual interest in the female and make no further mounts, but occasionally (Fig. 7(a) and (b)) males maintain their sexual arousal and, paradoxically, show increased mounting and thrusting prior to a loss of sexual interest. Moreover, if the oestrogenized female donor is given progesterone, her vaginal secretions lose their sexual stimulating properties when applied to the recipient. However, prior to the male's loss of sexual interest there is a marked increase in the male's mounting and thrusting (Fig. 7(c)). Since the only change in all these experiments is the odour of the female partner, I interpret this increased mounting behaviour as an increase in male sexual performance to compensate for the odour deficit of the female partner; that is, an increase in tactile input compensating for decreases in another sensory cue, namely olfactory. Similarly, following reversal of anosmia there may be an increase in male ejaculations with no marked increase in mounting (Fig. 7(d)). Here the introduction of
The olfactory sense with an attractive female initially improves the sexual performance of the male, and briefly increases his ejaculatory score.

It would appear from these results that at least two separate neural pathways are involved in the integration of olfactory cues. It is possible that sexual attraction involving releaser pheromones is brought about via olfactory connections to the pyriform cortex and other cortical regions.
before passing on to the limbic system via the amygdala and medial forebrain bundle to the hypothalamus. This I envisage as serving a filtering function, with the cortex analogous to a computer incorporating certain 'go' and 'no go' programmes. As we have already seen, the rhesus monkey's behaviour incorporates a number of 'no go' programmes, as for example the modifying effects of partner preferences, past experiences with certain females, and the presence of other males, etc. If we consider the human with infinitely complex behaviour patterns involving traditions, rituals, religions and past experiences, there are many variables which might constitute 'no go' programmes, making it pointless to look for any overt behavioural response. If, on the other hand, we consider sexual performance (as in Fig. 7 for the rhesus monkeys) it is possible that a more direct neural input to the hypothalamus is involved, possibly monosynaptic or probably involving only a few synapses. This I see as being analogous to tactile input as in genital stimulation (1), with the hypothalamus serving as an area of integration, while the threshold for response is modulated by hormonal status.

In conclusion, olfactory cues are of importance in the sexual behaviour of the male rhesus monkey but the behavioural response is far from stereotyped. This presents obvious problems when considering an attractant role for such odours in the human where social and cultural determinants of behaviour are even more complex. I would like to suggest that an alternative approach for the human might be in considering a role for these odours in sexual performance. This could be analysed objectively, and is less likely to be influenced by cultural variables.

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REFERENCES


