Social odours, sexual arousal and pairbonding in primates

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We describe the role of social odours in sexual arousal and maintaining pairbonds in biparental and cooperatively breeding primates. Social odours are complex chemical mixtures produced by an organism that can simultaneously provide information about species, kinship, sex, individuality and reproductive state. They are long lasting and have advantages over other modalities. Both sexes are sensitive to changes in odours over the reproductive cycle and experimental disruption of signals can lead to altered sexual behaviour within a pair. We demonstrate, using functional magnetic resonance imaging (fMRI), that social odours indicating reproductive state directly influence the brain areas responsible for sexual behaviour. Social odours also influence other brain areas typically involved in motivation, memory and decision making, suggesting that these signals have more complex functions in primates than mere sexual arousal. We demonstrate a rapid link between social odours and neuroendocrine responses that are modulated by a male's social status. Recent work on humans shows similar responses to social odours. We conclude with an integration of the importance of social odours on sexual arousal and maintaining pairbonds in socially biparental and cooperatively breeding species, suggesting new research directions to integrate social behaviour, neural activation and neuroendocrine responses.

Keywords: social odours; sexual arousal; pairbonds; primates; functional magnetic resonance imaging; neuroendocrine responses

1. INTRODUCTION

Evolutionary theorists have argued that in mammals, the sexes have fundamentally different reproductive strategies. Mammalian females have a greater certainty of maternity and greater energetic investment than do males, owing to gestation and lactation. Males can benefit from reduced post-conception energetic investment, but have a low certainty of paternity. As a result, females should be very choosy of mates, whereas males should compete with one another for as many conceptions as possible. However, in some mammalian species, including humans, mothers cannot rear infants successfully without some help from others. In such situations, either biparental care or infant care from a broader range of caregivers becomes essential. In these species, males and females have more congruent interests in reproduction. Some mechanisms become necessary not only to maintain a close social relationship between the breeding pair for infant care, but also to provide the male with confidence that the infant he is caring for is likely to be his. It has been argued (Snowdon 2001) that non-conceptive sex may be one proximal mechanism to form and sustain a pairbond. In this paper, we examine how social odours affect brain mechanisms and the neuroendocrine system to stimulate sexual behaviour, and how these odours may serve to sustain a relationship.

We first present the cooperatively breeding primates that we study, where both sexes are critical for infant survival and thus a close relationship between mates is critical. We then examine the features of olfactory signals and the potential role of these signals in regulating sexual behaviour and pairbonding along with the techniques available to study olfactory signals. We review behavioural evidence indicating the importance of social odours in reproduction in marmosets and tamarins and follow with our research on how social odours influence brain activity using functional magnetic resonance imaging (fMRI) as well as endocrine function and behaviour. We discuss some recent parallel studies on human responses to social odours and conclude with suggestions for future research to firmly link social odours, sexual arousal and pairbonding.

2. MARMOSETS AND TAMARINS: PRIMATES WITH OBLIGATE PAIRBONDING

As noted above, a close social relationship between mates is essential in those species where females are unable to rear infants successfully alone. Biparental species are those in which both parents are involved in taking care of infants. Cooperative breeders require not only both parents, but also additional helpers or alloparents which suppress their own reproduction to assist in the care of infants.

Callitrichid primates (marmosets and tamarins) are small monkeys (120–700 g) distributed throughout the

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Neotropics from Panama to southern Brazil. Characteristic of all of the species is a preponderance of giving birth to twins. In many natural habitats, as well as in captivity, females give birth twice a year. Gestation time is long compared with other small mammals, ranging from 4.5 to 6 months, which means that females generally become pregnant shortly after parturition while they are still nursing the current infants. Unlike birds, marmosets and tamarins do not build nests and so infants must be carried throughout the day as the group forages. Under such conditions, females are unlikely to be able to provide for all infants' care alone. In both field and captive environments, fathers and other group members are actively involved in transporting infants, share food with them as they are weaned, and probably assist infants with thermoregulation (Snowdon 1996). Fathers and other helpers are essential for infant survival (Snowdon 1996), and infant care is a significant energetic cost to males (Sanchez *et al.* 1999; Achenbach & Snowdon 2002).

Thus, in marmosets and tamarins both females and males have high stakes in maintaining a close social relationship. If a female is to be successful, she must keep her mate (and other helpers) with her during pregnancy and into the infant care period. In contrast with most other primate species, female marmosets and tamarins cannot rear infants alone and must maintain social ties with other animals to provide infant care. Similarly, if a male is to be reproductively successful, he must remain with his mate and invest significant energy in infant care. In order to do this, the father must have a high degree of confidence of paternity. Males would not benefit from providing infant care for infants they have not sired. Thus, it is critical to the self-interest of both females and males to develop and maintain a strong social relationship (or pairbond). We know relatively little about the mechanisms that lead to the formation and maintenance of bonds, but social odours appear to be one of the mechanisms by which bonds are maintained.

3. SOCIAL ODOURS

Olfaction is a sensory modality that is important in social communication in a wide array of species from insects to humans. There are many virtues of olfactory signals relative to other sensory modalities. Olfaction is useful where visual cues are difficult to detect and can be used at night and in visually obscured habitats. Olfactory signals may be energetically less expensive to produce than other types of signals and are long lasting relative to social signals. Olfactory cues have the advantage that they may be dissociated from the signaller if needed. Many species mark territorial boundaries through olfactory cues. This is an efficient way of defending a boundary since the odours will last after the producer has left. An organism can communicate without being directly located, providing reduced risk of detection by predators.

Odours used specifically for communication between animals within a species are called 'pheromones' in analogy to 'hormones'. Hormones are chemical signals that communicate from one part of the body to another, whereas pheromones are chemical signals that communicate from one organism to another. The original

research on pheromones was done with invertebrate species where there often appeared to be a fixed response to a signal. However, we take a broader view here (following Wyatt 2003). Pheromones are highly complex and variable mixtures of different chemicals and as a result will lead to different responses in recipients according to environmental and social variables. However, because discussion remains about the definition of a pheromone, here we use 'social odours' to describe chemical signals involved in regulating social interactions.

Social odours have a broad range of functions that vary within and between species. Odours can provide directional cues for orientation, serve as signals of alarm, mark territory boundaries, unify groups, direct foraging behaviour, attract mates, indicate reproductive and social status and provide information about species, subspecies, group, kin and individual identity (Wyatt 2003). Factors involved in mate choice and coordination of reproduction are of importance here. Social odours that serve to attract mates and communicate reproductive status are important for the coordination of reproductive behaviour, and odours that communicate species identity could limit reproduction to the appropriate species. Individual specific odours could be used to identify specific mates (Smith *et al.* 1997) and therefore be of value in maintaining relationships between mates.

Since social odours are usually a mixture of many substances, multiple levels of information can be provided simultaneously. Analyses of scent marks from Callitrichid primates (marmosets and tamarins) have revealed literally hundreds of chemical forms within a signal (Smith *et al.* 1976; Eppler *et al.* 1993). There are several implications to this finding. First, social odours have the complexity to encode multiple levels of information. The same signal might provide invariant information about the identity of species, subspecies, sex and individual while at the same time providing varying information such as the ovulatory state of a female. Chemicals of different molecular weight and molecular structure have different properties of diffusion. Thus, some components of a chemical signal may diffuse widely and attract a conspecific to the location of the signaller whereas larger, less well-diffusing molecules at the site of a scent mark can have a different effect once the receiver is attracted to the source.

In addition, there are two receptor pathways by which social odours can influence brain function. Each pathway can function simultaneously. The main olfactory system provides for transduction of airborne molecules at the nasal epithelium. Nerves from the nasal epithelium transmit information to the olfactory bulb, which in turn projects to the piriform and entorhinal cortices and subsequently to other cortical and subcortical areas, particularly the hippocampus. Some information may also be sent to the amygdala. The accessory olfactory system begins with chemicals transduced in the vomeronasal organ (VNO), which in many species is accessed via an aperture in the roof of the mouth. However, vomeronasal chemosignals can be taken into the VNO following direct contact by oral or nasal routes. Neurons from the VNO project to the accessory olfactory bulb, which connects directly to the amygdala and projects from there to other subcortical areas (Wyatt 2003).

There are several interesting and important points that emerge from a comparison of these two different systems for processing social odours. First, the main olfactory system is more likely to process volatile chemicals that can diffuse passively to the nasal epithelium, whereas the vomeronasal system appears better adapted to process less volatile chemicals that make direct contact by oral or nasal routes.

Second, the somewhat different brain pathways from the main olfactory bulb and the accessory olfactory bulb suggest that each area may process different potential functions of odours. Information from the accessory olfactory bulb goes directly to subcortical areas involved in sexual behaviour and neuroendocrine function, whereas information from the main olfactory bulb generally projects to many cortical areas and hippocampus first before being relayed to subcortical areas, although direct projections from the main olfactory bulb to the amygdala can be seen in rodents and probably in other species. Nonetheless, the main olfactory system provides greater flexibility in linking complex odours to different responses, including information requiring evaluation or cognitive processing.

4. TECHNIQUES TO STUDY SOCIAL ODOURS

It is difficult to study a sensory modality that we cannot perceive directly, and so determination of the role of olfactory signals requires careful methodology to (i) determine that odours are perceived, (ii) be certain that different odours may be discriminated, and (iii) know that odours have different functional effects. There are two major methods that have been used in studies of olfactory stimuli in mammals. First, one can use a behavioural bioassay to see if a participant can discriminate between different odours through preferences or other differential expression of behaviour. Second, one can look for a differential physiological response to different odours, either through peripheral measures or through changes in neural activity. We have used both methods in our research.

As an example of a behavioural bioassay, Ziegler *et al.* (1993) were interested in whether cotton-top tamarin males could detect signs of ovulation in their mates. Some authors (e.g. Burley 1979) had proposed that females manage monogamy by concealing the time of ovulation from their mate. Since the male cannot know when the female ovulates, he is prevented from seeking other mates. As noted, tamarins are cooperative breeders and male care of infants is critical to their survival. We had been unable to detect any changes in female behaviour or external physical changes that are related to ovulation. Thus, cotton-top tamarins appeared superficially to be a model of concealed ovulation. However, by monitoring hormonal states of females, we discovered that approximately 85% of ovulations resulted in conception (Ziegler *et al.* 1987). This suggested that some sort of communication of ovulatory status was happening. To test whether males could detect signs of ovulation, we collected daily scent marks (on ground glass stoppers) throughout the ovulatory cycle of a female and transferred the stoppers to cages housing pairs where the female was pregnant and not ovulating herself. In the periovulatory period of

the donor female, recipient males demonstrated increased rates and durations of erections and increased mounting of their own mates compared with days when the donor female was not ovulating. Although ovulation was concealed to human investigators, it was clearly not concealed to the tamarins.

An example of using a physiological response to determine if odours are perceived and have a functional effect comes from Ziegler *et al.* (2005). Male common marmosets were presented with small wooden disks containing odours from novel, ovulating females or of vehicle only, and a blood sample was taken 30 min later. Males had increased levels of testosterone following exposure to the odour of an ovulating female compared with exposure to the disk containing the vehicle.

5. THE ROLE OF SOCIAL ODOURS IN MARMOSETS AND TAMARINS

Owing to the importance of careful mate choice by both the sexes, each sex must evaluate carefully the quality and potential for a long-term relationship with the other. Social odours may play an important role in the evaluation of potential mates. Lazaro-Perea *et al.* (1999) studied the patterns of scent marking in wild groups of common marmosets and found that scent marking occurred in a variety of contexts in addition to the expected marking of territorial boundaries and food resources.

Studies on marmosets and tamarins in captivity have found that common marmosets of both the sexes and female cotton-top tamarins scent mark in response to presentation of a novel intruder (e.g. French & Snowdon 1981; Evans 1983). Lazaro-Perea *et al.* (1999) also found increased scent marking during intergroup encounters in wild common marmosets. In captive marmosets and tamarins, odours from reproductive females suppress ovulation in other females, providing a mechanism that could limit reproduction to a single female in a group (Epple & Katz 1984; Savage *et al.* 1988; Barrett *et al.* 1990). Although not reproductively active in the context of the family unit, subordinate females in the wild will scent mark at higher rates than reproductive females, particularly at territorial boundaries (Lazaro-Perea *et al.* 1999).

Subsequent research on the details of territorial interactions (Lazaro-Perea 2001) suggested that these interactions did not function solely to display aggression towards others, but also allowed marmosets to assess potential mates in other groups. In nearly every territorial encounter, a male from one group and a female from another group would cease behaving aggressively towards each other, move away from the rest of the group and copulate before returning to be aggressive to each other again. When a breeding animal disappeared from a group, the vacancy was filled rapidly, often by an animal previously seen engaged in territorial and assessment behaviour (Lazaro-Perea *et al.* 2000). Scent marks produced by non-reproductive males and females at territory boundaries may provide information about quality (physical health, stamina, reproductive competence) and also individual identity, information that can influence mate choice decisions.

These results suggest that social odours may serve as sexually selected traits in marmosets and tamarins by providing honest cues about the quality of the mate. This would be especially important in species that are dependent upon male infant care. Heymann (2003) has argued that scent marks are sexually selected traits, and he calls attention to an interesting sexual dimorphism in scent marking across different genera of Callitrichids. Scent marking is equally common in male and female marmosets, whereas it is rare among male tamarins. Male cotton-top tamarins scent mark when they are aggressive but not during sexual displays as common marmosets do. Evidence from both field and captivity has indicated that in *Saguinus* tamarins male care of infants is much more critical than in other species. Heymann (2003) argues that the sexual dimorphism in tamarin scent marking is functional because males will have a greater investment in infant care than in other genera and thus males rely on social odours from females to evaluate mate quality. In addition to the evidence of intersexual selection based on social odours, the evidence of olfactory suppression of reproduction in subordinate females cited above indicates that there is intrasexual selection in females based on social odours.

Another important function of social odours in marmosets and tamarins is in regulating sexual behaviour. These monkeys copulate throughout the ovarian cycle, as well as during pregnancy. This continuous receptivity is not an artefact of confined spaces that has been reported for other species (Wallen 1982). When we observed that the majority of ovulations that occurred in our captive tamarins resulted in conception, we began to look for potential signals by which females could communicate ovulation time to their mates. None of the traditional measures correlated. There was no obvious change in physical appearance, unlike the sexual swellings found in many old world primates (Zinner *et al.* 2004), and no changes in coloration. We find no evidence of menstruation, so males cannot be using menstruation to estimate when the next ovulation will occur. Given the importance of social odours already described, odours seemed a natural ovulatory signal, but we could find no changes in rates of scent marking by females that correlated with ovulation. However, it seemed likely that changes in odour quality might be an important cue.

Using the behavioural bioassay described above, Ziegler *et al.* (1993) collected scent marks deposited daily from an ovulating female on glass stoppers. The stoppers were then introduced to the cages of several mated pairs of tamarins where the females were pregnant and thus not ovulating themselves. We observed the behaviour of each pair in response to the odour and recorded all social and sexual behaviour that occurred during 10-min scent presentation. After all the behavioural data were gathered, we analysed the daily urine samples collected from the donor to determine when she had ovulated. We defined a periovulatory period as the day before, the day of and the day following the rise in luteinizing hormone (LH) that signals ovulation. Males showed increased frequency and duration of erection and increased rates of mounting their own mates on days of the donor's

periovulatory period. Females showed increased exploration of the platform containing the donor's periovulatory odours. Interestingly, males did not differ in rates of investigating, sniffing or licking at the donor's odours as a function of her cycle. This suggests that males are constantly monitoring social odours. Thus, female tamarins do communicate ovulatory status to males, but through changes in quality of the odour rather than frequency of marking.

A different type of experiment by Smith & Abbott (1998) found that male common marmosets could discriminate between odours of ovulatory versus anovulatory females. In an observational study on pygmy marmosets, Converse *et al.* (1995) described sexual behaviour occurring throughout the ovulatory cycle and found no changes in the rates of female scent-marking behaviour. However, males demonstrated increased rates of investigating scent marks from their mates at the time of ovulation as well as increased rates of courtship behaviour and mounting at ovulation. Female pygmy marmosets often displayed aggression towards male mounting attempts during the ovulatory cycle, but female aggression was never observed in the periovulatory period. Evidence from these three species taken together suggests strongly that social odours of females change through the ovulatory cycle and that males detect these cues.

Ziegler *et al.* (1993) demonstrated that the periovulatory odours of novel females could stimulate sexual arousal (erection and mounting behaviour) by males. The same result is found in common marmosets. Ziegler *et al.* (2005) presented male common marmosets with odours of novel ovulating females and compared behavioural response to this odour versus a vehicle control. Males showed increased rates of sniffing at the ovulatory odour as well as increased duration of erections during the 10-min tests. Although not significant, there were also decreases in latency to sniff at the odour, increases in licking, touching and male scent marking. Taken together, the results suggest the ability of odours of ovulating females to induce sexual arousal in males.

Washabaugh & Snowdon (1998) tested pairs of cotton-top tamarins with odours of the (i) resident female, (ii) unfamiliar females undergoing reproductive cycling, and (iii) unfamiliar females which were reproductively suppressed. The study was designed specifically to evaluate the response to odours independent of the ovarian cycle, by testing animals once each week for three weeks, with samples from the same females. The ovulatory cycle in tamarins is 23 days (French *et al.* 1984). Thus, by averaging observations across three weekly tests, the data represented responses to females in different reproductive conditions independent of ovulation. Males did not show increased sexual behaviour, but spent more time approaching and sniffing scents from the unfamiliar reproductive female. In contrast, females not only spent increased time investigating the odours of both unfamiliar reproductive females and unfamiliar non-cycling females, but also showed greatly increased rates of proceptive behaviour towards their mates in response to odours of unfamiliar reproductive females. These results taken together with those of Ziegler *et al.*

(1993) suggest that males respond with sexual arousal to novel females only at the time of ovulation, whereas females respond to odours of novel females at all stages of their cycle. Not only is information about ovulation conveyed, but there must also be some information in social odours independent of ovulation that allow females to recognize a reproductive female as novel at any stage in her cycle.

6. HOW SOCIAL ODOURS AFFECT THE BRAIN AND NEUROENDOCRINE SYSTEMS

How do odours affect the brain? Until recently, there has been no direct information directly linking olfactory stimuli to the specific brain areas known to be involved in sexual arousal. Given that there are direct pathways from the accessory olfactory system to the limbic system and other subcortical areas, the logical place to look for a direct influence of social odours is in these areas. Several studies implicate the anterior hypothalamus (AH) and medial preoptic areas (MPOA) as likely targets owing to their involvement in sexual arousal. In common marmosets, [Dixon & Lloyd \(1988\)](#) and [Lloyd & Dixon \(1988\)](#) lesioned the AH and MPOA in male common marmosets and found that the lesions reduced copulatory behaviour and male sexual interest in females without affecting grooming or affiliative behaviour with mates. In other species, the AH/MPOA has been implicated in sexual behaviour. [Paredes & Baum \(1995\)](#) studied ferrets and found that castrated females treated with oestradiol and tested in a T-maze preferred to approach a male and accept sexual behaviour, whereas intact males approached females and initiated sexual behaviour. However, castrated, oestrogen-treated males with AH/MPOA lesions showed reduced sexual behaviour towards females, and these castrated and lesioned males chose to approach sexually active males at the same rate as did control females. In a study on rats, [Paredes et al. \(1998\)](#) made lesions in the AH/MPOA of males and females and found no changes in female preferences for males as a function of either hormonal treatment or lesion condition. However, after AH/MPOA lesions, males changed partner preference and spent significantly more time in contact with sexually active males. Thus in rats and ferrets, AH/MPOA lesions in males, but not in females, can change preferences for sexual partners.

Based on these studies, we predicted that the odours of ovulating females would have a direct stimulatory effect on neurons in the AH and MPOA of males. To test this notion, we developed the technology and methods to image odour-evoked changes in brain activity of fully conscious monkeys using fMRI. First and foremost, we developed a restraint system that would keep the marmoset's head immobile during imaging. Built into the chassis of the marmoset restrainer were radiofrequency electronics for detecting subtle changes in MR signal from localized areas of the brain. Animals were lightly anaesthetized so that they could be placed in the restraints and then they were administered an antidote to the anaesthesia. We determined that each individual monkey recovered completely within 12–30 min after being given the

antidote. We took heart rate, respiratory rate and EEG data to demonstrate that animals were completely alert in the magnet, and documented normal physiological responses to the presentation of odours from ovulating females (increased heart rate and decreased respiration). In every session we compared images at the beginning and end of imaging and rejected any sessions where there was evidence of motion artefact. Since we were concerned about possible stress effects on the subjects owing to the procedure, we habituated monkeys to the procedures three times before testing. Measures of serum cortisol before and after imaging indicated some elevation of cortisol, but the elevation remained within the normal acceptable range for unrestrained controls. For more details on the methodology and the controls that are necessary see [Ferris & Snowdon \(2005\)](#).

We presented four male common marmosets with odours of novel females. Two types of odours were presented: scent marks of novel ovulating females and scent marks from novel ovariectomized females. The female scent marks were collected on glass stoppers, the scents were dissolved in a mixture of alcohol and deoxygenated water, and the extracts were stored at -80°C until they were used as a stimulus. Within each imaging session, the males were tested with an ovulatory odour, an ovariectomized odour and a vehicle control. Prior to each stimulus presentation, we also gathered data in the absence of any stimuli. We found support for our hypothesis ([Ferris et al. 2001](#)). There was a significantly increased activation of both the MPOA and AH in response to odours of both ovulatory and anovulatory females relative to vehicle control and no stimulus controls ([figure 1](#)). In addition, the activation in response to the ovulatory odour was significantly greater than the response to the anovulatory odour. Thus, social odours by themselves in the absence of any other sensory cues led to increased activation of the AH and MPOA, areas known to be involved in male sexual arousal.

There are many benefits in using fMRI. The technique is minimally invasive and thus the same animals can be tested repeatedly under different developmental and social conditions. Furthermore, one can carry out hypothesis-driven research such as described above, and at the same time, by collecting images from the entire brain, one can use fMRI for exploratory research as well. We further analysed the data from our marmosets to determine what other brain areas were involved in responding to sexual odours ([Ferris et al. 2004](#)). We specifically compared responses to the odours from novel ovulating females with responses to the odours from novel ovariectomized females. We found significant differences in positive MR signal in prefrontal cortex, temporal cortex, somatosensory cortex, insular cortex, cingulate cortex, caudate nucleus, putamen, hippocampus, septum, medial preoptic, AH, periaqueductal grey, Raphe nucleus and cerebellum. We also found significant differences between stimuli in reduced or negative MR signal in temporal cortex, cingulate cortex, putamen, substantia nigra, hippocampus, medial preoptic and cerebellum. In general, most of these areas have greater activation (positive signal) to the ovulatory odours (compared with the anovulatory

Figure 1. Activational maps at the level of the amygdala taken from a single animal. Significant changes in positive and negative BOLD signal are shown for presentation of the scent of novel, ovariectomized (OVX) females and those of novel, ovulating females. Regions of interest are delineated in the upper right-hand image. Note the greater overall degree of positive BOLD signal in response to the scent of ovulating females and the greater degree of negative BOLD signal in response to odours of ovariectomized females. Abbreviations: INS, insular cortex; CG, cingulate cortex; CD, caudate; SP, septum; PU, putamen; TP, temporal cortex; AM, amygdala; mPOA, medial preoptic area. (Reprinted from fig. 2, Ferris *et al.* 2004 *Journal of Magnetic Resonance Imaging* 2004, Wiley Liss.)

odours) and greater deactivation (negative signal) to anovulatory odours (figures 1 and 2).

These results indicate that sexual odours are not merely having an effect on areas directly involved in male sexual behaviour (AH/MPOA), but are also influencing the areas involved in memory (hippocampus, temporal cortex), emotional decision making (cingulate cortex), motivational systems (caudate, putamen, substantia nigra) and sensory integration (cerebellum, somatosensory cortex). If all of these areas are differentially involved in reaction to ovulatory versus anovulatory odours, then the odours cannot just be activating some sort of reflexive process, but some evaluative and recognition processes as well. These results lead us to hypothesize that male marmosets are using memory and decision-making processes to identify the source of the odour. For maintaining a pairbond, individual recognition of the mate becomes important and a male's mating decision may be based on the value of the relationship as well as whether the mate is detected or not.

Figure 2. Activational maps at the level of the thalamus. Images taken from a single animal. See figure 1 for detailed description. Abbreviations: SMC, sensory motor cortex; PT, posterior thalamus; MT, medial thalamus; HIP, hippocampus; SN, substantia nigra. (Reprinted from fig. 3, Ferris *et al.* 2004 *Journal of Magnetic Resonance Imaging* 2004, Wiley Liss.)

The hypothalamus including the AH and MPOA is intimately involved in regulating the neuroendocrine system. Is it possible to demonstrate that olfactory cues influence male neuroendocrine function? A few studies on rodents have shown an increase in LH or testosterone within a brief time of being presented with female odours. But in primates, only chronic exposure to odours over a few weeks has so far been related to increased hormonal activity. In a direct test of the hypothesis that female odours could have a rapid effect on endocrine responses, Ziegler *et al.* (2005) tested male common marmosets with odours of novel, ovulating females and compared these with responses to vehicle alone. Male marmosets showed increased erection rates and sniffing at the ovulatory scent. At the same time, Ziegler *et al.* (2005) took blood samples from males 30 min later and analysed these for testosterone and cortisol. The males were grouped according to their social condition (single, newly paired or fathers taking care of infants). Within 30 min of presenting the odour of a novel, ovulating female, single males and non-reproducing, paired males demonstrated a significant increase in testosterone levels but with no changes in cortisol levels. However, fathers showed no change in testosterone levels, reacting to the ovulatory odour as they did to the control. Something about being a father and caring for

infants prevented these marmosets from responding physiologically to ovulatory scents of a novel female.

Ziegler *et al.* (2004b) studied cotton-top tamarin males in the period around the post-partum ovulation of their mates. Females varied considerably in when they ovulated after giving birth (range 13–25 days), but males demonstrated significant increases in testosterone and dihydrotestosterone during the 5 days prior to the mate's ovulation. This hormonal anticipation of a mate's ovulation may prepare the male for copulation and mate guarding. The fact that the timing of increased hormonal levels in males anticipated precisely the timing of the mate's ovulation implies some sort of communication, and social odours appear the most likely modality.

7. SOCIAL ODOURS AND HUMAN REPRODUCTION

Do olfactory stimuli have any relationship to human reproductive behaviour? Hrdy (1999) has argued that humans are also cooperative breeders, since a single female is typically unable to rear an infant to adulthood without substantial support from others either in caregiving or financial support. Thus, we might expect to find similar importance in forming and maintaining pairbonds in humans, and it would not be surprising to find some similar mechanisms involved.

However, there are similar difficulties in studying social odours in humans as in monkeys. We often cannot perceive social odours at a conscious level. Sobel *et al.* (1999) used fMRI to measure response of subjects to oestra-2,3,5 (10), 16 tetraen-3yl acetate, an odour none of the subjects could consciously detect. At a low concentration, participants could not discriminate between the odour and a control but at high concentrations, they could discriminate despite being unaware of the presence of an odour. Nonetheless, fMRI revealed increased activation in the anterior medial thalamus and inferior frontal gyrus in response to both odours. Thus, although subjects were unaware of the odour at both the concentrations, they could discriminate between high concentrations and a control odour and had increased brain activation to both concentrations.

There has been considerable controversy over whether humans have a functional VNO. Trotier *et al.* (2000) found evidence of a vomeronasal pit bilaterally in 13% of more than 1800 subjects and unilaterally in another 26%. However, repeated sampling of a subset of 764 subjects found changes over time in whether a vomeronasal pit could be detected. There was no evidence of any nerve tract leaving the VNO, and the proteins expressed in the organ were different from those seen in other species. Although the VNO may be vestigial and ephemeral in humans, social odours may still be detected and processed by the nasal mucosa and main olfactory bulb.

As with non-human animals, behavioural and physiological bioassays are used to determine the presence and the effects of social odours in humans. Singh & Bronstad (2001) provide a typical example of a behavioural bioassay. Women wore clean T-shirts for three nights before menstruation (luteal phase) and another clean T-shirt for three nights at mid-cycle. Men were asked to smell the T-shirts and rate them on

qualities of pleasantness, attractiveness and sexiness. The T-shirts worn during ovulation were ranked higher than those worn during the luteal phase. Stern & McClintick (1998) illustrate a physiological bioassay. Axillary secretions were collected from women at either the early follicular phase or ovulation. Extracts of these odours were placed on the skin of recipient females between the upper lip and the nose. Over the subsequent two menstrual cycles, women receiving odours from ovulating women increased cycle length by 1.5 days and women receiving follicular odours shortened their cycles by a mean of 2 days. Thus, odours from women at different stages of their cycles can produce physiological effects on recipients. Stern & McClintick (1998) use these results to suggest a mechanism for menstrual synchrony.

In another study, Preti *et al.* (2003) collected axillary extracts from men and placed them under the noses of women who were being monitored for serum LH levels and mood. When presented with male axillary extracts, women showed more frequent LH pulses, reduced tension and increased relaxation, indicating both a physiological and emotional effect of male social odours.

The fact that axillary extracts of men and women have effects on physiology and mood led to a search for what might be key olfactory compounds. One compound of male axillary secretions is an androgen (4,16 androstadien-3-one; AND), and a less well-documented female equivalent is an oestrogen (1,3,5(10), 16-oestratetraen-3-ol; EST). How do these compounds influence behaviour and physiology in humans? Bensafi *et al.* (2003) presented AND and EST to heterosexual men and women while recording several measures of physiology and mood. The steroid, AND, affected the sexes differently, increasing physiological arousal in women, but decreasing arousal in men. EST, however, had no effect on either sex. Neither compound had a significant effect on mood.

In contrast, Savic *et al.* (2001) reported a double dissociation between AND and EST. They used positron emission tomography to measure neural activation in response to each compound. Women demonstrated a strong activation to AND and men demonstrated a strong activation to EST. There was a sex difference in the activated regions of the hypothalamus. AND activated the MPOA/AH and ventromedial hypothalamus in women, whereas EST activated the paraventricular and dorsomedial hypothalamus in men, although there was some overlap. The MPOA/AH was not activated in men in contrast to our results with marmosets, but the anterior cingulate and insula were activated in both sexes (men by EST and women by AND), comparable to our results with male marmosets. EST in men and AND in women also activated both left and right amygdala, but we found no differential responses in the amygdala of marmosets. In addition, EST increased activation in the fusiform and lingual gyrus in men, and AND activated the same areas in women. The fusiform gyrus is involved in individual face recognition and its activation by odours suggests a potential involvement in individual odour recognition as well. Neither men nor women rated the odours differently in terms of pleasantness, familiarity, intensity or irritability.

Savic *et al.* (2005) have extended their work with AND and EST to include homosexual men. They reported that EST did not produce increased neural activation in homosexual men, but AND did lead to increased activation in homosexual men in the same hypothalamic areas that were activated by AND in women. There were no differences between heterosexual and homosexual men to any of a variety of other steroid and peptide hormones that were sampled.

Research on determining putative social odours that affect reproductive behaviour in humans and identifying the relevant compounds is in its infancy, but it is becoming clear that human social odours may have influences on neural activity, neuroendocrine function and behaviour, somewhat similar to what we have documented in marmosets and tamarins.

8. RELATIONSHIP BETWEEN SEXUAL AROUSAL AND PAIRBONDS

Almost all of the studies we have reported so far have measured responses to odours of novel females. But this leads to a serious problem with respect to our initial arguments. We have shown that only ovulatory odours from novel females (and in women from novel males) can lead to sexual arousal, AH/MPOA activation and neuroendocrine responses, but how could odours work to maintain a pairbond that is essential for cooperative breeding?

Remember that (i) both male and female tamarins initiated sex with their mates when they are exposed to the odours of novel reproductive females (Ziegler *et al.* 1993; Washabaugh & Snowdon 1998), (ii) in common marmosets, fathers do not display an increased testosterone response to odours of novel females (Ziegler *et al.* 2005), and (iii) a variety of neural areas associated with recognition and memory are also activated by female odours (Ferris *et al.* 2004). Therefore, male marmosets and tamarins are not responding reflexively to sexual odours. If males can distinguish between odours from their own mate and that of a novel female and make decisions based on the value of the current mate versus the potential value of a novel female, we should be able to model this through a study of sexual conditioning to show that animals can learn specific olfactory cues associated with sexual activity.

We are completing a study on sexual conditioning in common marmosets. In our fMRI studies, we also used lemon extract as a non-sexual olfactory cue and as an additional control for novel female odours. Subsequently, these same males were trained to anticipate the opportunity of sex whenever they smelled lemon. In other words, on conditioning trials, males would receive lemon odour in the presence of a caged ovulating female and 3 min later the males had access to the female with whom they could copulate. On alternating trials, the males were presented with the vehicle, in the presence of a caged ovulating female, but the female was not released. The males rapidly displayed anticipatory sexual behaviour only when lemon was present. We are currently analysing the results from fMRI imaging to lemon before and after conditioning (Schultz-Darken *et al.* 2003, unpublished data). The demonstration of sexual conditioning to an arbitrary odour indicates that males can

learn to target sexual activity to those females associated with that odour. This, in turn, suggests that males can rapidly learn about the individual odours of their mates and thus limit their sexual reactions to their mates (or at least inhibit responses to other females in the presence of their mates).

How does this work to maintain a pairbond? Data from a variety of studies suggest that non-conceptive sex is important in forming and maintaining pairbonds (Snowdon 2001). Not only is sexual activity greater at the beginning of a relationship than later on, but also various experimental disruptions to a relationship, such as brief separation from mate, presenting a novel animal, either directly or indirectly through odour cues, lead to increased levels of sexual activity among mated pairs as though non-conceptive sex was acting to reaffirm or restore the relationship. We hypothesize that the rewards of non-conceptive sex condition mates to the individual-specific cues of one another and that these cues may serve as secondary reinforcement for maintaining a close relationship. Thus, social odours lead to sexual arousal and conceptive or non-conceptive sex with the mate. This, in turn, leads to learning about mate-specific cues that may then serve to maintain a strong relationship.

9. FUTURE DIRECTIONS

Our research to date suggests several interesting future studies. We know that male common marmosets are likely to be interested in and copulate with novel females at the time of ovulation, but males appear to be much less interested in novel, non-ovulating females. However, mated pairs of common marmosets engage in sexual activity throughout the cycle. This suggests that the sexual arousal of male marmosets by novel females is much more sensitive to their reproductive condition, whereas arousal to their own mates is less linked to ovulation. It follows then that males should display equal interest in the odours of their mates throughout the ovarian cycle. Thus, although activation of the MPOA and AH is clear to novel, ovulating females, we predict that activation of the MPOA and AH would be equally strong to the mate's odour at all phases of the ovarian cycle. Alternatively, owing to long-term habituation to odours of the mate, the mate's odours alone might not induce as much activation at any time in the reproductive cycle, compared with a novel female's odours.

Several studies have shown that male marmosets react differently to a novel female depending on whether his mate is present or not. Evans (1983) showed that when a novel female intruder was presented to paired common marmosets, both male and female engaged in aggressive behaviour towards the intruder. However, when the male of the pair was tested alone with a novel female, he demonstrated affiliative behaviour with little aggressive behaviour. In an extension of this paradigm, Anzenberger (1985) tested males separately from their mates but with the mates visible behind a one-way window. In this condition, males displayed much more aggression and less affiliation towards a novel female than when they were tested in an environment where they could not see their mates. Clearly, some aspect about the presence of

the mate inhibits a male from demonstrating sexual interest in a novel female.

Could this be done with odours as well and what effect might these have on brain activity? In parallel with the studies using visual cues, we predict that a male should demonstrate a much lower level of sexual interest when tested with odours of a novel female in the presence of olfactory cues from his mate. Erection rates would be lower and sniffs and licks at the novel female odour would be fewer and latency to approach the odour would be less in the presence of odours from the mate. With respect to neural activity, we predict that the presence of the mate's odour along with the odour of a novel ovulating female should suppress the response of the AH and MPOA. We have preliminary data suggesting that this is the case (C. F. Ferris *et al.* 2004, unpublished data). The males were presented with odours from a novel, ovulating female and displayed the robust neural response in AH/MPOA described earlier. However, when an odour from the male's mate was presented in addition to that of the novel female, there was an immediate inhibition of AH and MPOA activation suggesting that, as with visual stimuli, olfactory stimuli can inhibit a male's sexual reaction to a novel female. Since odours last a relatively long time and can be effective even in the absence of the animal producing the odour, an inhibition of a male's sexual response suggests that females can control the sexual behaviour of the mate even without being visible or present.

We found a rapid increase in serum testosterone within 30 min of presenting the odour of an ovulating novel female, but this hormonal response was limited to singly housed and non-reproducing, paired males and not to fathers (Ziegler *et al.* 2005). Thus, the sexual response to social odours varies with the male's reproductive history. One of the great advantages of fMRI as a tool to study the nervous system is that the same individuals can be tested repeatedly. All of the males that we have studied with fMRI to date have been either sexually naive males living together or non-reproductive pairs. We predict that virgin males and non-reproductive paired males should continue to demonstrate a robust response of AH and MPOA, but that the same males, when retested as fathers, should display a muted response or no response. Furthermore, since Ziegler *et al.* (2004a) showed that male cotton-top tamarins begin to exhibit a hormonal cascade halfway through pregnancy, shortly after the foetal adrenal begins to become active, it is possible that males tested late in their mate's pregnancy would also demonstrate neural inhibition to odours of novel females.

All of the research to date on neural and endocrine changes on common marmosets in response to odours of novel animals has involved the study of males. However, we have shown in the related cotton-top tamarins that females also reacted to the odours of novel females by increasing proceptive behaviour towards their mate (Ziegler *et al.* 1993; Washabaugh & Snowdon 1998). In a monogamous or cooperatively breeding species, both the sexes should be involved in the maintenance of the relationship if infant care is to be successful. The cotton-top tamarin males rarely scent mark (French & Cleveland

1984), and we cannot study how female tamarins react to male odours. However, in common marmosets, both the sexes use social odours about equally and therefore a parallel series of studies could be done with females in response to male social odours. Single and newly paired females should be much more interested in odours of novel males and should demonstrate greater neural activation than females either late in pregnancy or with dependent infants.

10. CONCLUSIONS

Social odours play an important role in regulating sexual behaviour in cooperatively breeding primates, marmosets and tamarins. Odours appear to be important in marking territories, suppressing the fertility in subordinate females and, possibly, evaluating potential mates. Mated marmosets and tamarins engage in pair maintenance behaviour in the presence of odours from novel, reproductive females and males are sensitive to odour cues of ovulation. We have shown that it is feasible to use fMRI in conscious marmosets as a tool to study odour-induced changes in brain activity in response to signals inducing sexual arousal. fMRI indicated activation, not only of areas involved in sexual arousal, but also brain areas involved in motivational processes, memory and decision making. Odour cues from novel ovulating females also elicit a rapid increase in testosterone secretion in single and non-reproducing, paired males, but not in fathers, suggesting that male reproductive status affects how he responds to female odours. These findings taken together illustrate the importance of social odours not only in sexual arousal, but also in identifying a mate and regulating neuroendocrine function. Since fMRI allows one to study activation throughout the brain and over the course of an animal's reproductive life, the technique holds great promise when used in conjunction with behavioural and neuroendocrine methods for understanding the brain mechanisms involved in linking sexual arousal with forming and maintaining the strong pair relationship needed to rear infants successfully. The finding of somewhat similar effects in humans suggests the potential importance of this research to better understand the formation and maintenance of human relationships.

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