

Multimodal signalling of ovulation in human and non-human primates

Signalisation multimodale de l'ovulation chez les primates humains et non-humains

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Abstract Communication in primates is based on multiple elements of signals, often expressed in different modalities. While some individual primate signals are relatively well described for a particular cue (e.g. copulation calls, sexual swellings) or for one specific dimension of a signal (e.g. the size of sexual swellings), few studies have simultaneously investigated the role of multiple signals and cues in the same communicative context. This paper reviews comparative evidence on primate sexual communication, specifically concerning multimodal sexual signalling of ovulation and mating strategies. A comparison is made across primate species, including humans, of the characteristics of different female sexual cues and signals (behavioural, visual, auditory and olfactory) and of their potential roles in the discrimination of the timing of ovulation. The possible selective reasons for such multimodal signalling are discussed.

Keywords Sexual signals · Communication · Ovulation · Mating choices · Reproductive strategies

Résumé La communication chez les primates est basée sur de multiples éléments de signaux, souvent exprimés via différentes modalités. Alors que certains signaux (e.g. cris de copulation, gonflement sexuel) ou certaines composantes particulières d'un signal (e.g. la taille du gonflement sexuel) ont été relativement bien décrits, peu d'études ont simultanément analysé le rôle de multiples signaux dans un même contexte de communication. Cette revue présente des données comparatives relatives à la communication sexuelle chez les primates et concernant la signalisation multimodale de l'ovulation et les stratégies reproductives. Je compare les caractéristiques des différents indices et signaux sexuels des femelles (comportementaux, visuels, auditifs et olfactifs) chez différentes espèces de primates dont l'Homme, et leurs rôles potentiels dans la détermination du moment de

l'ovulation. Les possibles raisons sélectives expliquant une telle signalisation multimodale sont discutées.

Mots clés Signaux sexuels · Communication · Ovulation · Choix copulatoires · Stratégies de reproduction

Introduction

Animal communication generally depends on multiple elements of signals expressed by several modalities [1]. These signals could provide information on individual characteristics, such as identity, dominance rank, nutritional condition or reproductive status. Their evolution may be inherent to sexual selection as they have major consequences on fitness and reproductive success. Recent studies underline the importance of studying multi-component signals [2] and non-human primates are an excellent model for anthropological studies of fertility signalling. Human and non-human primates share a long evolutionary history, and have a similar anatomy and physiology. Therefore, comparative studies on the different types of pressures and related adaptations of non-human primates can help to answer specific questions on the evolution of humans, but also to identify general principles that apply across species. Concerning studies on reproduction, Old World monkeys (i.e. baboons, chimpanzees, macaques etc.) are excellent models for holistic studies on the evolution of reproductive function and ovulatory signalling. Women and Old World primate females share a similar pattern of ovarian cycles, where the menstrual cycle is divided into the follicular phase preceding ovulation, the luteal phase following ovulation, and menstruation [3]. Cycle lengths are quite homogenous among primates (e.g. humans: 29.1 days; catarrhines: 31.0 days [3]), and studies on non-human primates also underline the similarity of their hormonal profiles to those of humans (e.g. female baboons and women [4]). Moreover, as in humans, mating behaviours in some primate species (e.g. baboons, bonobos and capuchins) are not restricted to the most conceptive days of the

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cycle (i.e. the ovulation window), and copulations can also occur after conception (i.e. during the gestation period) [5–7]. Finally, studying the adaptation of the reproductive function in different primate species could improve our general understanding of the evolution of human sexual communication and its biological and physiological mechanisms. Using several primate models with different mating processes and ovulatory signalling as an evolutionary continuum could thus help to answer specific questions on the specific features of the *Homo sapiens* mating system.

This paper briefly reviews the most relevant findings on the role of each female sexual signal in indicating the likely fertile phase and the timing of ovulation. We then discuss the consequences of multimodal ovulatory signalling on female and male mating strategies, and the importance of these findings for a better understanding of human sexual communication and its evolution.

A complex set of female sexual signals indicates the fertile phase and the timing of ovulation in primates

In a number of primate species, males tend to mate during the period of highest probability of ovulation (i.e. the fertile phase) [8–10]. This suggests that they are able to discriminate between periods of low and high probability of conception during the menstrual cycle. However, the signals and cues available to males for their mating decisions, and their relative reliability, are still poorly understood. There are several potential cues involved in ovulatory signalling in human and non-human primates: behavioural signals (i.e. proceptive behaviours directed by the female toward males, such as approaches and presentations) [11–13], visual signals (e.g. skin colour and sexual swellings) [14–16], auditory signals (e.g. human voice and copulation calls) [17–19], and olfactory cues (e.g. female body odours and vaginal secretions) [20–22]. While most studies have generally focused on one or two cues (e.g. copulation calls and sexual swellings) or on one specific dimension (e.g. size of the sexual swelling), few attempts have been made to investigate whether females simultaneously advertise their fertile status through a combination of several complex signals. Therefore, the question of whether primate females signal fertility in multiple modalities and the extent to which these may influence male and female mating strategies are still not well understood.

Studies investigating the role of female sexual behaviours have yielded a contrasting picture of how proceptive behaviours might encode information concerning the likely fertile phase in primates. It has been suggested that female behaviours are linked to the timing of ovulation in some primate species (humans [11], olive baboons [22], tufted capuchins

[23], crested macaques [24]), but this may not be universal (Japanese macaques: [9], Barbary macaques [25]). Moreover, it is important to note that even within a species, the relationship between female proceptive behaviours and the timing of ovulation may differ, depending on the behaviours of interest. For example, our recent study on olive baboons [22] showed that female approaches contained information on the likely fertile phase, whereas sexual presentations of the anogenital area did not. Moreover, social behaviours in sexual contexts (e.g. lip-smacking, eye contact, grooming) or indicators of the female's willingness to copulate (i.e. female refusal of males mounts or interruptions of copulation) are less studied. However, these female behaviours might contain reliable information about female's motivation to copulate [see 13, 22, 23]. More studies are therefore needed to fully understand the role of female behaviours in primate sexual communication.

In several primate species (e.g. baboons, chimpanzees and mandrills) the anogenital skin gradually swells during the menstrual cycle, changing in shape, turgidity and colour. The swelling reaches its maximum size around the time of ovulation, before the skin rapidly returns to its non-swollen state [26]. Studies on visual signals have generally focused on the size of the sexual swelling, whereas few studies have simultaneously investigated the role of its other components. These include skin colour or shape, which may also contain reliable information about the timing of the fertile phase. For example, the size of the swelling in baboons has been found to contain relevant information on the timing of ovulation [10, 22], whereas sexual skin colour seems to be uninformative concerning the intra-cycle probability of fertility [16, 22]. Besides size and colour, the shape of the swelling may also contain information on female intra-cycle differences in chacma baboons and mandrills [26]. Taken together, these results confirm that, in order to understand the role of one complex signal in the framework of multimodal sexual communication, it is important to investigate the role of each dimension of a signal. Besides olive baboons [16, 22], the relationship between sexual skin coloration and the cycle phase has been studied in some primate species lacking obvious signals of fertility (e.g. swellings). Changes in face coloration, but not in hindquarters, were found to be related to the timing of ovulation [rhesus macaques: 15]. Similarly, women's facial attractiveness was found to increase around ovulation, suggesting that visual cues also advertise fertility status in humans [14]. Nevertheless, the role of the different visual signals and the function of red skin coloration in ovulatory signalling and mating choices are still far from fully understood.

Among primate species, auditory cues in a sexual context (e.g. copulation calls) have been particularly well described [baboons: 19, chimpanzees: 18, macaques: 27]. Maestripieri and Roney [28] have suggested that copulation calls play an important role in female postcopulatory strategies. These

auditory cues may promote competition between males, and potentially between sperm, as well as mate-guarding by the consorting male, by informing other males that copulation has occurred. Therefore, females may simultaneously assure and confuse paternity by copulating with several males, including the dominant one, and thus reduce the risk of infanticide. However, the question of whether copulation calls act as a cue of ovulatory signalling in primate species is still open. In humans, the attractiveness of a woman's voice is known to be greater during the fertile phase [17], and it has been suggested that auditory cues are linked to sexual hormone levels (e.g. oestrogen and progesterone), but do not accurately indicate the probability of ovulation in non-human primates [29]. This contrasts with recent studies on crested macaques [24] and olive baboons [22], which both reported an increase in calls during the expected timing of ovulation. Moreover, our study [22] found that the proportion of ejaculatory mounts that elicited a call tended to be higher during the fertile phase. Thus, it seems premature to assume that copulation calls are uninformative about the timing of ovulation in all primate species.

Finally, whereas olfactory cues are known to play an important role in sexual communication in a number of mammal species, few studies have investigated their role in primate ovulatory signalling [30, 31]. Olfactory cues are known to provide information on individual identity or rank in lemurs and mandrills [32, 33], and to influence human mating preferences [20]. Among non-human primates, sniffing behaviours have been reported in sexual contexts [21, 34]. Therefore, there is ample reason to suspect that olfactory cues may play a greater role in primate ovulatory signalling than previously suggested. Along with Clarke et al [21], Rigail et al [22] found that male baboons tended to perform more olfactory inspections during the fertile and post-fertile phases (i.e. when consorting is established), and that those inspections were mostly associated with post-inspection ejaculatory mounts. These results suggest that males may have access to olfactory cues that may either encode information about the timing of ovulation, through subtle changes in vaginal secretions' composition, or may promote male mounting behaviours and sperm production. These results in baboons are in agreement with findings in macaques showing that olfactory cues elicited both endocrinological (i.e. increased testosterone levels) and behavioural responses (e.g. ejaculatory mounts) in males [35]. However, it is important to note that few studies have investigated the composition of vaginal secretions [33] in detail, so that their role in ovulatory signalling remains unclear for most primate species including humans.

All together, studies assessing how different signals might combine to influence patterns of male mating choices suggest that females exhibit several cues that could contain information about the timing of ovulation (sexual behaviours, size of

the swelling or skin colour, copulation calls and olfactory cues). However, the potential interactions between these cues have been less investigated and little is known about their spatial and chronological distribution. Our recent results for olive baboons [22] suggest that different types of cues, i.e. long and short-distance cues, may interact and create a complex framework of ovulatory signalling.

Male responses to female sexual signals and the establishment of male and female mating strategies

As suggested by Candolin [1], the use of multiple cues and signals may allow a more accurate assessment of female reproductive status and a decrease in mate choice errors, as females are less able to "cheat" about their fertility when displaying multiple cues. The repertoire of signals includes long-distance and short-distance cues, for which various males may have a differential access.

Visual (e.g. face and hindquarters coloration, swelling size) and auditory signals (e.g. copulation calls), may act as long-distance cues allowing all males to discriminate intra-cycle differences in fertility. In baboons, the frequencies of some female proceptive behaviours are positively correlated with the swelling size during the fertile phase [22]. This suggests that behavioural signals may act redundant signals by reinforcing the information already perceived through visual cues. Whereas those signals seem to be accessible to all males, olfactory cues may only be accessible at close range (short-distance cues), i.e. to the consorting male, due to the different active spaces of signals [21, 22]. Therefore, all males may be able to discriminate the fertile phase, but only consorting males would be supposed to accurately determine the timing of ovulation and concentrate their mating efforts. This spatial dissimilarity in the availability of sexual signals may allow males and females to establish different mating strategies.

These results thus suggest that the use of sexual signals by males and females enable them to establish different mating strategies. We suggest that males may gain more information about the probability of ovulation, by combining multiple cues, and thus reduce the time and energy spent on inspecting females. Males may use a first cue which is less costly to investigate (e.g. swelling size) and then a second one that may be more informative while more costly (e.g. olfactory cues) [see 22]. They may also be able to discriminate "cheaters", i.e. females who display misleading information about their reproductive status (e.g. by exhibiting a large swelling outside the fertile phase), by using a set of different informative cues, which decreases the risks of mate choice errors. Males could thus reduce the cost of mating (sperm production and mate-guarding) by focusing their sexual interest on

the most reliable mates (i.e. cycling females in the fertile phase). On the other hand, we suggest that the use of multiple sexual signals by females may be a trade-off between the costs of ovulatory signalling (e.g. changes in swelling size and skin colour) and the benefits of mating (i.e. mate-guarding). By combining long-distance cues with short-distance cues, such as olfactory signals, to which different males (consorting and non-consorting) have a differential access, females may assure paternity (by promoting mate-guarding by the consorting male) and simultaneously confuse paternity (by increasing competition between males). Moreover, this spatial difference in the availability of sexual signals may allow an indirect female mate choice, as only a subset of males will have access to reliable cues of ovulation.

Conclusion

This review shows that in most primate species, including humans, ovulation does not seem to be concealed. Non-human and human primate females display several ovulatory cues or signals, which are more or less advertised (e.g. exaggerated sexual swellings) and others more subtle (olfactory cues). This complex set of sexual signals may allow males to determine the fertile phase with more or less accuracy. Our review underlines that human and non-human primates share a general pattern of ovulatory signalling. However, the expression of sexual signals or cues varies among primate species at different levels, for example baboons or macaques display obvious visual signals such as swellings or changes in skin redness whereas visual cues of ovulation are more subtle in humans. This wide diversity of signals may be due to the different types of pressures (e.g. environmental, sexual) that species may have undergone. As a result, some particular adaptations of ovulatory signalling might evolve as specific derived traits in some species, and be lost in others. More comparative studies on multimodal ovulatory signalling would be needed to fully understand the underlying ecological pressures underlying the evolution and function of female sexual signals in human and non-human primates.

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