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ORIGINAL ARTICLE

Phylogenesis of mammal sexuality. Analysis of the evolution of proximal factors☆

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Summary The aim of this article is to make a precise identification of the factors involved in the evolution of human sexuality. The analyses presented concern mainly the evolution of proximal factors that govern prototypical heterosexual copulation in mammals. The data was collected from a review of the literature concerning the evolution of neurobiological factors of sexual behaviour in mammals. Several studies, in biology, genetics and neurosciences, have shown that some of these factors have changed over the course of evolution. In primates, the olfactory circuits are impaired, sexual activities are dissociated from hormone cycles (reproduction and sexual behavior have become independent one from the other), the lordotic mating reflex is no longer functional and the cortex is highly developed in human beings. For these reasons, the analysis of available data suggests that: (1) the dynamics of sexual behaviour has significantly evolved from the anthropoid primates; (2) the functional dynamic of heterosexual copulation is very probably disorganized; (3) the behavioural dynamics that emerge with the hominidae — from factors that still exist in heterosexual copulation — would seem to be based on a quest for erotic reward, by stimulation of the erogenous zones; and (4) in humans, due to the extensive cognitive development, sexuality is structured by cultural representations.

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Introduction

Ethological observations of sexual behaviour in mammals show that there are major differences between ''the stereotyped sexual behaviour in non-primate mammals and the astounding variety of human sexual behaviours'' (Agmo, 2007). Physiological and neurobiological data have shown the changes in some of the factors that govern mammal reproduction, and which appear to explain the evolution of sexuality.

The aim of this article is to review the literature that addresses these biological changes, to relate these to the

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behavioural changes that have been observed, and to look for correspondence between structural changes and functional evolution.

Proximal and ultimate causes of evolution

To achieve better understanding of how these behaviours have evolved, it is useful to distinguish several types of cause for these behaviours: distal or ultimate causes (functional and phylogenetic causes) and proximal causes (ontogenetic, structural and immediate causes). Distal or ultimate causes are (in simple terms) all the factors that influenced ancestral species; conversely, proximal causes are factors that influence current species and organisms, particularly in their immediate environment.

Functional causes are linked to basic biological functions. Under the influence of natural selection, some behaviours have evolved because they were better adapted to ensure the survival of the individual and/or the species. Phylogenetic causes are causes that are inherited via the ancestral phylum. For example, pheromones are one of the causes of mammal behaviour, because this type of olfactory organisation is common to all vertebrates. Ontogenetic causes are factors that emerge as an organism develops. For example, hormones cause the development of motor and olfactory structures that enable heterosexual copulation. Structural causes are the factors that govern a behaviour that is specifically organised within the organism. An example of this is the hard-wired circuits responsible for the sexual lordotic reflex in females. Immediate causes are internal stimuli (hormone balance, body clock, etc.) or external stimuli (sensory stimulus) that trigger a behaviour.

In general, it is difficult to describe in a reliable way, and to understand, the ultimate causes of evolution. Ancestral species have disappeared, and archaeological material is rare and can be difficult to interpret. Ecological and/or evolutionary causes are not always easy to identify (Young et al., 2010), and can depend on unpredictable phenomena (Nei et al., 2008, and see Jacob, 1977). New discoveries and concepts can lead to profound changes to theoretical models, such as epigenetic mutations in evolution (Cubas et al., 1999), ''group selection'' (Wilson and Wilson, 2007), and coevolution (using the example of humans and dogs). Another example, the theory of replacement, which was dominant in the 1990s, assumed that *Homo sapiens* had ''replaced'' the other species in the genus *Homo* (by eliminating them or because they had a better capacity to adapt). Recent studies in genetics, however, suggest that there are interbreeding between these species (Green et al., 2010; Seguin-Orlando et al., 2014), suggesting that a different theoretical model of evolution is required (the interbreeding theory) and suggests that the sexuality of some species in the *Homo* genus could cross species lines and that some species could be interfertile (Condemi et al., 2013).

Conversely, it is easier to identify proximal causes, as current species can be observed and studied experimentally. For this reason, this article primarily examines the proximal causes of the evolution of mammal sexual behaviour. The study focuses on copulation, the crucial behaviour in which sperm is deposited in the vagina, which in turn enables fertilisation. As copulation is a fundamental behaviour that is absolutely necessary for the survival of a species, it is likely that it is subject to intense pressure from the mechanisms of natural selection. This is why a study of the evolution of the factors that govern copulation is likely to shed light on the evolution of sexual behaviour, particularly in primates and in humans. Data on female mammals are given most attention, as the evolution of sexual behaviour in female mammals is well-understood, and in particular the behavioural differences between species are large, easy to understand, and significant. The case of male mammals is a little more complex, but fairly similar in terms of the evolution of the main factors (see Wunsch, 2014 for additional explanation).

Main biological factors governing mammal sexuality

In a behavioural study, it is very important to identify the primordial factors, in other words the factors that are most important, which are quasi-innate (Kobayakawa et al., 2007; Moncho-Bogani et al., 2002) and that act first. Mammals have great capacity for learning, and many characteristics that are observed in adults are acquired during development and via interaction with the environment and members of the same species. Many studies, particularly rodent studies, have sought to identify the main factors that govern sexual behaviour (Knobil and Neill, 2005). These factors, both primordial and proximal, govern the reciprocal attraction of male and female (the appetitive phase), copulation (consummation phase), sexual learning, and overall control of reproduction.

Hormones are a major factor in mammal reproduction. They play two main roles: an organisational role during development, and an activation role in adults. Sex hormones activate, co-ordinate and control most other factors involved in reproductive behaviour (Thibault and Levasseur, 2001).

The olfactory circuits (olfactory epithelium, vomeronasal organ, vomeronasal amygdala), which detect and process sex pheromeones, are responsible for the initial part of reproductive behaviour, i.e. evaluation of partner, arousal, and then reciprocal attraction of the partners (Keller et al., 2009).

Sexual reflexes, which are hard-wired into the nervous system, enable copulation and fertilisation of gametes, once the partners are in physical contact. In mammals, there are three types of innate sexual reflexes: motor, autonomous and neuroendocrine reflexes. The motor reflexes are the lordotic reflex (Pfaff et al., 1994) and immobilisation in females, and pelvic thrusts and intromission in males (Meisel and Sachs, 1994). Autonomous reflexes are vaginal lubrication in females, and erection (Giuliano and Rampin, 2004) and ejaculation (Allard et al., 2005) in males. In some species, there is a neuroendocrine ovulation reflex, which is triggered by coitus (Spies et al., 1997). This reflex, which appears to have existed in all the ancestral species (Pavlicev and Wagner, 2016), optimises fertilisation by releasing the egg when sperm is deposited in the vagina.

The reward system, which is primarily activated by the stimulation of erogenous zones during copulation (Cibrian-Llanderal et al., 2010; Matsumoto et al., 2012), takes part in many sexual learning (Pfaus et al., 2012).

Finally, cognitive processes adapt the sexual behaviour to the environment, and further improve adaptation via memory and evaluation of previous sexual experiences.

The remarkable fact is that all these factors are responsible for true reproductive behaviour. These factors mean that without prior learning, heterosexual arousal can be triggered (Sachs, 1997), and an autonomous or motor copulation sequence can be executed (Pfaff et al., 1994). They also mean that learning can be directed towards optimisation of heterosexual copulation (Pfaus et al., 2012). This means that everything is organised in order to ensure heterosexual copulation and fertilisation, when mature gametes are present, and at the right time in seasonal breeding species.

However, in primates, it is observed that several of these proximal factors have undergone changes, which has led to evolution of the dynamics of sexual behaviour.

Evolution of proximal factors of sexuality

Recent studies have shown that in mammals in general, and primates in particular, the proximal factors that govern sexual behaviour have evolved (Fig. 1).

In the following sections, the main observed changes to the proximal factors that govern sexual behaviour are shown, along with the probable implications of these changes on the dynamics of such behaviour. It should be noted that ultimately only those analyses of evolution that shed light on human sexuality are shown.

Impairments in olfaction in the Catarrhini

In mammals, olfaction is composed of several sub-systems, which are generally located in the nasal cavity, usually the olfactory epithelium and the vomeronasal organ. Several molecular constituents of these sub-systems have changed with evolution, which has impaired inter-animal communication that uses chemical signals.

Evolution observed

In the olfactory epithelium, there have been particularly significant changes in humans: around 60% of the genes for olfactory receptors have become pseudogenes (Gilad et al., 2003). The vomeronasal organ, which plays a major role in the detection of innate olfactory signals, is impaired in old-world primates (the Catarrhini: Cercopithecidae, Hylobatidae and Hominidae). Genes for protein TRPC2, an ion channel that is essential for the sensory activity of the vomeronasal organ, have become pseudogenes (Zhang and Webb, 2003). More specifically, in humans, around 90% of genes for pheromone receptors (the *VR1*, *VR2* and *TAAR* genes) are altered, both in the vomeronasal organ and in the olfactory epithelium — Nei et al., 2008.

These alterations in several types of olfactory genes are not isolated incidents. A general evolutionary trend can be observed: chemically-mediated senses (smell and taste), which are so fundamental in animals (Brennan and Zufall, 2006; Wyatt, 2009), lose their importance in primates (Liman, 2006; Swaney and Keverne, 2009).

Functional implications

Pheromones are involved in numerous functions (Keller and Bakker, 2009), such as partner evaluation (Hurst, 2009), heterosexual orientation (Martinez-Ricos et al., 2008; Roberts et al., 2010; Stowers et al., 2002; but also see Pankevich et al., 2006; and Kimchi et al., 2007), the forming of attachment between copulation partners (Young and Wang, 2004) and sexual conditioning (Lanuza et al., 2008). An impairment in pheromone detection capacity leads to an impairment in these functions, the extent of which will vary depending on the number of genes that have changed into pseudogenes in each species. This is what is seen in the Hominidae — and in the species that is probably closest to humans, *Pan paniscus* (bonobos) — in which each Hominidae engages in both heterosexual and homosexual activities, with no exclusive attachment to one partner (Bagemihl, 2000; De Waal, 1988).

Functional disappearance of the lordotic reflex in the Hominidae

In mammals, once animals are in physical contact, copulation occurs via a succession of sexual reflexes (lordosis, vaginal lubrication, pelvic thrusts, ejaculation, etc.). From the Hominidae onwards (orangutans, gorillas, chimpanzees and humans), the lordotic reflex function disappears and reflex-governed copulatory activities become acquired sexual activities.

Evolution observed

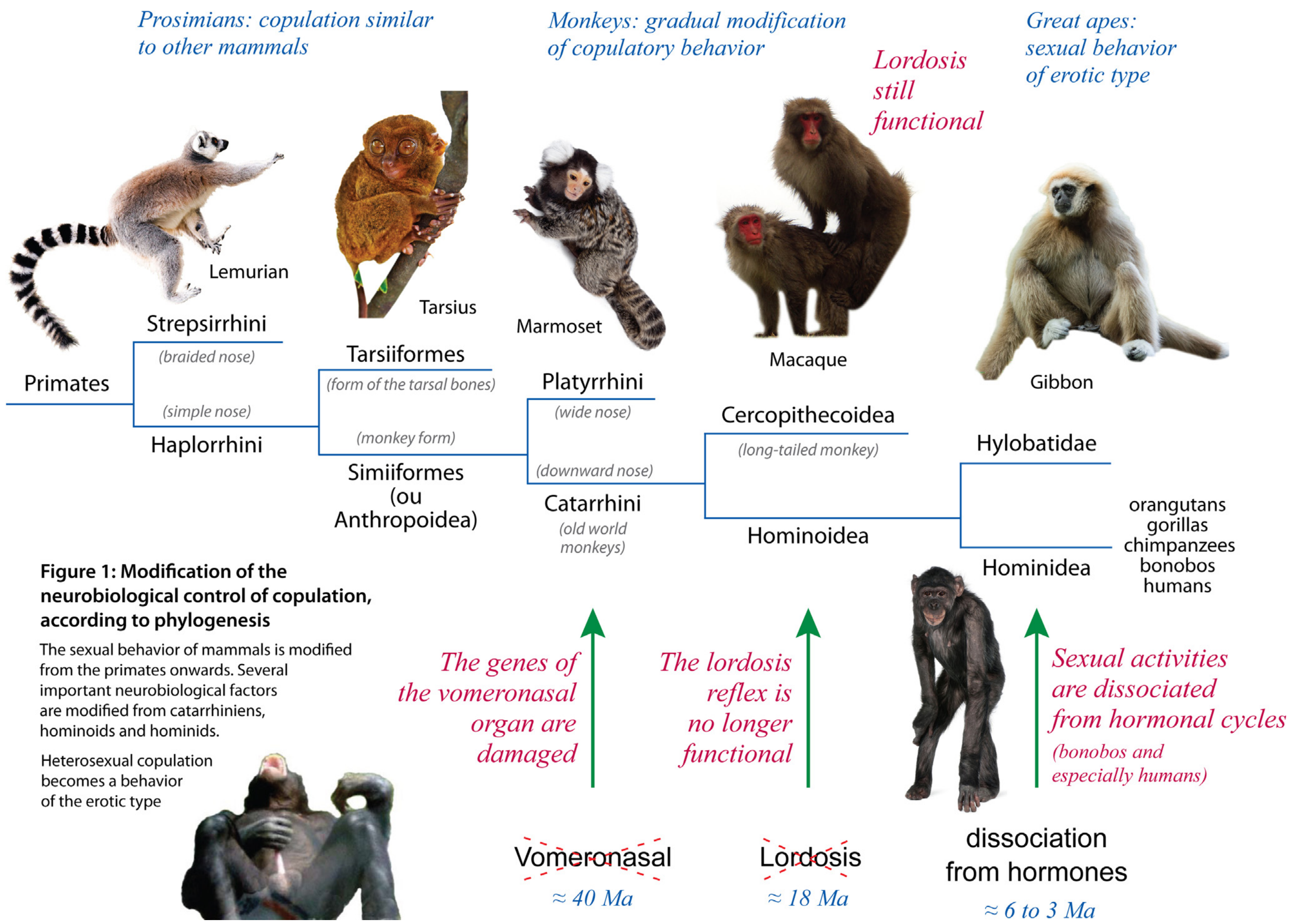
The sexual lordotic motor reflex, which is essential to copulation for females of many species, is hard-wired into the nervous system (Pfaff et al., 1994). It has been observed that this lordotic reflex, as well as the immobilisation reflex, is present in non-primate mammals. It is also present in prosimian primates (lemurs, tarsiers, etc.).

From the anthropoids onwards (simians/monkeys) there is a gradual loss of the lordotic reflex, in parallel with the loss of major hormone effects and oestrus (Dixson, 2009: 101—102). In the Cercopithecidae (macaques, etc.), the lordotic reflex is still functional, but it is part of sexual and sociosexual activities such as presenting. This sociosexual presenting (which follows the same sequence as lordosis: curvature of the back and lateral movement of the tail, which presents the genital region to view) is no longer dependent on hormonal control, but occurs in response to a social situation (Hanby, 1976).

In the Hominidae, lordosis and immobilisation are absent, even during the phase around ovulation. Female receptiveness is neither obligatory nor passive. The female can actively avoid or refuse the male, or can terminate the encounter (Dixson, 2009: 101—102). In female humans, sexual stimulation of the rump no longer triggers immobilisation or the lordotic reflex position. A woman can have a full sexual life without ever adopting a lordotic position.

Functional implications

In females of the Hominidae, the motor reflexes involved in copulation have been replaced by new sexual activities, several of which have nothing to do with copulation or fertilisation. For instance, activities that involve sexual stimulation of the milk-producing organs (breasts) or the



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extremities of the digestive tract (the mouth, via kissing, and the anus via sodomy), or mutual masturbation. Even for copulation, the innate female lordotic position has been replaced by learned positions such as face-to-face coitus. Functionally, we thus observe in sexual behavior a transition in the motor control of sexual activities: in particular, in females, the innate sexual motor reflexes that enable copulation have been replaced by learned erotic behaviour (Wunsch, 2014).

Dissociation of sexual activity from hormone cycles in the Hominidae

In mammals, sex hormones (oestrogens, androgens, etc.) play a major role in governing sexual behaviour. From the Hominoid primates (chimpanzees and humans) onwards, it is observed that sexual activity has gradually become dissociated from the hormone cycles that govern reproduction.

Evolution observed

The evolution of hormonal control is particularly easy to observe in female mammals. In non-anthropoid females (nearly all mammals apart from monkeys), sexual activity depends on the presence of a maximum hormone concentration, particularly oestrogen. As a simplification, peak oestrogen concentrations simultaneously trigger ovulation (physiological effect) and reproductive behaviour (motivational and behavioural effects), such that copulation is coupled with ovulation (Fig. 2, top, female rat). In most mammals, an increase in blood oestrogen concentration simultaneously triggers physiological and behavioural effects, such that sexual activity only takes place when the reproductive organs are in a fertile phase. Sperm is thus only deposited in the vagina when a mature egg is present (Thibault and Levasseur, 2001).

However, a major evolutionary step has been observed, starting with the anthropoid mammals. Sexual activity for females is no longer limited to the period around ovulation. It can even take place after oophorectomy. Pre-pubescent females can engage in sexual activity, unlike non-anthropoid females (Dixson, 2009: 93). This dissociation of sexual activity and hormone cycles becomes obvious when drawing comparisons of hormone cycles and periods of sexual activity between species (Fig. 2).

This dissociation of sexual activity and reproduction has occurred gradually, and became significant in the hominInae. There is a major dissociation in *Pan paniscus* (bonobo) (Fig. 3 — Furuichi, 2011). There is a nearly complete dissociation in female humans, who can engage in sexual activity throughout the cycle. Although there is a residual oestrous

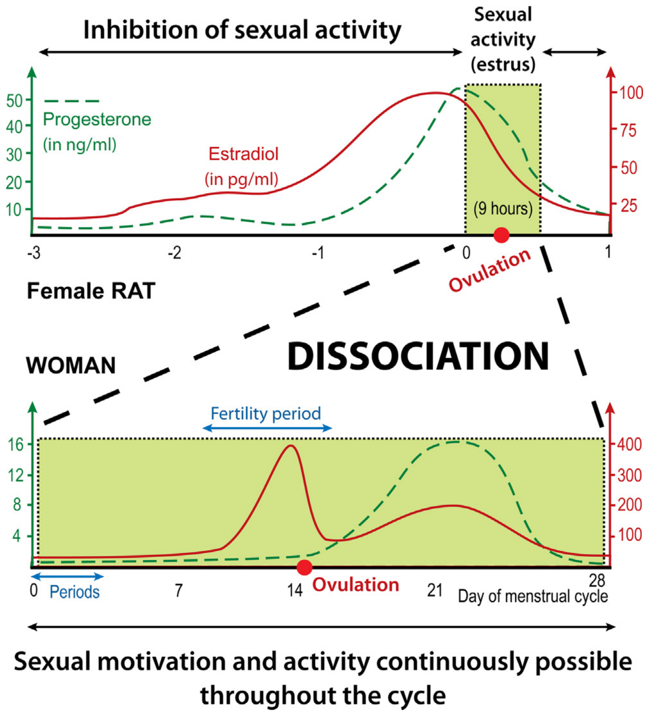

Figure 2 Dissociation of sexual activity from reproduction. In female rodents, sexual activity only takes place during the period in which hormone concentration is maximum and when ovulation takes place, while in female humans, activity can take place at any time in the cycle. Sexual activity gradually becomes independent of variations in hormone levels (Hormone graphs from Thibault and Levasseur, 2001). Shaded (or green), periods in the cycle when sexual activity is possible (in female rats, around 9 hours in a cycle lasting 4—5 days).

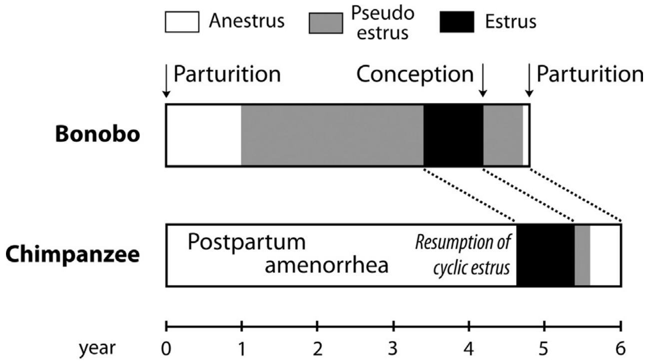

Figure 3 Dissociation of sexual activity from reproduction in *Pan*. There appears to be a meaningful dissociation of sexual activity from hormone cycles in *Pan paniscus* (bonobo). The most noticeable difference is the long period of postpartum amenorrhoea in *Pan troglodytes* (common chimpanzee). Female chimpanzees are only in oestrus and receptive for on average 12.5 days in a cycle lasting 11.5 months, before 5 years of postpartum anoestrus. Bonobos' receptiveness does not reduce during lactation (De Waal, 1988). Female bonobos are in oestrus or pseudo-oestrus and receptive most of the time between births (Furuichi, 2011). Diagram adapted from Furuichi (2011).

influence (Tarin and Gomez-Piquer, 2002) and a seasonal influence (Foster and Roenneberg, 2008), there is no longer any behavioural inhibition.

Functional implications

It is very important to note that hormones still play a major biological role in all primates. The evolution of the role of hormones has affected how hormones govern sexual behaviour before puberty and during the oestrous and seasonal cycle. In most mammal species, sexual activity — particularly for females — is inhibited at all times apart from during oestrus and the reproductive season (in seasonal breeders). Conversely, in humans, these hormonal influences have weakened (Brown et al., 2011) and sexual activity can take place at any time in the year and in the hormone cycle (Dixson, 2009).

Human sexuality has become a continuous phenomenon, and is now almost totally independent of the physiological control of reproduction. Unlike most mammals, male and female human beings can be sexually motivated, can engage in erotic activities and can experience erotic pleasure at any time in the hormone cycle and at any time of year. Sexuality is practically dissociated from reproduction.

The functional importance of erotic reward

The reward system (or appetitive reinforcement system), as well as the aversive system (or negative reinforcement) are two basic systems that enable learning of behaviours that are adapted for the survival of the organism and the species (Kolb and Whishaw, 2008). It is observed that from the anthropoid primates onwards, the reward system associated with erogenous zones becomes continuously functional.

Evolution observed

The structural organisation of this reward system, which is linked to the primary erogenous zones (penis and clitoris) has not evolved significantly in mammals (Berridge and Kringelbach, 2008). Functionally, experiments have shown that the reward system is governed by sex hormones, in order to favours types of learning that optimise reproduction (copulation, attachment, breastfeeding, etc. — Ferris et al., 2005).

However, because of the hormonal, olfactory and motor changes described in the previous sections, changes have occurred in the functional dynamics of this system. In the anthropoid primates, it has become continuously functional. Humans can obtain erotic reward (via masturbation, for example) at any time in the hormone cycle and at any time of year.

There has also been an observed evolution in erogenous zones: several regions of the human body, not including the genitals, can become erogenous (Turnbull et al., 2013; Wunsch, 2007). The body hair, which plays a social role in mammals (Morrison et al., 2010), can transmit erotic sensations in humans (Jonsson et al., 2015). The physiological mechanisms responsible for the erogenous nature of a large part of the body are poorly understood; it appears that the erogenous zones must be made of mucocutaneous tissue, must have a high density of receptors, must cause high levels of arousal in the brain, and must have a relationship

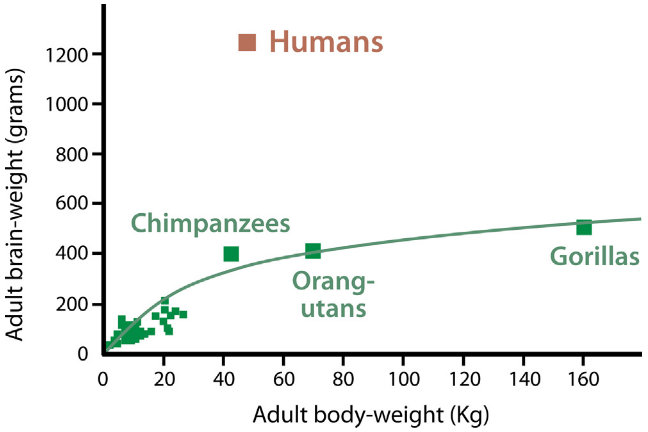

Figure 4 Corticalisation index for primates.

with the reward system (Schober et al., 2011; Winkelmann, 1959).

Functional implications

In non-primate mammals, because of hormone and pheromone constraints, the reward system relating to the erogenous zones (penis and clitoris) is mainly activated during heterosexual copulation and the breeding season (just a few days per year in females from seasonally breeding species).

Conversely, since hormone, olfactory and motor constraints have weakened in the Hominidae, sexual activity is no longer limited to reproductive seasons or to an opposite sex partner, and the reward system can then be activated each time the erogenous zones are stimulated (via masturbation, with one or more partners; and at any frequency up to several times per day throughout the year — Bagemihl, 2000). Because sexual activity has become dissociated from the hormonal reproductive cycles, sexual reward is now barely dependent on physiological constraints on reproduction, although there is still some residual influence (Dreher et al., 2007). And every action that activates the reward system — which is perceived as a feeling of erotic pleasure — can result in a learned motivation to repeat this erotic activity (Georgiadis et al., 2012). For all these reasons, learned sexual motivation in humans is no longer limited to heterosexual copulation, but extends to all types of erotic stimulation of the body (Pfaus et al., 2012; and see Agmo, 2007).

Corticalisation of the nervous system in mammals

In mammals, there is a relatively gradual development of the neocortex, which a process known as corticalisation (or encephalisation, or telencephalisation). This development of the multimodal associative areas in the cortex leads to the gradual emergence of complex cognitive abilities, which have enabled the human species to develop culture.

Evolution observed

It has been noted that this corticalisation is particularly advanced in humans (Fig. 4), as the encephalisation index (brain weight/body weight ratio) is 3.5 times higher in humans than in the other Hominidae (Bogin, 1997; Gilbert, 2013).

In particular, the development of the prefrontal cortex became significant in various Homininae species (*Homo habilis*, *Homo erectus*, *Homo neanderthalensis*, etc.) and this process culminated in *Homo sapiens* (Gazzaniga et al., 2002) (Fig. 5).

Functional implications

As the prefrontal cortex receives information from all the main brain structures, its specific anatomical and functional organisation allows higher cognitive functions to emerge (in particular language, working memory, reasoning, and executive functions in general — Miller et al., 2002). These complex cognitive processes can have an influence on the activity of subcortical structures (top—down processing), such as sensory circuits and the reward system (McCabe et al., 2008).

All these cognitive abilities, particularly categorisation, planning, generalisation, abstraction and symbolic thought, are necessary to the creation of rules, norms, beliefs, values, morals and ethics. Because of the sophistication of these types of cognitive processing, erotic activities are no longer simple responses to the characteristics of an environment or partner. Human sexual behaviour is no longer simply erotic behaviour, and attachment is no longer just a way of seeking physical closeness. Sexual pleasure, and individual and social significations of pleasure, can be incorporated into complex behaviours or symbolic situations.

Functionally, cognitive capacity enables human beings to interpret what they observe and feel, and to create prescriptive norms and values. For example, love can be characterised as free, romantic, courtly or platonic, while variations in sexual differentiation (Blackless et al., 2000) can be interpreted as additional genders (up to 5—6 genders — Herdt, 1996; Ringrose, 2003). Human beings can even designate sexual pleasure as an evil phenomenon and can enforce the suppression of all sexual desire, idealising chastity and purity (Brundage, 1987).

Functional analysis: evolution of sexual behaviour

In humans, several of the factors that govern mammal sexuality have evolved out: the sexual lordotic reflex; olfactory circuits, particularly those involving pheromones; sexual activity and hormone cycles are now practically dissociated; the reward system is continuously functional; and cognition has developed to such an extent that culture has emerged (Fig. 6).

What are the functional implications of these various structural changes and impairments in terms of the overall dynamic of sexual behaviour?

In anthropoid primates, we observe a gradual ''disorganization'' of heterosexual copulation, and in parallel there emerges in the Hominidae a behaviour of stimulation of the erogenous zones. In humans, we also see that cultural cognitive representations structure sexuality.

It should also be noted that, as the Hominidae form only about 0.1% of mammal species (Wilson and Reeder, 2005),

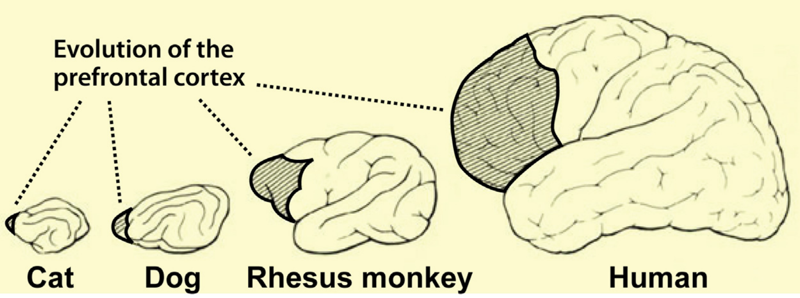

Figure 5 Development of cortical areas that are involved in cognition. The prefrontal cortex (grey) is the brain structure that has evolved to the greatest extent in humans. The prefrontal cortex is responsible for the most complex cognitive processes (e.g. symbolic thought, planning, reflection).

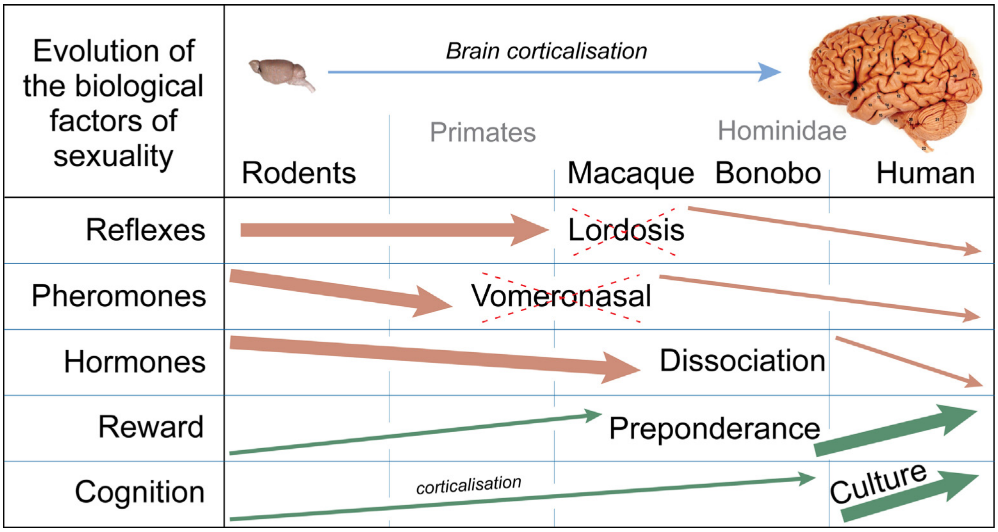

Figure 6 Summary diagram: evolution of the main factors that govern sexual behaviour in mammals. From Wunsch (2014).

the sexuality of humans is not representative of mammal sexuality in general.

Disorganization of copulation and emergence of ''erotic'' behaviour

In mammals, and in particular in primates, gradual changes (such as corticalisation) or rapid changes (such as changes to the vomeronasal organ) appear at different era and do not affect all species. This is why each species has specific biological characteristics, and has a sexuality that is to some extent distinct to that seen in other mammals and primates.

However, there do not appear to be any major transformations of these various factors. The overall organisation is maintained, and it appears to be just some genetic or cellular elements that are altered. Functionally, these single changes appear to lead to a gradual ''disorganization'' of heterosexual copulation. The dissociation of sexual activity from hormone cycles means that such activity can take place at any time, even if there are no mature gametes available. The change in olfaction weakens the attraction to the opposite sex. The functional disappearance of the lordotic reflex leads to the disappearance of immobilisation and a specific position for copulation. Because of these changes, the initial functional dynamic, in which sexual behaviour is optimised for heterosexual copulation when mature gametes are present, no longer prevails. The proportion of sexual activity, which cannot result in reproduction increases.

In parallel, as the reward system associated with the primary erogenous zones is always functional, it appears that the behavioural dynamic evolves towards activities in which these erogenous zones are stimulated (Fig. 7). This functional model appears to be corroborated by ethological, ethnological and experimental observations. Ethological observations show that sexual activity in the Hominidae is no longer primarily directed towards heterosexual copulation, but towards the stimulation of the genital erogenous zones (Bagemihl, 2000). This is particularly evident in *Pan paniscus* (bonobo — De Waal, 1988), in which there has been the maximum number of changes in the factors that govern copulation. Even social non-sexual contact primarily involves the genitals (Hanby, 1976). In humans, observations of hunter-gatherer societies, which are considered to be close to the origins of the human species (Konner, 2010), suggest that sexuality develops in the early years of life via various activities in which the genital erogenous zones are stimulated (genital play, masturbation, mutual masturbation, penetration, coitus — Henry, 1949; Henry and Henry, 1974). This type of sexuality appears to become in adults a

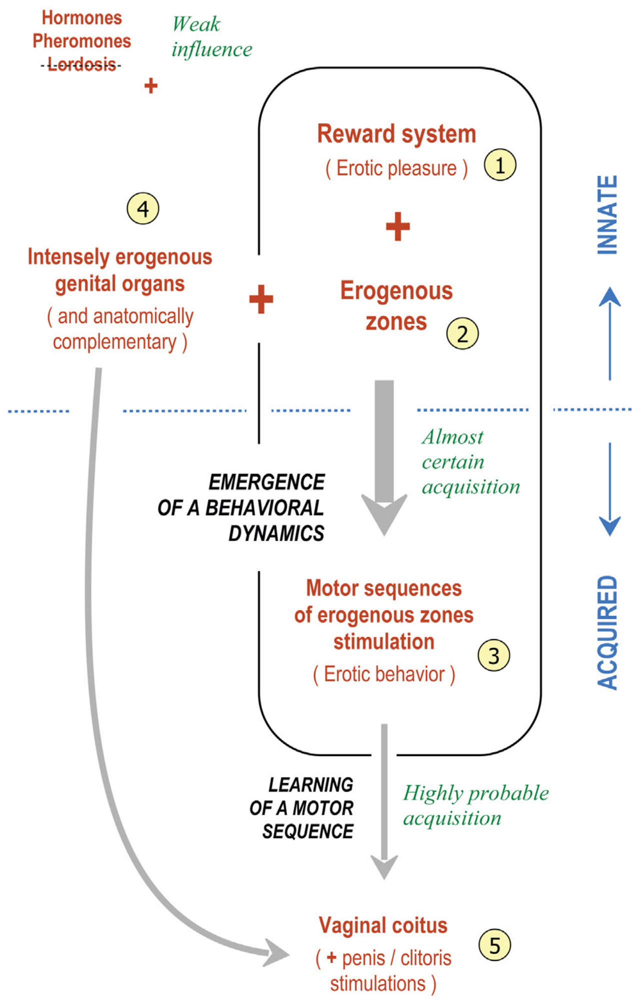

Figure 7 Probable dynamic of Hominidae sexual behaviour. Functional modifications, which are triggered by the structural evolution described in Fig. 6, are shown schematically in the model above. In the Hominidae, the lordosis reflex is no longer functional, hormones and pheromones play a less important role. The reward system [1] associated with erogenous zones [2] becomes functionally more important and appears to lead in nearly all subjects to the acquisition and repetition of a variety of motor sequences involving erogenous zone stimulation [3]. The existence of innate genital organs that are complementary and that are intensely erogenous (lead to orgasm) [4], appears, during erotic activity, to lead to a greater probability of vaginal coitus [5], which is necessary for reproduction (Wunsch, 2007, 2014).

mainly genital sexuality (Stephens, 1972). This developmental and functional dynamic, which is focused on the primary erogenous zones, seems to have been confirmed experimentally; analysis of human sexual activity suggests that — if the cultural context permits — individuals prefer to engage in activity ''that procures the most intense stimulation of the most erogenous areas of the body (penis/clitoris, vagina)'' (Wunsch, 2007).

In a functional analysis, it has been observed that the heterosexual copulatory behaviour seen in mammals appears to have evolved, in the Hominidae, into erotic behaviour.

Erotic and cultural sexuality in humans

As previously stated, the cortex, and particularly the prefrontal cortex, is highly developed in humans. This large increase in cognitive capacity over the course of evolution means that signification and particular values can be created and attributed to the stimulation of erogenous zones. Humans can invent refined erotic practices (e.g. the Kāmasūtra of Vātsyāyana) or indeed can confine sex to the purposes of reproduction. Sexual activity can be experienced as a ritual or duty (conjugal duty), or can be purely hedonistic, or can be instrumentalised (Meston and Buss, 2007). All human activity can be imbued with interiorised norms or symbolic meaning, which are transmitted by social learning and which accumulate over the generations (Dean et al., 2012). Here we see what divides the human species from others: the development of culture.

Historical (Aries, 1973; Cantarella, 2002; Rocke, 1998) and ethnological data (Ford and Beach, 1952; Gregersen, 1983; Marshall and Suggs, 1971; Miletsky, 2002; Werner, 1986) show the diversity of sexual values and cultural practices, which vary widely from one society to the next. Sociological studies such as those by Ira Reiss (1986), and William Simon and John Gagnon (2008) have shown the major importance that culture has for human sexuality. And this cultural influence appears to be exercised via cognitive processes, partly via the unconscious influence of cultural representations (Custers and Aarts, 2010), or via social mimetism (Lebreton et al., 2012).

In a functional analysis, it is observed that erotic behaviour in the Hominidae evolves into erotic and cultural sexuality in humans.

Conclusion

In most mammals, it is reasonable to state that there is a specific biological system for heterosexual copulation, which enables fertilisation via a deposit of sperm into the vagina.

In the evolutionary process, it appears that several proximal factors that govern heterosexual copulation have undergone change, particularly in primates. In particular, pheromone receptor genes are impaired, sexual activity is dissociated from hormone cycles (behavior and reproduction are dissociated), the lordotic copulation reflex is no longer functional and the cortex is highly developed in human beings. As a simplification, it is possible to say that the more these main neurobiological factors change, the more change is found in the sexual behaviour of a mammal species.

In the Hominidae, in which all these changes and evolutionary features are brought together, the functional dynamic of sexual behaviour has been significantly altered. The only system that remains wholly functional is the system of reward associated with the erogenous zones. For these reasons, the neurobiological factors that have changed shift the orientation of sexual activity away from heterosexual copulation and towards erotic stimulation of the most erogenous areas of the body. Functionally, it appears that heterosexual copulation has become ''disorganized'' and that the functional dynamic has evolved in favour of behaviour in which erogenous zones are stimulated.

In humans, because of the highly developed cortex, this behaviour involving stimulation of the erogenous zones (which can be qualified as ''erotic'') appears to be heavily structured by cognition and, in particular, by culture.

A functional analysis of the available data suggests that the heterosexual copulation dynamic that prevails among mammals has evolved, in humans, into an erotic and cultural sexuality.

Disclosure of interest

The author declares that he has no competing interest.

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