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ORIGINAL ARTICLE

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

S. Wunsch*

École pratique des hautes études (EPHE), 33000 Bordeaux, France

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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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* Appt 23, 68, rue Lamartine, 33400 Talence, France.
E-mail address: serge.wunsch@ouvaton.org

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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).

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