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Evolution from mammals' heterosexual reproductive behavior to human erotic bisexuality

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Abstract

What is the neurobiological dynamics of mammal and human sexuality ?

In rodents, mainly sexual hormones and pheromones, and secondarily sexual reflexes and reinforcement processes, would be the main innate factors at the origin of a genuine heterosexual reproductive behavior, the purpose of which is, at the favorable season, to achieve copulation permitting fecundation.

It would seem that during evolution, owing to the modifications of the brain of rodents into that of Man's, the hormonal and pheromonal factors have become secondary, whereas the cognitive factors and the reinforcement processes (or reward systems) have become predominant.

For these reasons, in Man, the behavior that leads to reproduction may be conceived not as an innate "reproductive behavior", but as an acquired "erotic behavior" involving behavioral sequences of stimulation of the most erogenous body zones by a partner – no matter his sex.

Keywords

Reproductive behavior, sexual behavior, bisexuality, heterosexuality, reinforcement, reward, erogenous zones, sexuality, Human.

NB: figures and references updated (02/2013)

1. Introduction

Fundamentally, is human sexuality heterosexual or rather bisexual ? What are the factors at the origin of human sexuality and reproductive behavior ? What are the most fundamental neurobiological processes which underlie the development and the dynamics of these behaviors? How does these behaviors emerge from the interaction between the various biological and environmental factors?

We first chose to study reproductive behavior, rather than sexuality, because it is the fundamental behavior, absolutely necessary for the survival of the species, and, therefore, probably subject to intense pressure from natural selection mechanisms. For that reason, the study of this behavior should allow us to highlight the main biological means which were selected by evolution to implement and control Man's various fundamental behaviors, including sexual behavior and sexuality. Furthermore, the understanding of reproduction and sexual behaviors is an important issue, for basic research as well as for sexual education, daily emotional life or sexology.

At present, it is generally assumed that sex hormones are the main factor at the origin of heterosexual reproductive behavior, by controlling the development of a neural circuit specific to sexual behavior and by activating it at puberty (e.g., see Fiske, 2004). However, it would seem that this model, highlighted in nonprimate mammals, is no longer valid for the most corticalized species.

Recent data suggest that probably during evolution the influence of hormones and pheromones decreased, whereas in hominoid primates it was reinforcement processes (or reward systems) that became the main factor at the origin of the learning of a behavior that enables reproduction (Agmo 2007).

This article presents a synthesis of the literature. All this data makes it possible to suggest an archetypical model of the reproductive behavior of mammals, and its evolution from rodents to Mankind.

2. Archetype of mammalian reproductive behavior

In the least corticalized mammals (nonprimates), current research has made it possible to identify many innate elements that can directly and indirectly take part in the appropriate realization of the fertilizing vaginal coitus. These innate elements can be instinctual as well as physiological or autonomous: the hormones can control a seasonal inhibition (copulation only takes place during the favorable season), a puberty inhibition (copulation only takes place at the period of maturity of the reproductive organs), an estrous inhibition (copulation only takes place at the periovulatory period); the pheromones allow the recognition of the partner of the opposite sex, whereas sexual reflexes (lordosis, erection, pelvic thrusts, ejaculation, reflex ovulation triggered by coitus) enable the innate motor execution of the vaginal coitus and fecundation.

These various elements, which are complementary, do not all exist simultaneously in the current mammal species. However, when trying to recreate the first mammalian organism, in particular by grouping together these various complementary elements, a genuine reproductive behavior appears in the original organization plan of mammals in a remarkable way: its sole purpose and behavioral sequences are the achievement of a heterosexual fertilizing copulation, carried out at the favorable season.

Thus, by carrying out a synthesis of current knowledge, completed by the last data which challenge the current accepted theories (Kimchi & Al 2007, Agmo 2007), it seems possible to model the factors and the dynamics of the archetypical reproductive behavior of mammals.

2.1 Innate primary factors of reproductive behavior

What would the innate primary factors that originate reproductive behavior be, and what would their respective functions be?

Research carried out for several decades in mammals has highlighted the existence of four innate primary factors: hormones, pheromones, sexual reflexes and reinforcement processes.

- **Hormones**. They regulate and coordinate most of the other factors of reproductive behavior (Balthazart & Fabre-Nys, 2001). Initially, during the organism development (organizational phase) they control the sexual differentiation of certain neural structures (preoptic nucleus, hypothalamus) involved in reproductive behavior (Simerly, 2002). Then, at adulthood (activational phase), they are involved in:
  - The activation of sexual behavior during: (1) the season favorable to reproduction (Aleandri & al., 1996), and (2) the favorable period of the physiological cycle of the female reproductive apparatus (estrous period).
  - A general sexual motivation.
  - The facilitation of sexual reflexes.
  - The emission of sexual pheromones.

- **Pheromones**. They especially enable the triggering of sexual motivation (via the principal and vomeronasal olfactory system; Keller & al., 2009; Moncho-Bogani & al., 2004; Yoon & al., 2005) and distinction of a reproductive partner of the opposite sex (via the vomeronasal system; Roberts & al., 2010; Stowers & al., 2002; Dulac & Torello, 2003).

- **Sexual reflexes** (motor, autonomous and neuroendocrinous).
  The motor sexual reflexes allow the attainment of the last phase of copulation. These reflexes are:
  - Lordosis (Kow & al., 2007; Pfaff & al., 1994) and / or immobilization.
  - Intromission (Meisel & Sachs, 1994).
  - Pelvic thrusts (Hart, 1968; Comarr & Gunderson, 1975).

  The autonomous and neuroendocrinous sexual reflexes facilitate copulation and allow fertilization. These reflexes are:
  - Erection and lubrication (Giuliano, 2011).
  - Ejaculation (Allard & al., 2005; Coolen, 2005).
  - Ovulation reflex, caused by coitus (Spies & al., 1997) and pheromones (More 2006).

- **Reinforcement processes** (on the neurobiological level) or **reward system** (at the psychological level). These processes, associated with the hairy skin (Olausson & al., 2002), the erogenous zones, copulation (Caggiula & Hoebel, 1966) as well as with ejaculation and orgasm (Holstege & al., 2003), would then be at the origin of repeating all the activities stimulating the body and especially the genital zones. These processes would also, although indirectly, be at the origin of learning the majority of the sequences of reproductive behavior that are not innate (Agmo 2007).

2.2. Acquired primary factors of reproductive behavior.

In addition to these innate factors, a certain number of research studies have highlighted crucial elements, absolutely necessary to the realization of reproductive behavior, which, on the contrary, would not be innate. These elements, which would be acquired during the development period of the organism, are:

– The recognition of congeners, that is, partners of the same species (Kendrick & al., 1998).

– The sexual motivation to seek genital physical contact.

– Sexual socialization (Spevak & al., 1973).

– The capability for the appropriate genito-genital positioning of the bodies (Gruendel & Arnold, 1969; Missiakan, 1969; Turner & al., 1969).

According to current knowledge and understanding of the way the nervous system functions, it is likely and consistent that these capacities must be acquired. Indeed, we notice that these capacities are in fact those that are the most difficult to hardwire or to code genetically. These capacities require the innate existence of elaborated representations of the body (individual's body and partner's body), which could be coded only in the most complex areas of the nervous system. According to current neurobiological knowledge, the innate implementation of such complex cognitive capacities is difficult to explain (Wunsch, 2007).

To give a precise example of the difficulty of "hardwiring" or "programming" innate cognitive characteristics, one can study in detail the hypothesis of Desmond Morris (1971), which supposes buttocks and breasts could be innate visual signals. According to this hypothesis, the similarity between the shape of breasts and buttocks is explained by the need in the human species to transpose a specific posterior excitatory signal, the buttocks, into a similar anterior signal, the breasts, and this because of face-to-face coitus. The breasts would thus be "front buttocks", an excitatory adaptive signal specific to the human species. Various declarative and behavioral investigations have shown that the buttocks and the breasts were indeed the most attractive sexual signals for human males. However, if these visual signals are really innate – and not acquired by association or conditioning processes during previous sexual experiences – then it must be possible to highlight innate characteristics specific to these signals in the visual areas of the nervous system.

Genetic, developmental, anatomical and functional studies of the visual system (summarized in Breedlove & al. 2007), show that the visual system is composed of a great number of small structures (functional modules) that each have a limited role in visual data processing. For example, the retina processes the signal's luminosity, the generation of saccadic eye movements is processed by the interstitial rostral nucleus of the median longitudinal bundle, colors are processed by visual area 4, and certain dynamic characteristics (movement, direction) by visual area 5, and so on. Vision is originated through the coordination of all these elementary processes. According to all this current knowledge, the hypothesis of the innateness of a visual information system hardly seems plausible because it seems impossible to explain the genetic (or possibly epigenetic) coding and the localization of the preformed prototypical image of the buttocks and the breasts, to which complex visual information of the congeners' morphology must be compared. Indeed, the recognition of complex patterns is located in the associative cortical areas (Gazzaniga & al., 2002), which are the most complex regions of the brain. However, with regard to the development of the nervous system, only the main pathways of the visual system connections seem to be genetically coded, and a number of the visual system's capacities develop in interaction with the environment. Furthermore, a gene codes a protein, which, in a best-case scenario, can only be used as a global guidance molecule for the synaptic connections (Chilton, 2006). Then how can we explain the specific and precise coding of billions of nervous synapses that would probably be necessary to interpret the complex pattern of buttocks and breasts in the inferior temporal cortex associative areas? How can we explain the stability of this coding in areas known to be the center of plasticity, selective stabilization and reorganization phenomena? And last, how would this signal participate in the execution of fertilizing vaginal coitus?

In addition, in subprimate mammals, it is mainly the chemical signals that control reproduction, within phylogenetically old neural structures. This communication channel seems the best adapted to the biological realities of mammalian organisms: a few molecules, a few receivers and a simple neural network are enough to distinguish partners, to activate sensory and motor pathways and to trigger behavioral sequences. For what evolutionary reasons would this simple and effective system have been replaced by a complex system of visual data processing within the most phylogenetically recent cortical areas?

Moreover, and above all, as buttocks and breasts do not have the same appearance in women and in female monkeys, and as the human species differs genetically from the other primates by only a few percent of genes, according to present knowledge, it is almost impossible to conceive the following point: how can random changes or genetic modifications in a protohuman organism and on a restricted number of genes have coded by anticipation a prototypical image of the new final morphology of the buttocks and breasts of *homo sapiens*? This phenomenon is, according to present knowledge, rigorously impossible.

In conclusion, the coding of specific innate cognitive characteristics of reproductive behavior is unlikely. On the other hand, by studying the environment in which young mammals develop, one notices that all the capacities that are not innate (recognition of congeners, sexual motivation to seek genital physical contact, sexual socialization and the capacity for the appropriate genito-genital positioning of the bodies) can be learnt during the numerous physical and social interactions with the mother and the peers (Ward, 1992; Gruendel & Arnold, 1969). In the following paragraphs we present the data that suggest that these capacities are not innate, and the experimental arguments that give indications as to the likely conditions of their being learned.

The recognition of congeners is not innate. Indeed, animals raised from birth by a mother of another species (a kid by a ewe and a lamb by a goat) express a sexual attraction for the animals of their adoptive species and not for those of their genetic species (Kendrick & al., 1998). These data suggest that there is apparently no innate information relating to the specific characteristics of congeners in ovidae, and, probably, in other mammals. It can also be noted that there is no necessity to code this information genetically, because the morphological, olfactive, auditive and visual characteristics of the congeners would inevitably always be learnt: except in exceptional cases, a newborn animal is always in contact and develops with members of its species. The learning of the congeners' characteristics is thus predetermined by the context of development, and it always takes place.

Sexual socialization, that is, the entirety of attitudes and reactions appropriate to sexual social interaction with congeners, is not innate. Indeed, it is observed that animals raised in social isolation from birth are incapable of normal social and sexual interactions (Spevak & al., 1973). It is moreover difficult to explain, from current knowledge, how all the sensory, emotional and cognitive capacities necessary for the appropriate social and sexual interactions can be programmed into the nervous system (cf. the similar example of buttocks and breasts, detailed in the previous paragraphs). Sexual socialization is learnt during the many and frequent social games in which young mammals take part throughout their development (Vanderschuren & al., 1997). These playful activities are frequently repeated because they are reinforcing, in particular during the developmental period (Trezza & al., 2011; Douglas & al., 2004).

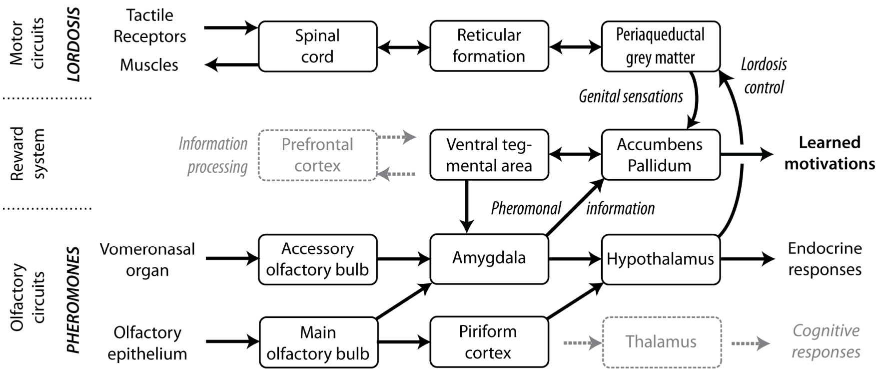

Figure 1: Female sexual circuits
(Brennan & Zufall 2006 ; Pfaff & al 1994 ; Kringelbach & Berridge 2010).

Schematic innate connections between olfactory, motor and reward circuits. Pheromonal information (Novejarque & al 2011 ; Wenkstern & al 1993 ; Lanuza & al 2008) and genital sensations (Cibrian-Llanderal & al 2010 ; Matsumoto & al 2012) to the reward system enable the learning of sexual motivation.

The sexual motivation to seek genital physical contact is not innate. Indeed, what would the neurobiological processes be that enable mutual attraction between a male and a female, then provoke copulation? According to present knowledge, one can explain the recognition of the partner and the state of sexual arousal by pheromones and hormones. Apparently, to schematize, sexual pheromones would enable the recognition of the partner of the opposite sex (Roberts & al., 2010; Stowers & al., 2002; Dulac & Torello, 2003). They also induce a state of sexual excitement (Moncho-Bogani & al., 2004, 2005, 2002), by connections between the olfactory receptors and GnRH neurons (Yoon & al., 2005; Boehm & al., 2005), which control the sex hormones. However, once the male and the female are in an aroused state – a neural state appropriate for the release of various physiological or motor actions – what are the processes that will bring them to copulation? One can envisage that there could be innate knowledge, representations or motor sequences, specific to vaginal coitus. However, no current data makes it possible to prove or even to explain how cognitive phenomena as complex as knowledge or representations specific to copulation can be coded in the associative cortices. As for the innate motor sequences, the only ones currently known are lordosis and intromission, which enable the achievement of the final part of copulation. To sum up, the known innate processes explain the sexual arousal of animals, and only if the animals come into genito-genital contact will the innate reflexes permit vaginal coitus. But the specific motivation to come into appropriate physical contact on the level of the genital zones is lacking. Nevertheless, it would seem possible that this specific motivation is acquired during development, due notably to the processes of reinforcement (or reward system – Figure 1). Indeed, physical stimulation, especially around the genital zones, is particularly reinforcing. The postnatal physical contacts with the mother and with the other newborn animals, and in particular anogenital licking (Moore, 1992; Baum & al., 1996; Ward, 1992) as well as sexual games with the other congeners, and especially the regular pheromone-dependent investigation of the peers' anogenital area (Spevak & al., 1973), could gradually develop a sexual motivation to seek genital stimulations. This acquired sexual motivation is then strongly enhanced at puberty under the effect of the sex hormones, probably by a modulating action by testosterone on the enzymes controlling the synthesis of neurotransmitters involved in the sexual processes (Du & Hull, 1999).

The ability for the appropriate genito-genital positioning of the bodies (the mounting sequence in the nonprimate mammals) is not innate. Indeed, it is observed that when nonhuman mammals, and especially primates, are put in conditions where they cannot learn any element of reproductive behavior, the male is systematically incapable of coitus (Gruendel & Arnold, 1969; Missakian, 1969; Turner & al., 1969; Ward, 1992). This incapacity of the male to practice coitus without prior experience has been verified in several species (guinea pigs, rats, cats, dogs, rhesus monkeys, chimpanzees), and it is systematic in all primates. By varying the experimental conditions, it appears that it is probably the deprivation of physical contact, and not of the sight, sounds or odors of congeners, which is the critical factor originating the lack of coitus (Ward, 1992; Gruendel & Arnold, 1969). One can thus observe sexually naive males expressing many specific behaviors of reproduction (arousal, erection, contacts with the partner), but they do not manage to copulate. Although there are also related problems of socialization and fear of the other congeners (Goldfoot, 1977), one of the main problems could be related to a deficiency in the building of the "body schema" and is characterized by an incapacity to correctly position the body to succeed in intromission (Hard & Larsson, 1971). The absence of innateness of the genito-genital positioning is hardly surprising. How could this complex cognitive ability, which requires the innate existence of representations and specific body positions in space, be preprogrammed in the nervous system? From what is known at present, it is apparently unexplainable. On the other hand, this ability could be learnt during physical interactions and from the sexual games with congeners. These activities would be frequently repeated because of their reinforcing characteristic (Trezza & al., 2011; Douglas, 2004). The first postnatal body contacts and more particularly all types of contacts and body explorations carried out during social games could originate the building of an individual and congeners' "body schema". The learning of a body schema enables the animal to find and adapt postural adjustments – including genito-genital positioning – during specific body interactions with its congeners (grooming, aggression, copulation).

Moreover, during all these physical interactions, all those in connection with the genital regions or that trigger sexual reflexes could thus initiate partial sexual sequences (sexual games), which are gradually integrated into more global motor schemas (Hard & Larsson, 1971), therefore progressively initiating the learning of a more complete reproductive behavior. All the learning that takes place thanks to these physical activities and stimulations concretely results in the neural structures' development involved in controlling sexual behavior (medial amygdala, median preoptical nucleus, medullary motor nuclei; Moore & al., 1992; Baum & al., 1995; Cooke & al., 2000). The control exerted on reproductive behavior by these structures is therefore not an innate control, dependent on a genetically or hormonally "programmed" organization of these structures, but a control that is mainly acquired. That way, the interaction between the environmental factors and the innate factors enables the nervous system's structural and functional development, and the development of the specific sexual behavior neural circuit.

These data and analyses clearly show that even in the simplest or the most primitive mammals reproductive behavior is not completely innate (Wunsch & Brenot, 2004), and that all mammals at least have to learn, during their development, how to recognize congeners, sexual motivation to seek genital physical contact, sexual socialization and the ability of the appropriate genito-genital positioning of the bodies to be able to reproduce.

In conclusion of all these analyses, even if the data presented above do not allow us to explain exactly all the details of all the learning necessary for the achievement of reproductive behavior, it seems to be very likely that the most cognitive capacities necessary for the achievement of this behavior are not innate, but that they are learnt thanks to the many physical and social interactions that take place during the development period. That way, at puberty, all the factors and processes necessary for the achievement of heterosexual reproductive behavior are functional.

2.3. Emergence and dynamics of reproductive behavior

In agreement with all the data presented in the previous sections, and from an analysis of the various biological processes identified in the nonprimate mammals, in broad outline, what would the dynamics of the heterosexual reproductive behavior of a prototypical mammal be?

Hormones would be a major factor. With regard to behavior, they mainly have a role of coordination and modulation, by simultaneously activating the various neurobiological processes involved in the reproductive behavior. The melatonin, by its action on GnRH neurons, activates sexual behavior during the season favorable to reproduction (Aleandri & al., 1996). Sex hormones initiate reproductive behavior at puberty (Sisk & Foster, 2004), lift the tonic inhibitions on the sexual reflexes, lower the sensory thresholds (Gandelman, 1983), activate the synthesis and release of sexual pheromones and would maximize sexual motivation. The organism is thereby ready to carry out the behavioral sequences leading to fecundation.

Then, during what is generally called the motivational phase, when sexually naive animals are present, pheromones that are specific to sex, that is, which are released only by the partner of the opposite sex, would be the main primary signals that enable the triggering of the heterosexual sexual motivation (Moncho-Bogani, 2005) and the heterosexual distinction of the sexual partner of the opposite sex (Roberts & al., 2010 ; Stowers & al., 2002; Dulac & Torello, 2003).

Sexual socialization, the sexual motivation to seek genital physical contact and the ability for the appropriate genito-genital positioning of the bodies – abilities probably learned during development – enable animals to interact in an adapted way, to come into physical contact, and to position their bodies correctly.

Finally, during the consummatory phase, when the animals are in physical contact, the physical stimuli provoked by each action constitutes the release stimuli of the following reflex action (Balthazar & Fabre-Nys, 2001): mounting, lordosis (Pfaff & al., 1994), intromission and pelvic thrusts (Meisel & Sachs, 1994), ejaculation (Allard & al., 2005) and release of the ovum (Spies & al., 1997).

Once the naive animal has achieved its first sexual behavior, and with the progressive increase of its sexual experiences and concomitant learning (Woodson, 2002), the various motor sequences will be performed more effectively, other signals (visual, auditive, gustatory, etc.) can become sexual by conditioning (Pfaus & al., 2012 & 2001), and reproductive behavior can take place in spite of the absence of certain signals crucial for the sexually naive animal (Meredith, 1991; Balthazar & Fabre-Nys, 2001).

We thus observe that reproductive heterosexual behavior emerges mainly from the functional coordination of various reflexes and innate sexual processes, from interactions with congeners and from various learning experiences that always take place through development in the normal ecological environment.

It should be noted that for an external observer, reproductive behavior can appear instinctual, insofar as the learning experiences, such as those induced by ano-genital licking, are not apparent, are not directly related to reproduction or are not regarded as "sexual".

It should also be noted that this is a prototypical and general model, which highlights especially the main factors. However, minor variations exist from one species to the other: seasonal inhibition may not exist, some processes (reflexes, reinforcement, neurotransmitter enhancement) are not under hormonal control (Park & Rissman, 2007), masculinization or feminization may occur (Aron, 1996), the layout in the brain of oxytocin receptors may vary (Insel & Shapiro, 1992) and so on. These neurobiological variations from the general model explain the behavioral variations observed in nonprimate mammals: sometimes continuous sexual behavior throughout the year, some homosexual activities, other monogamous or polygamous sexuality and so on.

2.4. Concept of "partial instinct"

The above study about the innate and acquired factors at the origin of reproductive behavior suggests that there would seem to be no instinct, that is, an innate central programming of the various motor sequences necessary for the achievement of this behavior. Instead there is the possibility of the coordination of various innate but elementary functional modules, which after some essential learning enables the emergence of a reproductive behavior.

These particular characteristics lead us to suggest the concept of a "partial instinct", that is, an incomplete set of innate elements. However, because these elements are associated with specific environmental circumstances that almost always exist during development (e.g., physical contacts, sensory stimuli, the mother-child interactions), the missing elements are, in an indirect way, always acquired. Therefore the "partially instinctual" behavior is carried out correctly at its maturity period, without the need for specific learning.

Does this archetypical model of reproductive heterosexual behavior presented in the preceding sections, with its innate primary factors and its developmental learning, exist in all mammals and in particular in Man?

3. Evolution of reproductive behavior

By studying the modifications of the organization of the nervous system of the various mammalian species during evolution, one notices important structural and functional changes that directly influence the innate primary factors of reproductive behavior.

The main modifications, from rodents to Man, are as follows:

– An important development of the prosencephalon.

– A functional deterioration of the olfactory systems.

– Human sexual activities are dissociated from hormonal cycles

The significant development of the neocortex, the seat of cognitive functions, infers an increase in the importance of cognitive factors in reproductive behavior. Apparently, the more the neocortex is developed in a given species, the more one observes variations and behavioral adaptations due to the capacity of analyzing context and individual experience. In Man, the cortex, which has developed to constitute three fourths of the brain, is the medium that has enabled the emergence of culture and its determining influence on human sexuality.

The vomeronasal system’s deterioration in Old World primates (Zhang & Webb, 2003) and the deterioration of 90 % of pheromone receptor genes in Man (Nei & al., 2008) causes the deterioration of the functions provided by pheromones, in particular the heterosexual distinction of the reproductive partner of the opposite sex. Indeed, when the vomeronasal organ is not functional, sexual behavior becomes bisexual (Stowers & al., 2002; Dulac & Torello, 2003; but see Pankevich & al., 2006; then see Kimchi & al., 2007). Moreover, although pheromones can still be perceived at the level of the main olfactory system (Liberles & Buck, 2006; Savic & Berglund, 2010; Savic & al., 2009), one observes that their residual effects, in particular behavioral, are weak in human beings (Havlicek & al., 2010; Winman, 2004; Foidart & al., 1994).

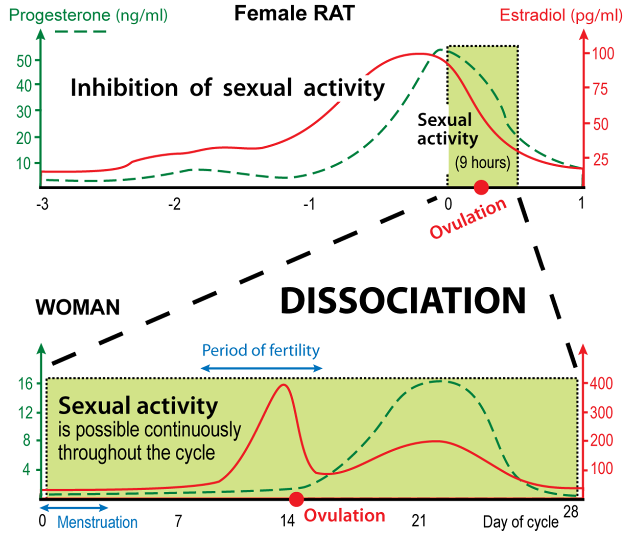

Figure 2: Human sexual activities are dissociated from hormonal cycles

As for the hormonal factors, which play a major role in the control of reproductive behavior, one notices that human sexual activities are dissociated from hormonal cycles (Figure 2). Seasonal control has almost disappeared: sexual activity and human reproduction exist throughout the year and only in the Nordic countries can one observe the seasons having only a minor effect on reproductive behavior. (Aleandri & al., 1996; Pandi-Perumal & al., 2006). Oestrous control is weakened: women can have sexual activities throughout their cycle, even if one still observes a hormonal effect during the period of fertility (Brown & al., 2010 ; Foster & Roenneberg, 2008). The puberty hormones are no longer determinants of the initiation of sexual behavior: in bonobos (Hashimoto, 1997; De Waal, 1990b) and in Man (Suggs, 1966; Malinowski, 1929; Ford & Beach, 1965; Marshall & Suggs, 1971; Henry & Henry, 1974; Diamond, 2004; Martinson, 1994), if the context permits, sexual activities begin in the first years of life. Finally, the neuroendocrine ovulation reflex provoked by coitus is no longer functional in many species of mammals, including primates.

Therefore, in Man, there only remains the innate primary factors at the origin of the last part of reproductive behavior: the sexual reflexes (not lordosis, but erection, lubrication, intromission, pelvic thrusts, ejaculation), which enable copulation to be achieved. And reinforcement processes also remain, associated with the hairy skin and the erogenous zones, which are at the origin of the reiteration of body stimulation activities, especially the genital zones. Besides, and above all, it should be noted that in Man sexual reinforcements and sexual reflexes are active throughout the year and can take place in many nonreproductive situations (masturbation, for example).

What general rules concerning the evolution of the reproductive behavior of mammals can one deduce from all these observations?

It appears that the various primary factors are relatively independent of each other and can be modified or disappear, without necessarily compromising reproduction. In these cases, one observes that reproductive behavior develops according to the characteristics of the factors that still exist. If seasonal control weakens, the behavior is expressed continuously but with seasonal variations of frequency; if the heterosexual distinction of the appropriate partner disappears, the behavior becomes bisexual (Dulac & Torello, 2003) and so on. Apparently, whatever the modifications caused by evolution in a species, as long as a behavior leading to fertilizing vaginal coitus can develop on the basis of the modified characteristics of the primary factors, this species can survive and reproduce.

In conclusion, the evolution of mammalian reproductive behavior depends on the modifications or deteriorations that the evolution of the nervous system structure causes in the various primary factors. For each species, the basic characteristics of reproductive behavior depend on the characteristics of the primary factors that still exist in this species.

What characteristics of primates’ reproductive behavior can one deduce from these evolutionary tendencies?

In synthesis, in primates and especially in Man, the hormonal and pheromonal innate primary factors become secondary, nearly all the copulatory reflexes are preserved, and it is the cognitive and reinforcement factors which are at the origin of the initial part (motivation, orientation) of reproductive behavior.

These important evolutions of the main behavioral factors are very likely to have a major impact on human reproductive behavior. Hence, by taking account of all these analyses, and starting from these factors modified by evolution, what would the development and the dynamics of human reproductive behavior be?

4. Behavioral model in primates and Man.

In particular, is it possible that only the reinforcement processes (or reward system) are sufficient to initiate the development of a behavior enabling reproduction in primates? And if the answer is *yes*, what would the dynamics of this behavior then be?

At present, at least two somatosensory systems are known that are associated with the reinforcement processes. The first one, apparently the most general, is a system located in the hairy skin of the body and probably constituted by fibers with slow conduction, which are not myelinized and originating in the plexus of the hair roots. This system responds to light touching and projects itself in the limbic areas and in the reward system (McCabe & al., 2008; Olausson & al., 2002), which implies that it is functional in the emotional responses provoked by pleasant physical contacts (Olausson & al., 2010; Wessberg & al., 2003). It may then be responsible for searching physical contact and explains the reason for primates being contact animals (Morrison & al., 2010). The second system, more specific, is that of the erogenous zones. These zones are constituted by muco-cutaneous tissue, which is a transitional tissue between the external skin and the internal mucous membranes. This particular skin is characterized by a lesser thickness of the dermis and the neural sensory structures are closer to the epidermis than in the other types of skin (glabrous or hairy). Erogenous zones constituted by muco-cutaneous tissue are the penis/clitoris, the foreskin, the external part of the vulva, the perianal skin, nipples and lips (Winkelmann, 1959). The most erogenous zones would also have a densely innervated skin and a strong capacity for stimulating central nervous system arousal (Schobert & al., 2011). Moreover, the significant erogeneity of the genital erogenous zones was highlighted by the works of Masters and Johnson (1980): from the observation and measurement of various anatomical and physiological parameters, during more than 10,000 sexual response cycles with 694 men and women, they showed that the penis and the clitoris were the main source areas of sexual pleasure.

In theory, after the first initiating stimulations have occurred, these two somatosensory systems should induce the search for and repetition of hedonic and erotic physical contacts. It is observed that these first initiating stimulations can be very diverse, and that they can come, at first, from parental care (nursing, grooming, physical affection …), then, at a later time, from physical or sexual play with peers, from initiation by a more experienced partner, or from masturbation (Constantine & Martinson, 1981; Martinson, 1994). Self-stimulation of the genitals, especially manually because of the anatomical arrangement of the forelimbs that is particularly convenient for this activity, could be at the origin of the first erotic stimulations as early as the foetal period: indeed, before birth, using echography one can observe erection (Shirozu & al., 1995), masturbatory-like stimulations (Meizner, 1987; Broussin & Brenot, 1995) and perhaps orgasm (Giorgi & Siccardi, 1996; Broussin & Brenot, 1996). In conclusion, it is completely plausible that during all these foetal and infantile experiments, the subject acquires and develops a motivation to seek hedonic and erotic physical contacts, and learns motor sequences and situations allowing enabling him or her to be obtained.

Thus, due partly to the functional association between somatosensory systems and reinforcement processes, which induce the search for and repetition of physical contact, during their development and interactions with their congeners, human beings can learn sexual socialization, sexual motivation to seek genital physical contact, and the capability of appropriate genito-genital positioning of the bodies.

This model is not incompatible with a concomitant, but weaker, effect of hormones or possibly of pheromones. For example, the puberty hormones, among others, should increase the frequency of sexual activities in adolescence, and pheromones could increase the heterosexual element of these activities. As for the cognitive factors, they modulate the development of sexual behavior through the analysis of past experiences, but especially through the elaboration of values, beliefs, prohibitions or obligations (prohibitions of masturbation or homosexuality, valorization of virginity, obligation of chastity, etc.).

All of these data have led to us to elaborate a learning model of a particular sexual behavior, specific to hominoid primates, which would no longer be a "heterosexual reproductive behavior", but which nevertheless would indirectly enable the reproduction necessary for the survival of the species. The crucial hypothesis is that the acquisition of a human behavior enabling reproduction would depend – mainly but indirectly – on the activation of reinforcement processes, provoked by the genital erogenous zones' stimulation. In other words, it is mainly the existence of erogenous zones and especially the intense erogeneity of the penis, the clitoris and the vagina that provoke the discovery then the repetition of various motor sequences of body and genitalia stimulation, including the sequence of vaginal sexual coitus.

The reinforcement processes, the erogenous zones and the intense erogeneity and anatomical complementarity of the penis and the vagina would seem to be at the origin of two singular phenomena: (1) the emergence of a particular behavioral dynamics: erotic behavior, and (2) the learning of a specific motor sequence: vaginal coitus (Figure 3).

Emergence of a behavioral dynamics: Erotic behavior. The association of two innate biological factors, the processes of reinforcement (or reward system – Fig. 3, part 1) with the erogenous body zones (Fig. 3, part 2), creates a functional system. This system originates the emergence of erotic behavior, characterized by the repetition of the motor sequences of erogenous zones' stimulation (Fig. 3, part 3).

The existence of these erogenous zones and these reinforcement processes implies a very high probability that each subject, during its development and during interaction with others – no matter their sex – discover the erogenous zones, and, through the medium of the reinforcement processes, learn to repeat the stimulation of these erogenous zones. Erotic activities are thus gradually acquired during development, in a few months or several years, depending on the learning undergone, the quantity and the quality of the erotic experiences.

Learning of a specific motor sequence: Vaginal coitus. During erotic behavior, in the course of searching for physical pleasures, the existence of complementary genitals (penis and vagina) having highly erogenous zones (Fig. 3, part 4) would be a characteristic that would induce a high probability that vaginal coitus becomes one of the preferred erotic practices (Fig. 3, part 5).

The fact that the stimulation of the genitals may generally provoke highly intense erotic pleasure, including orgasm, is one of the main factors facilitating the acquisition and repetition of vaginal coitus. This characteristic leads erotic activities to be mainly centered on the genitals, thus increasing the probability of discovering several genital activities, among which vaginal coitus. Moreover, curiosity, the search for novelty and cognitive capacities are also factors increasing the probability of discovering this sequence. The heterosexual sequence of vaginal coitus would thus be acquired during the development and diversification of the activities of stimulation of the erogenous zones.

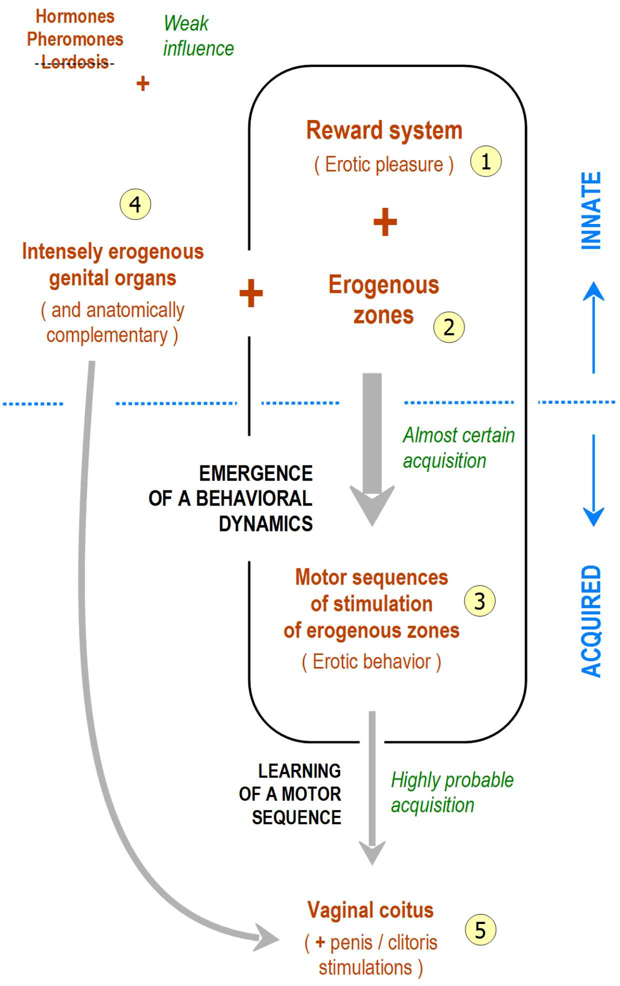

Figure 3: Acquisition of a behavior allowing the reproduction

It should be noted that in this model, if fertilizing vaginal coitus is practiced, it is not because this activity is "planned" by a specific structural and functional organization, but because, in spite of the unforeseen nature of evolution and the modifications of the primary factors, this activity is (fortunately) one of the erotic activities that brings most pleasure.

In the following section we present ethological, clinical and experimental data that apparently corroborate this behavioral model.

5. Elements of corroboration

The exhaustive and multidisciplinary experimental verification of this behavioral model largely exceeds the limits of this article. For that reason, we are only going to present the main animal and human data that permit us to assess this model.

First and foremost, the recent work of Anders Agmo, *Functional and Dysfunctional Sexual Behavior* (2007), presents analyses of a very large number of experimental data that show the major importance of reinforcements in the learning of human sexual activities. Agmo's analyses corroborate thus, in our behavioral model, the importance of reinforcements.

To test our behavioral model, we initially sought in the ethological, ethnological and clinical knowledge of the data that already exists which would corroborate or refute the model. Our neurobiological hypothesis of the functional prevalence of the"reinforcement / erogenous zones" system should induce a behavior of body stimulation, and not a heterosexual reproductive behavior centered on vaginal coitus. Do the ecological or medical observations corroborate this behavioral forecast?

5.1. Animal data

For the ethological data, we limit ourselves to the *pan paniscus* chimpanzee (Bonobos), which is the animal species closest to Man, as much on the genetic and hormonal (Figure 4 – Furuichi, 2011) level, as on the cognitive and behavioral ones. It is the most corticalized animal species, therefore the most appropriate to test the hypothesis; however, contrary to Man, it is difficult to invalidate the behavioral observations on the basis that its sexuality could be "denatured" through culture's influence.

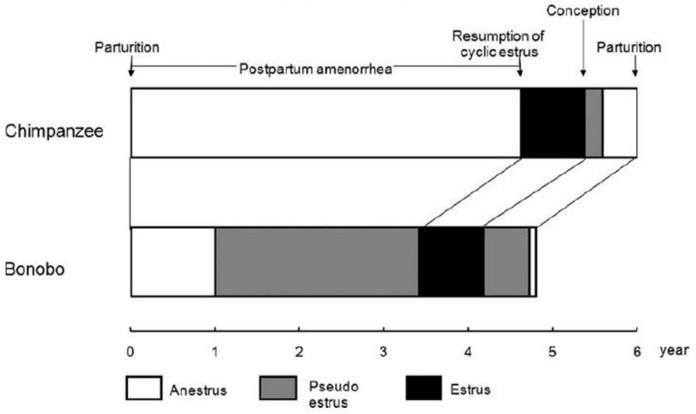

Figure 4: Estrus and pseudo-estrus in female chimpanzees and bonobos. Unlike chimpanzees, bonobos are receptive for most of the ovarian cycle and during nursing.

To summarize the essentials, the sexuality of captive or wild Bonobos is continuous throughout the year and begins toward the age of 1, so well before puberty. These prepubescent activities account for almost one fourth of all sexual activities, the activities of teenagers represent approximately one half, and that of adults a little more than one fourth. The sexual activities are bisexual (approximately one third of activities are homosexual and two thirds heterosexual, but never exclusively homosexual or heterosexual), and one observes many nonreproductive activities: masturbation, use of objects, mutual masturbation, genito-genital rubbing, kissing, oro-genital activities, in groups, and so on. It is noticed that these nonreproductive activities account for approximately three fourths of all the sexual activities (Hashimoto, 1997; De Waal, 1990a, 1990b; Bagemihl, 2000).

In conclusion, one observes that Bonobos' sexuality consists of various activities involving the stimulation of the body and erogenous zones, and not of heterosexual reproductive behavior centred on vaginal coitus. These observations thus corroborate the hypothesis of the functional prevalence of the "reinforcement / erogenous zones" system in hominoid primates' sexuality.

Furthermore, Bonobos' sexuality demonstrates that the evolution of the prototypical heterosexual reproductive behavior into a behavior of body stimulation by no means prevents reproduction and survival of the species.

5.2. Human data

This behavioral dynamics of body stimulation by partners – no matter their sex – predicted by the behavioral model, is extremely different from a heterosexual reproductive behavior focused only on vaginal coitus, and is in conformity with the observations of human sexual activity. These descriptions can be found in the sexological literature (Langis & Germain, 2010; LeVay & Baldwin, 2009), in handbooks of sexuality (Comfort, 1992; Remes, 2004) or in the great classics of erotic literature (e.g. the *Kama Sutra* of Vatsayana). These data suggest, in the past and today, that human sexual activities consist primarily of erotic stimulation of the bodies.

Moreover, the clinical data coming from the pathology of spina bifida are very interesting to corroborate, and even validate the behavioral model. Spina bifida is characterized mainly by a vertebral malformation, involving the crushing of the spinal cord between vertebrae or by the cerebrospinal liquid. In certain cases the neurological impact causes an absence of sensitivity in the genital area. Unlike accidental medullary sections, people thus affected have never in their life experienced genital feelings. It is observed in such cases that the patients do not masturbate and are not interested by this type of activity. Moreover, genital orgasm is absent. Vaginal coitus, when pathology has not impaired the sexual reflexes, is carried out only in a voluntary way with the intention of procreating. It is thus observed that erotic activity is absent from the insensitive erogenous zones. On the other hand, the patients perceive and seek feelings of an erotic nature ("thrills or particular sensations"; "impression of hot flushes"; para-orgasm) caused by the stimulation of the upper part of the body (Soulier, 2001; Labat & Mauduyt De La Grève, 1996; Cass & al., 1986). It is thus observed that the sexual activity is organized around the preserved or new erogenous zones.

What is remarkable it is that one observes a total dissociation between the innate reproductive behavior (or rather what remains of it in Man) and the acquired erotic behavior. The erotic activity is acquired and develops on the basis of new or preserved erogenous zones, and no longer has any connection with reproduction, whereas the sexual reflexes that permit the innate achievement of the final sequences of copulation (erection, ejaculation) still exist but are no longer included in erotic behavior.

6. Discussion

What can one conclude from the whole of these data and analyses presented in the previous paragraphs?

The most plausible interpretation of all these data is that because of the nervous system's transformations during evolution, in Man, the prototypical heterosexual reproductive behavior of the first mammals no longer exists but is replaced by a modified behavior, the goal of which is body and erogenous zones stimulation. Reproduction is nevertheless preserved, because of the intense erogeneity of the penis / clitoris that favors genital activities, including the vaginal coitus that is essential for fertilization.

It is even possible to speak about erotic behavior, insofar as the reinforcements (perceived consciously as a sensation of erotic pleasure) act as an organizing and structuring principle: in the course of time and experience, one observes that erotic activities become increasingly typical, elaborate, identified, conscious and deliberate. At maturity, the mental behavior pattern and the motor activities are organized around a specific purpose: obtaining erotic sensations, and especially, orgasmic pleasure.

In addition, with regard to the main erogenous zones (genital, anal, oral and pectoral in women), a remarkable characteristic is that they are constituted by muco-cutaneous tissue and that they correspond to organism openings that are involved in the entries and exits of matters. These data suggest the existence of a particular and fundamental somatosensory system, in the interface between the inside and the outside of the organism. This system could participate in the emergence and acquisition of behaviors involved in the control of energy and matter flows (gametes, food, waste), necessary for the organism to function. These crucial behaviors (excretion, alimentation, breast feeding, coitus) are absolutely necessary for the survival of the individual and the species. If complementary studies confirm the existence of this functional system (i.e., muco-cutaneous tissue associated with reinforcement processes), the primary erogenous zones' presence around the main orifices of the organism would thus have an adaptive functional meaning. As for erotic behavior, its functional dynamics would be clarified: this behavior would appear, would develop and would be organized according to the search for optimal stimulations of the muco-cutaneous tissue. The revealing of these dynamics would enable us to understand the reason for which human erotic activities develop primarily around the main openings of the organism and have no direct link with reproduction.

What is also striking is that this erotic behavior does not seem to be the result of a progressive optimization during evolution. Indeed, it is difficult to interpret the vomeronasal system's functional deterioration and the weakening of hormonal and pheromonal effects as being functional characteristics that optimize reproductive behavior. On the contrary, it would seem that a true and relatively optimized heterosexual reproductive behavior exists in rodents, of which certain optimization factors (seasonal control, estrus, recognition of the heterosexual partner) have been lost or weakened through the hazardous process of mammals' evolution. What is also noticeable is that, in Man, the reproduction function does not seem to be achieved by a biological organization, the goal of which being fertilization, but by stimulation of the erogenous zones. This means that a fundamental function, absolutely necessary to the survival of the species, could be indirectly achieved by a neurobiological organization that has a different goal.

What main objections can one raise to this behavioral model (Figure 3), based on the hypothesis of the functional prevalence of the "reinforcement / erogenous zones" system?

The most intuitive objection is the absence of bisexual activities. Indeed, the behavioral model implies that a proportion of sexual activities should be bisexual. However, in current Western societies one observes an almost heterosexual sexuality, which, *a priori*, refutes the model. But do Western societies adequately represent humanity (Arnett, 2008 ; Henrich & al., 2010) ? Ethnology and ethology show that almost all the primates have bisexual activities (Wallen & Parsons, 1997; Bagemihl, 2000), in particular the chimpanzees *pan paniscus* (Bonobo) (De Waal, 1990a), that in sexually liberal societies children and teenagers have bisexual activities (Ford & Beach, 1965; Henry & Henry, 1974; Malinowski, 1929; Diamond, 2004), and that apparently in all the ancient warrior societies generalized bisexual practices existed, that is before the advent of the current religions that are unfavorable to sexuality (Neill, 2009 ; Sergent, 1986). All these data suggest that there is a significant tendency towards bisexuality in human beings. Furthermore, in the West we need to take into account the great cultural value of the heterosexual couple, a very strong homophobia (Bagley & Tremblay, 2000), the fact that bisexual individuals are also often rejected by homosexuals, that bisexuality does not exist on a practical level or in cultural values (Rodriguez-Rust, 2002), and that it is thus extremely difficult to live in a bisexual way (Evans, 2003). To understand the major effect of the pressures of conformity and the cultural context, one can give as an example the social standards that apply to clothing. Although there are no laws or formal taboos and people are *a priori* "free", it is observed that almost all men never wear women's clothes. All men conform to the implicit Western codes of masculinity (Connell, 1993). This example, relatively close to the field of sexuality but not dependent on any biological factor, should allow us to understand the determining effect of homophobia and heterocentrism on sexual affects and behavior. Despite all of this, one should observe nonetheless that between a third and one half of Western people have had at least one bisexual experience (Kinsey, 1948), but that probably the majority of people conform to the dominant practices and values because of all the difficulties and psychological pressures exposed previously.

Another possible refutation apparently would be the existence of an innate sexual orientation, which is suggested mainly by positron emission tomography scan studies. When exposed to pheromones, the homosexual male brain and heterosexual female brain showed the same pattern of activation, different from the heterosexual male pattern, suggesting that homosexual men have an anatomical and functional "female" diencephalic region (LeVay, 1991; Savic & al., 2005; Berglund & al., 2006 ; but see Ciumas 2009). Nevertheless, even if these results – although they currently do not allow us to know if these functional characteristics are innate or acquired – correspond effectively to an innate sexual orientation, that does not refute the behavioral model. Indeed, this multifactorial model (Figure 3 & Figure 5) supposes only the prevalence of the erotic reinforcement/reward process. The residual behavioral effects of hormones and pheromones exist, but would be weaker.

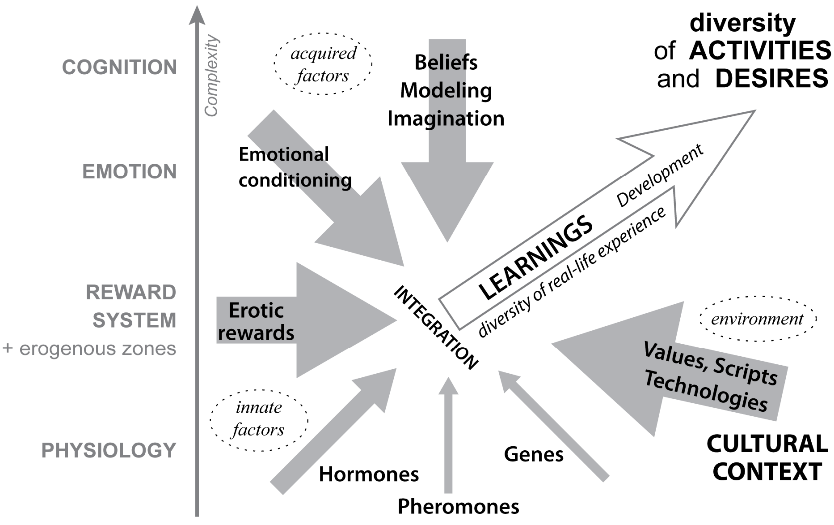

Figure 5: Modelisation of the multifactorial dynamics of human sexuality

Finally, the last main objection would be that such a behavior, the majority of activities of which do not enable reproduction, are not adaptive and would probably be eliminated during evolution by natural selection mechanisms. However, given the existence of oddities and imperfections of structure and function in the living world, it would seem that the major effect of natural selection would not be the optimization but rather the elimination of nonviable organisms. In other words, it is necessary to get past the idea that everything that is not optimized is impossible in evolutionary terms, and get to the idea that everything that survives – no matter the way – is possible (Jacob, 1977). Macaques (*macaca fuscata*) and especially bonobo chimpanzees (*pan paniscus*), whose sexuality is also characterized by a bisexual behavior of stimulation of the erogenous zones (De Waal, 1990a, 1990b; Hashimoto, 1997; Vasey & Duckworth, 2006), seem to be good examples showing that bisexual erotic behavior, although not optimized for fertilization, is by no means an obstacle to reproduction and to the survival of the species.

Obviously, the scientific validation of such a behavioral model cannot be limited to an analysis of the literature. Multidisciplinary complementary studies are necessary to confirm this behavioral model, and to clarify the three factors' importance and their respective roles that seem to be a determinant in the development of human sexualization and sexuality: sex hormones, reinforcement processes and cognitive processes. This first study lets us show that this hypothesis of the "reinforcement process / erogenous zones" system prevalence is plausible, and also, the study of reward systems and the somatosensory system in human behaviors' emergence and dynamics is a research area to develop.

7. Conclusion

At the end of the analysis of the available phylogenetic data, it would seem that the main innate biological factors (seasonal inhibition of sexual behavior, sex hormones, sexual pheromones, reinforcements, lordosis, erection, pelvic thrusts, ejaculatory reflex, release of the ovum triggered by coitus) that are at the origin of nonprimate mammals' reproductive behavior were modified during evolution. In the most corticalized mammals, the hormonal and pheromonal factors have become secondary whereas the reinforcement processes and the emotional and cognitive factors have become predominant. Apparently, it is always the same factors that are at the origin of reproductive behavior among all mammals; however, as the characteristics and the relative importance of these factors were modified during evolution, the behavioral dynamics are different.

Schematically, the results of the current study suggests that there are not "instincts" or complete and innate "programmings" of reproductive behavior, but rather (and perhaps for all behaviors) a whole set of neurobiological processes, innate but elementary, only at the origin of global and approximate tendencies. These tendencies, during development and interaction with the environment, enable the learning of behaviors by trial and error, not optimized behaviors, but relatively adapted and suited to the survival of the individual and the species.

It seems, in Man, that innate heterosexual reproductive behavior no longer exists; however, due to the specific relations between reinforcement processes and erogenous zones, a new behavior has appeared, the goal of which would be bodily stimulation. This behavior, that we describe as erotic behavior, induces the learning of many auto-, hetero-, homo- and bisexual activities, among which, indirectly, is the crucial vaginal coitus sequence. Thus human reproduction, however fundamental to the survival of the species, would, paradoxically, only be an almost fortuitous consequence of the search for physical pleasures.

In conclusion, in the absence of cultural values stigmatizing particular sexual behaviors (i.e., homophobia), it seems that the innate tendency to search for erogenous zones' stimulations by partners, as seen in the Bonobos, leads to the learning of a sexuality that would in most cases be bisexual and diversified (Figure 5).

References

NB : references updated (02/2013)

Agmo, A. (2007). Functional and dysfunctional sexual behavior : a synthesis of neuroscience and comparative psychology. Elsevier.

Aleandri, V., Spina, V., & Morini, A. (1996). The pineal gland and reproduction. Human reproduction update., 2, 225-235.

Allard, J., Truitt, W. A., McKenna, K. E., & Coolen, L. M. (2005). Spinal cord control of ejaculation. World journal of urology., 23, 119-126.

Arnett J.J. (2008) The neglected 95%: why American psychology needs to become less American. The American Psychologist, 63(7):602-614.

Aron, C. (1996). [Bisexuality and natural order]. Paris: Odile Jacob.

Bagemihl B. (2000) Biological Exuberance. St Martin's Press.

Bagley, C. & Tremblay, P. (2000). Elevated rates of suicidal behavior in gay, lesbian, and bisexual youth. Crisis, 21, 111-117.

Balthazart, J., Fabre-Nys, C. (2001) Sexual behavior. in Thibault, C. , Levasseur, M.-C. (Eds.), Reproduction among mammals and Man (pp. 611-637). Paris: INRA Ellipse.

Baum, M. J., Bressler, S. C., Daum, M. C., Veiga, C. A., & McNamee, C. S. (1996). Ferret mothers provide more anogenital licking to male offspring: possible contribution to psychosexual differentiation. Physiology & Behavior, 60, 353-359.

Berglund, H., Lindstrom, P., & Savic, I. (2006). Brain response to putative pheromones in lesbian women. Proceedings of the National Academy of Sciences of the United States of America, 103, 8269-8274.

Boehm, U., Zou, Z., & Buck, L. B. (2005). Feedback loops link odor and pheromone signaling with reproduction. Cell, 123, 683-695.

Breedlove S.M., Rosenzweig M.R., Watson N.V. (2007) Biological Psychology. An introduction to behavioral, cognitive, and clinical neuroscience. Sinauer Associates, Fifth edition.

Brennan P.A., Zufall F. (2006) Pheromonal communication in vertebrates. Nature, 444(7117):308-315.

Broussin, B., Brenot, P. (1995). Is there a sexuality of the fœtus? Fertilité, contraception, sexualité, 23(11), 696-698.

Broussin, B., Brenot, P. (1996). Orgasm in utero? Sexologies, 21(5), 15-16.

Brown S.G., Calibuso M.J., Roedl A.L. (2011) Women's sexuality, well-being, and the menstrual cycle: methodological issues and their interrelationships. Archives of Sexual Behavior, 40(4):755-765.

Caggiula, A. R. & Hoebel, B. G. (1966). "Copulation-reward site" in the posterior hypothalamus. Science, 153, 1284-1285.

Cass, A. S., Bloom, B. A., & Luxenberg, M. (1986). Sexual fonction in adults with myelomeningocele. The Journal of Urology, 136, 425-426.

Chilton, J. K. (2006). Molecular mechanisms of axon guidance. Dev.Biol., 292, 13-24.

Cibrian-Llanderal T., Tecamachaltzi-Silvaran M., Triana-Del R.R., Pfaus J.G., Manzo J., Coria-Avila G.A. (2010) Clitoral stimulation modu-lates appetitive sexual behavior and facilitates reproduction in rats. Physiology & Behavior, 100(2):148-153.

Ciumas C., Linden H.A., Savic I. (2009) High fetal testosterone and sexually dimorphic cerebral networks in females . Cerebral Cortex, 19(5):1167-1174.

Comarr A.E., Gunderson B.B. (1975) Sexual function in traumatic paraplegia and quadriplegia. Am. J. Nurs., 75:250-255.

Comfort, A. (1992). Joy of sex. Paris: Arthaud.

Connell R.W. (1993) Masculinities in recent world history. Theory and society, 22:597-623.

Constantine, L. L., Martinson, F. M. (Eds.) (1981). Children and sex : new findings, new perspectives. Boston: Little, Brown and Co.

Cooke, B. M., Chowanadisai, W., & Breedlove, S. M. (2000). Post-weaning social isolation of male rats reduces the volume of the medial amygdala and leads to deficits in adult sexual behavior. Behavioural Brain Research, 117, 107-113.

Coolen, L. M. (2005). Neural control of ejaculation. The Journal of Comparative Neurology, 493, 39-45.

De Waal, F. B. M. (1990a). Peacemaking Among Primates. Harvard University Press.

De Waal, F. B. M. (1990b). Sociosexual behavior used for tension regulation in all age and sex combinations among Bonobos. Berlin: Springer-Ferlag.

Diamond, M. (2004). Sexual behavior in pre contact Hawai'i : a sexological ethnography. Re vista Española del Pacifico, 16:37-58.

Douglas, L. A., Varlinskaya, E. I., & Spear, L. P. (2004). Rewarding properties of social interactions in adolescent and adult male and female rats: impact of social versus isolate housing of subjects and partners. Dev.Psychobiol., 45, 153-162.

Du, J. & Hull, E. M. (1999). Effects of testosterone on neuronal nitric oxide synthase and tyrosine hydroxylase. Brain Research, 836, 90-98.

Dulac, C. & Torello, A. T. (2003). Molecular detection of pheromone signals in mammals: from genes to behaviour. Nature Reviews. Neuroscience, 4, 551-562.

Evans, T. (2003). Bisexuality : negotiating lives between two cultures. Journal of bisexuality, 3, 91-108.

Fiske, B. (2004). The sexual brain. Nature Neuroscience, 7, 1029.

Foidart, A., Legros, J. J., Balthazart, J. (1994) [Human pheromones: animal vestige or unrecognized reality]. Revue médicale de Liège, 49(12), 662-680.

Ford, C. S., Beach, F. A. (1965). Patterns of sexual behavior. London: Methuen & Co.

Foster RG, Roenneberg T. (2008) Human responses to the geophysical daily, annual and lunar cycles. Curr. Biol., 18(17):R784-R794.

Furuichi T. Female contributions to the peaceful nature of bonobo society. Evolutionary Anthropology, 20(4):131-142, 2011.

Gandelman, R. (1983) Gonadal hormone and sensory function. Neuroscience and Biobehavioral Reviews, 7: 1-18.

Gazzaniga, M. S., Ivry R. B., Mangun, G. R, (2002) Cognitive neuroscience: the biology of the mind. Norton & Company, 2nd edition, pp. 195-204.

Giorgi, G. & Siccardi, M. (1996). Ultrasonographic observation of a female fetus' sexual behavior in utero. American Journal of Obstetrics and Gynecology, 175, 753.

Giuliano F. (2011) Neurophysiology of erection and ejaculation. J. Sex Med., 8 Suppl 4:310-315.

Goldfoot, D. A. (1977) Rearing conditions which support or inhibit later sexual potential of laboratory-born rhesus monkeys: hypothesis and diagnostic behaviors. Lab Anim Sci 27: 548-556.

Gruendel, A. D. & Arnold, W. J. (1969). Effects of early social deprivation on reproductive behavior of male rats. Journal of Comparative & Physiological Psychology, 67, 123-128.

Hard, E. & Larsson, K. (1971). Climbing behavior patterns in prepubertal rats. Effects of hormones, rearing conditions, and sensory cues. Brain, Behavior and Evolution, 4, 151-161.

Hart B.L. (1968) Alteration of quantitative aspects of sexual reflexes in spinal male dogs by testosterone. J. Comp. Physiol. Psychol., 66:726-730.

Hashimoto, C. (1997). Context and development of sexual behavior of wild bonobos (pan paniscus) at Wamba, Zaire. International Journal of Primatology, 18, 1-21.

Havlicek J., Murray A.K., Saxton T.K., Roberts S.C. (2010) Current issues in the study of androstenes in human chemosignaling. Vitam. Horm., 83:47-81.

Henrich J., Heine S.J., Norenzayan A. (2010) The weirdest people in the world? Behav. Brain Sci., 33(2-3):61-83.

Henry J., Henry Z. (1974) Doll play of Pilaga indian children. First Vintage Books Edition.

Holstege, G., Georgiadis, J. R., Paans, A. M., Meiners, L. C., van der Graaf, F. H., & Reinders, A. A. (2003). Brain activation during human male ejaculation. The Journal of Neuroscience, 23, 9185-9193.

Insel, T. R., & Shapiro, L. E. (1992). Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. Proceedings of the National Academy of Sciences of the United States of America, 89(13), 5981–5985.

Jacob, F. (1977). Evolution and tinkering. Science, 196, 1161-1166.

Keller M., Bakker J. (2009) [Special issue, 12 articles] Pheromonal communication in higher vertebrates and its implication on reproductive function. Editorial. Behavioural Brain Research, 200(2):237-238.

Kendrick, K. M., Hinton, M. R., Atkins, K., Haupt, M. A., & Skinner, J. D. (1998). Mothers determine sexual preferences. Nature, 395, 229-230.

Kimchi, T., XU, J., Dulac, C. (2007). A functional circuit underlying male sexual behaviour in the female mouse brain. Nature, 448(7157):1009-1014.

Kinsey, A. C., Pomeroy, W. B., Martin, C. E. (1948). Sexual Behavior in the Human Male. Philadelphia: W B Saunders Co.

Kow L.M., Florea C., Schwanzel-Fukuda M., Devidze N., Kami K.H., Lee A., Zhou J., Maclaughlin D., Donahoe P., Pfaff D. (2007) Development of a sexually differentiated behavior [lordosis] and its underlying CNS arousal functions. Curr. Top. Dev. Biol., 79:37-59.

Kringelbach M.L., Berridge K.C. (2010) Pleasures of the brain. Oxford University Press.

Labat, J. J. & Mauduyt de la Grève, I. (1996). [Genito-sexual disorders of the spina bifida paralytic]. In P.Costa, S. Lopez, & J. Pélissier (Eds.), Sexualité, fertilité et handicap (pp. 161-169).

Langis P., Germain B. [Human sexuality]. De Boeck, 2010

Lanuza E., Novejarque A., Martinez-Ricos J., Martinez-Hernandez J., & al. (2008) Sexual pheromones and the evolution of the reward system of the brain: the chemosensory function of the amygdala. Brain Research Bulletin, 75(2-4):460-466.

LeVay S., Baldwin J. Human Sexuality. Sinauer Associates, 3e edition, 2009

LeVay, S. (1991). A difference in hypothalamic structure between heterosexual and homosexual men. Science, 253, 1034-1037.

Liberles, S. D. & Buck, L. B. (2006). A second class of chemosensory receptors in the olfactory epithelium. Nature, 442, 645-650.

McCabe C., Rolls E.T., Bilderbeck A., McGlone F. (2008) Cognitive influences on the affective representation of touch and the sight of touch in the human brain. Soc. Cogn Affect. Neurosci., 3(2):97-108.

Malinowski, B. (1929) The Sexual Life of Savages in North-western Melanesia. New York: Harcourt, Brace, and World.

Marshall D.S., Suggs R.C. (1971) Human sexual behavior: Variations in the ethnographic spectrum. Basic Books.

Martinson, F. M. (1994). The sexual life of children. Westport, Connecticut, Bergin & Garvey.

Masters, W. H., Johnson, V. E. (1980). Human sexual response. New York: Bantam Books 1980.

Matsumoto J., Urakawa S., Hori E., de Araujo M.F., Sakuma Y., Ono T., Nishijo H. 2012) Neuronal responses in the nucleus accumbens shell during sexual behavior in male rats. The Journal of Neuroscience, 32(5):1672-1686.

Meisel, R. L., Sachs, B. D. (1994). The physiology of male sexual behavior. in Knobil, E., Neill, J. D. The physiology of reproduction. New York: Raven Press, 2nd edition.

Meizner, I. (1987). Sonographic observation of in utero fetal "masturbation". Journal of Ultrasound in Medicine, 6, 111.

Meredith, M. (1991) Sensory processing in the main and accessory olfactory systems : comparisons and contrasts. Journal of steroid biochemistry and molecular biology, 39: 601-614.

Missakian, E. A. (1969). Reproductive behavior of socially deprived male rhesus monkeys (Macaca mulatta). Journal of Comparative & Physiological Psychology, 69, 403-407.

Moncho-Bogani, J., Lanuza, E., Hernandez, A., Novejarque, A., & Martinez-Garcia, F. (2002). Attractive properties of sexual pheromones in mice: innate or learned? Physiology & Behavior, 77, 167-176.

Moncho-Bogani, J., Lanuza, E., Lorente, M. J., & Martinez-Garcia, F. (2004). Attraction to male pheromones and sexual behaviour show different regulatory mechanisms in female mice. Physiology & Behavior, 81, 427-434.

Moncho-Bogani, J., Martinez-Garcia, F., Novejarque, A., & Lanuza, E. (2005). Attraction to sexual pheromones and associated odorants in female mice involves activation of the reward system and basolateral amygdala. European Journal of Neuroscience, 21, 2186-2198.

Moore, C. L. (1992). The role of maternal stimulation in the development of sexual behavior and its neural basis. Annals of the New York Academy of Sciences, 662, 160-177.

More L. (2006) Mouse major urinary proteins trigger ovulation via the vomeronasal organ. Chem. Senses, 31(5):393-401.

Morris D. (1971) Intimate behavior. London: Randam House.

Morrison I., Loken L.S., Olausson H. (2010) The skin as a social organ. Exp. Brain Res., 204(3):305-314.

Nei M., Niimura Y., Nozawa M. (2008) The evolution of animal chemosensory receptor gene repertoires: roles of chance and necessity. Nat. Rev. Genet., 9(12):951-963.

Neill J. (2009) The origins and role of same-sex relations in human societies. McFarland & Company.

Novejarque A., Gutierrez-Castellanos N., Lanuza E., Martinez-Garcia F. (2011) Amygdaloid projections to the ventral striatum in mice: direct and indirect chemosensory inputs to the brain reward system. Front Neuroanat., 5:54.

Olausson, H., Wessberg, J., Morrison, I., McGlone, F., & Vallbo, A. (2010). The neurophysiology of unmyelinated tactile afferents. Neuroscience and Biobehavioral Reviews, 34(2), 185–191.

Olausson, H., Lamarre, Y., Backlund, H., Morin, C., Wallin, B. G., Starck, G. et al. (2002). Unmyelinated tactile afferents signal touch and project to insular cortex. Nature Neuroscience, 5, 900-904.

Pandi-Perumal, S. R., Srinivasan, V., Maestroni, G. J., Cardinali, D. P., Poeggeler, B., & Hardeland, R. (2006). Melatonin: Nature's most versatile biological signal? FEBS Journal, 273, 2813-2838.

Pankevich D.E., Cherry J.A., Baum M.J. (2006) Effect of vomeronasal organ removal from male mice on their preference for and neural Fos responses to female urinary odors. Behavioral Neuroscience, 120(4):925-936.

Park J.H., Rissman E. (2007) The male sexual revolution: Independence from testosterone. Annual Review of Sex Research, 18:23-59.

Pfaff, D. W., Schwartz-Giblin S., McCarthy M. M., Kow L.-M. (1994). Cellular and molecular mechanisms of female reproductive behaviors. in Knobil, E., Neill, J. D. The physiology of reproduction. New York: Raven Press, 2nd edition.

Pfaus J.G., Kippin T.E., Coria-Avila G.A., Gelez H., Afonso V.M., Ismail N., Parada M. (2012) Who, what, where, when (and maybe even why)? How the experience of sexual reward connects sexual desire, preference, and performance. Archives of Sexual Behav-ior, 41(1):31-62.

Pfaus J.G., Kippin T.E., Centeno S. (2001) Conditioning and sexual behavior: a review. Hormones and Behavior, 40(2):291-321.

Rémès, É. (2004). Sex guides. Paris: Éditions blanche.

Roberts S.A., Simpson D.M., Armstrong S.D., Davidson A.J., Robertson D.H., McLean L., Beynon R.J., Hurst J.L. (2010) Darcin: a male pheromone that stimulates female memory and sexual attraction to an individual male's odour. BMC. Biol., 8(1):75.

Rodriguez-Rust, P. C. (2002). Bisexuality : the state of the union. Annual Review of Sex Research, 13, 180-240.

Savic I., Berglund H. (2010) Androstenol--a steroid derived odor activates the hypothalamus in women. PLoS. One., 5(2):e8651.

Savic, I., Berglund, H., & Lindstrom, P. (2005). Brain response to putative pheromones in homosexual men. Proceedings of the National Academy of Sciences of the United States of America, 102, 7356-7361.

Savic I., Heden-Blomqvist E., Berglund H. (2009) Pheromone signal transduction in humans: what can be learned from olfactory loss. Human Brain Mapping, 30(9):3057-3065.

Schober J., Weil Z., Pfaff D. (2011) How generalized CNS arousal strengthens sexual arousal (and vice versa). Hormones and Behavior, 59(5):689-695.

Sergent, B. (1986). Initiatory homosexuality in ancient Europe. Paris: Payot.

Shirozu, H., Koyanagi, T., Takashima, T., Horimoto, N., Akazawa, K., & Nakano, H. (1995). Penile tumescence in the human fetus at term--a preliminary report. Early Human Development, 41, 159-166.

Simerly, R. B. (2002) Wired for reproduction: organization and development of sexually dimorphic circuits in the mammalian forebrain. Annual Review Neurosciences, 25:507-536.

Sisk, C. L. & Foster, D. L. (2004). The neural basis of puberty and adolescence. Nature Neuroscience, 7, 1040-1047.

Soulier, B. (2001) [A love like so many others? Motor handicaps and sexuality]. Paris: Association des paralysés de France.

Spevak, A. M., Quadagno, D. M., & Knoeppel, D. (1973). The effects of isolation on sexual and social behavior in the rat. Behavioral Biology, 8, 63-73.

Spies, H. G., Pau, K. Y., & Yang, S. P. (1997). Coital and estrogen signals: a contrast in the preovulatory neuroendocrine networks of rabbits and rhesus monkeys. Biology of Reproduction, 56, 310-319.

Stowers, L., Holy, T. E., Meister, M., Dulac, C., & Koentges, G. (2002). Loss of sex discrimination and male-male aggression in mice deficient for TRP2. Science, 295, 1493-1500.

Suggs, R. C. (1966). Marquesan sexual behavior: an anthropological study of polynesian practices. New York: Harcourt, Brace & World.

Trezza V., Campolongo P., Vanderschuren L.J. Evaluating the rewarding nature of social interactions in laboratory animals. Dev. Cogn Neurosci., 1(4):444-458, 2011

Turner, C. H., Davenport, R. K., & Rogers, C. M. (1969). The effect of early deprivation on the social behavior of adolescent chimpanzees. The American Journal of Psychiatry, 125, 1531-1536.

Vanderschuren, L. J., Niesink, R. J., & van Ree, J. M. (1997). The neurobiology of social play behavior in rats. Neuroscience and Biobehavioral Reviews, 21, 309-326.

Vasey, P. L. & Duckworth, N. (2006). Sexual reward via vulvar, perineal, and anal stimulation: a proximate mechanism for female homosexual mounting in Japanese macaques. Archives of Sexual Behavior, 35, 523-532.

Wallen, K. & Parsons, W. A. (1997). Sexual behavior in same-sexed nonhuman primates: is it relevant to understanding human homosexuality? Annual Review of Sex Research, 8, 195-223.

Ward, I. L. (1992). Sexual behavior : the product of perinatal hormonal and prepubertal social factors. in Geral, A. A., Moltz, H., Ward, I. L. (Eds.). Sexual differentiation, vol 11, Handbook of behavioral neurobiology. New York: Plenum Press.

Wenkstern D., Pfaus J.G., Fibiger H.C. (1993) Dopamine transmission increases in the nucleus accumbens of male rats during their first exposure to sexually receptive female rats. Brain Research, 618(1):41-46.

Wessberg, J., Olausson, H., Fernstrom, K. W., & Vallbo, A. B. (2003). Receptive field properties of unmyelinated tactile afferents in the human skin. Journal of Neurophysiology, 89, 1567-1575.

Winkelmann, R. K. (1959). The erogenous zones: their nerve supply and its significance. Mayo Clinic Proceedings, 34, 39-47.

Winman A. (2004) Do perfume additives termed human pheromones warrant being termed pheromones? Physiology & Behavior, 82(4):697-701.

Woodson, J. C. (2002). Including 'learned sexuality' in the organization of sexual behavior. Neuroscience and Biobehavioral Reviews, 26, 69-80.

Wunsch S. (2007) [Doctoral thesis: Role and importance of reinforcement processes in the learning of the reproductive behavior in humans]. EPHE-Sorbonne, Paris.

Wunsch, S., Brenot, P. (2004). Does a sexual instinct exist? Sexologies, 13(48), 30-36.

Yoon, H., Enquist, L. W., & Dulac, C. (2005). Olfactory inputs to hypothalamic neurons controlling reproduction and fertility. Cell, 123, 669-682.

Zhang, J. & Webb, D. M. (2003). Evolutionary deterioration of the vomeronasal pheromone transduction pathway in catarrhine primates. Proceedings of the National Academy of Sciences of the United States of America, 100, 8337-8341.