Primordial Factors of Reproduction Behavior and their Evolution in Human

Wunsch Serge, department of neuroscience, EPHE, Paris

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, whose purpose is the achievement at the favorable season of copulation permitting fecundation.

It would seem that during evolution, by reason of the modifications of the brain of rodents into that of Human, the hormonal and pheromonal factors would have become secondary, whereas the cognitive factors and the reinforcement processes (or reward systems) would have become predominant.

For these reasons, in Human, the behavior which some times leads to reproduction would not be an innate "reproductive behavior", but an acquired "erotic behavior" involving behavioral sequences of stimulation of the most erogenous body zones (oral, anal and genital).

Keywords

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

1. Introduction

What are the factors at the origin of human sexuality and reproductive behavior ? What are the most primordial 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 the various fundamental behaviors of human being, 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 this at puberty (for example, 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 and that 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 allows reproduction (Agmo 2007).

This article presents a synthesis of the literature. All these data make it possible to propose an ***archetypical*** model of the reproductive behavior of mammals, and its evolution from rodents to Human.

2. Archetype of mammalian reproductive behavior

In the simplest mammals (non-primates), current research made it possible to identify many innate elements, as well instinctual as physiological or autonomous, which can take part directly and indirectly in the appropriate realization of the fertilizing vaginal coitus: the hormones can control a seasonal inhibition (copulation takes place only at the favorable season), and a puberty inhibition (copulation takes place only at the period of maturity of the reproductive organs), and an estrous inhibition (copulation takes place only at the periovulatory period); the pheromones allow the recognition of the appropriated partner, while sexual reflexes (lordosis, erection, pelvic thrusts, ejaculation, reflex ovulation triggered by coitus...) allow the innate motor execution of the vaginal coitus and also optimize fecundation.

These various elements, which are complementary, do not all simultaneously exist in the current species of mammals. But when trying to reconstitute the first mammalian organism, in particular by grouping together these various complementary elements, it appears in a remarkable way in the original organization plan of mammals *a genuine reproductive behavior*, ***whose only purpose and only 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* primordial factors of reproductive behavior

What would be the main *innate primordial factors* at the origin of reproductive behavior and which would be their respective functions?

Research carried out for several decades in mammals has highlighted the existence of four *innate primordial 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). They regulate mainly:
  Initially, during the organism development (organizational phase) they control the sexual differentiation of some neural structures (preoptic nucleus, hypothalamus...) involved in the reproductive behavior (Simerly 2002).
  And next, at adulthood (activational phase), they are involved in:
  - The activation of sexual behavior during: a) the season favorable to reproduction (Aleandri & al., 1996), and b) 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 would allow especially the triggering of sexual motivation (via the principal and vomeronasal olfactory system; Moncho-Bogani & al., 2004; Yoon & al., 2005) and discrimination of an adequate reproductive partner (via the vomeronasal system; Stowers & al., 2002; Dulac & Torello, 2003).

– The *sexual reflexes* (motor, autonomous and neuroendocrinous).
The motor sexual reflexes allow the attainment of the last phase of copulation. These reflexes are:
  – Lordosis (Pfaff & al., 1994) and / or immobilization.
  – Intromission (Meisel & Sachs, 1994).
  – Pelvic thrusts.

The autonomous and neuroendocrinous sexual reflexes facilitate copulation and allow fertilization. These reflexes are:
  – Erection and lubrication (Giuliano & Rampin, 2004).
  – Ejaculation (Allard & al., 2005; Coolen, 2005).
  – Ovulation reflex, caused by coitus (Spies & al., 1997).

– *Reinforcement processes* (on the neurobiological level) or reward systems (at the psychological level). These processes, associated with body 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 the reiteration of all the activities of stimulation of the body and especially of the genital zones. These processes would also, although indirectly, be at the origin of the learning of the majority of the noninnate sequences of reproductive behavior (Agmo 2007).

2.2. *Acquired* primordial 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, but which would not seem to be innate. These elements, which would be acquired during the development period of the organism, would be:

– The recognition of congeners (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 which would be the most difficult to hard-wire or to code genetically*. These capacities would 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.

To give a precise example of the difficulty of "hardwiring" or "programming" innate cognitive characteristics, one can study in detail the hypothesis of Morris Desmond (1970), which supposes buttocks and breasts could be innate visual signals. According to this hypothesis, the similarity between the shape of the breasts and the buttocks is explained by the need in the human race, and because of face to face coitus, to transpose a specific posterior excitatory signal, the buttocks, into a similar anterior signal, the breasts. The breasts would thus be "front buttocks", an excitatory adaptive signal specific to the human race. Various declarative and behavioral investigations have shown that the buttocks and the breasts were indeed both the most attractive sexual signals for human males. 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 ROSENZWEIG & al. 2002), show that the visual system is composed of a great number of small structures (functional modules) which have each a *limited role* in visual data processing. For example, the processing of the luminosity of the signal is carried out by the retina, the generation of saccadic eye movements by the interstitial rostral nucleus of the median longitudinal bundle, the processing of colors by visual area 4, and certain dynamic characteristics (movement, direction ...) by visual area 5, etc. It is *the coordination of all these elementary processes* which is at the origin of vision. According to all this current knowledge, the hypothesis of the inneity of a system of visual information 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 morphology of the congeners 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 numerous capacities of the visual system develop in interaction with the environment. Furthermore, a gene codes a protein, which, in the best case, can be used only 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 which would probably be necessary for the interpretation of the complex pattern of buttocks and breasts in the associative areas of the inferior temporal cortex? How can we explain the stability of this coding in areas known to be the center of the phenomena of plasticity, selective stabilization and reorganization? How finally 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: some molecules, some 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 especially – knowing that buttocks and breasts do not have the same appearance in women and in female monkeys, and knowing that the human race differs genetically from the other primates by only a few percent, it is almost impossible, according to current knowledge, to conceive how random changes or genetic modifications in a protohuman organism and on a restricted number of genes can 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 current 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 noninnate capacities (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 will present the data which suggest that these capacities are not innate, and the experimental arguments which give indications as to the likely conditions of their being learned.

The recognition of congeners would not be 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 the Ovidae, and, probably, in the other mammals. It can also be noted that there is no necessity to code this information genetically, since the morphological, olfactive, auditive and visual characteristics of the congeners would inevitably always be learnt: except in exceptional cases, a new-born animal is always in contact and develops with members of his species. The learning of the congeners' characteristics is thus *predetermined* by the context of the development and it is *always* carried out.

Sexual socialization, i.e. the whole of the attitudes and reactions appropriate to sexual social interaction with congeners, would not be 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, according to current knowledge, how all the sensory, emotional and cognitive capacities necessary for the appropriate social and sexual interactions can be programmed in the nervous system (cf. the similar example of buttocks and breasts, detailed in the previous paragraphs). Sexual socialization would be learnt during the many and frequent social games which are practised by young mammals throughout their development (Vanderschuren & al., 1997). These play activities are frequently repeated because they are reinforcing, in particular during the developmental period (Douglas & al., 2004).

The sexual motivation to seek genital physical contact would not be innate. Indeed, what would be the neurobiological processes which can allow the reciprocal attraction of a male and a female and then provoke copulation? According to current knowledge, one can explain the recognition of the partner and the state of sexual excitation by pheromones and hormones. Apparently, to schematize, the sexual pheromones would allow the recognition of the partner (Stowers & al., 2002; Dulac & Torello, 2003) and the induction of a state of sexual excitation (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. But, once the male and the female are in a state of excitation – a neural state appropriate for the release of various physiological or motor actions – what are the processes which will bring them to copulation? One can envisage that there could

be innate knowledge, representations or motor sequences, specific to vaginal coitus. But 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 allow the achievement of the final part of copulation. To recapitulate, the known innate processes explain the sexual excitation 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 particular motivation is acquired during development, due in particular to the processes of reinforcement. Indeed, physical stimulation, in particular at the level of the genital zones, would be particularly reinforcing. The postnatal physical contacts with the mother and with the other newborn animals, and in particular ano-genital 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' ano-genital area (Spevak & al., 1973), could gradually develop a sexual motivation to seek genital stimulations. This acquired sexual motivation could then be strongly potentiated 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 capacity for the appropriate genito-genital positioning of the bodies (the mounting sequence in the lower mammals) would not be innate. Indeed, it is observed that when nonhuman mammals, and especially the primates, are put in conditions where they cannot learn any element of the reproductive behavior, in a systematic way the male is incapable of coitus (Gruendel & Arnold, 1969; Missakian, 1969; Turner & al., 1969; Ward, 1992). This incapacity of the male to practise coitus in the absence of any preliminary experience has been verified in several species (guinea-pig, rat, cat, dog, rhesus monkey, chimpanzee), and it is systematic in all the 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 the congeners, which is the critical factor at the origin of the lack of coitus (Ward, 1992; Gruendel & Arnold, 1969). One can thus observe sexually naive males expressing many specific behaviors of reproduction (excitation, erection, contacts with the partner…) but they do not manage to copulate. One of the main problems, although there are also related problems of socialization and fear of the other congeners (Goldfoot, 1977), could be related to a construction deficit in the "body schema" and is characterized by an incapacity to correctly position the body in order to succeed in practising intromission (Hard & Larsson, 1971). The absence of inneity of the genito-genital positioning is hardly surprising. How could this complex cognitive capacity, which requires the innate existence of representations and specific positions of the body in space, be preprogrammed in the nervous system? According to current knowledge, it is apparently unexplainable. On the other hand, this capacity could be learnt during bodily interactions and from the sexual games with congeners. These activities would be frequently repeated because of their reinforcing characteristic (Douglas & al., 2004). The first postnatal body contacts and more particularly all the types of contacts and body explorations carried out during social games could be at the origin of the construction of a "body schema" of the individual and of the congeners. The learning of a body schema would permit the animal to be able to carry out adapted 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 which would trigger sexual reflexes could thus initiate partial sexual sequences (sexual games), which would be gradually integrated in more global motor schemas (Hard & Larsson, 1971), thus gradually initiating the learning of a more complete reproductive behavior. All the learning carried out due to these physical activities and stimulations would concretely result in the development of the neural structures involved in the control of sexual behavior (medial amygdala, median preoptical nucleus, medullary motor nuclei…; Moore & al., 1992; Baum & al., 1995; Cooke & al., 2000). The control which these structures exert on reproductive behavior would thus not be an innate control, dependent on a genetically or hormonally "programmed" organization of these structures, but a mainly acquired control. In this way, the interaction between the environmental factors and the innate factors allows the structural and functional development of the nervous system, and the development of the specific neural circuit of the sexual behavior.

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

In conclusion from 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 would not be innate, but that they would be learnt due to the numerous physical and social interactions taking place during the development period. In this way, at puberty, all the factors and the processes necessary for the achievement of heterosexual reproductive behavior would be functional.

2.3. Emergence and dynamics of reproductive behavior

According to all the data presented in the previous sections, and from an analysis of the various biological processes identified in the lower mammals, what would schematically be the dynamics of the heterosexual reproductive behavior of a *prototypical* mammal?

Hormones would be a major factor. With regard to behavior, they would 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 neurones, would activate sexual behavior during the season favorable to reproduction (Aleandri & al., 1996). Sex hormones would initiate reproductive behavior at puberty (Sisk & Foster, 2004), would lift the tonic inhibitions on the sexual reflexes, would lower the sensory thresholds (Gandelman, 1983), would activate the synthesis and release of sexual pheromones and would potentiate sexual motivation. The organism is thus ready to carry out the behavioral sequences leading to fecundation.

Then, during what is generally called the motivational phase, when sexually naive animals would be present, pheromones would be the main primary signals which would allow the triggering of the innate and acquired sexual motivation (Moncho-Bogani, 2005) and the discrimination of the *appropriate* ***heterosexual*** *sexual partner* (Stowers & al., 2002; Dulac & Torello, 2003).

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

Finally, during the consumatory phase, when the animals are in physical contact, the physical stimuli provoked by each action would constitute 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 carried out a first sexual behavior, and progressively with the increase of its sexual experiences and concomitant learning (Woodson, 2002), the various motor sequences will be carried out more effectively, other signals (visual, auditive, gustatory, etc.) can become sexual by conditioning, and reproductive behavior can be carried out in spite of the absence of certain signals crucial for the sexually naive animal (Meredith, 1991; Signoret, 1996).

We thus observe that reproductive heterosexual behavior would emerge mainly from the functional coordination of various reflexes and innate sexual processes, from interactions with congeners and from various learning experiences which are always carried out during 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 those induced by ano-genital licking, are not apparent, are not directly related to reproduction or are not regarded as "sexual".

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 be no instinct, i.e. an innate central programming of the various motor sequences necessary for the achievement of this behavior. Instead there would be the possibility of the coordination of various innate but elementary functional modules, which after some essential learning would enable the emergence of a reproductive behavior.

These particular characteristics lead us to suggest the concept of a "partial instinct", i.e. an incomplete set of innate elements, but, because they are associated with specific environmental circumstances which almost always exist during development (for example physical contacts, sensory stimuli, the mother-child interactions …), the missing elements are indirectly always acquired and 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 primordial factors and its developmental learning, exist in all mammals and in particular in Human?

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 which directly influence the innate primordial factors of reproductive behavior.

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

– An important development of the prosencephalon.

– A major decrease in the influence of hormones and pheromones.

– A functional deterioration of the vomeronasal system.

The significant development of the neocortex, the seat of the 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 Human, the cortex, which has developed to constitute three quarters of the brain, would be the medium which has allowed the emergence of culture and its determining influence on human sexuality.

As for the hormonal factors, which play a major role in the control of reproductive behavior, one notices that their influence decreases gradually until it becomes minor in human beings. 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 (Wilcox & al., 2004). The puberty hormones are no longer determinants of the initiation of sexual behavior: both in chimpanzees (Hashimoto, 1997; De Waal, 1990) and in Human (Suggs, 1966; Malinowski, 1929; 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.

The deterioration of the vomeronasal system in Old World primates (Zhang & Webb, 2003) causes the disappearance of the functions provided by this organ, in particular the ***heterosexual discrimination*** of the *appropriate reproductive partner* (Stowers & al., 2002; Dulac & Torello, 2003). Moreover, although pheromones can still be perceived at the level of the main olfactory system (Liberles & Buck, 2006), one observes that their effects, in particular behavioral, are weak in human beings (Foidart & al., 1994).

In Human therefore there only remain the innate primordial factors at the origin of the last part of reproductive behavior: the sexual reflexes (erection, lubrication, intromission, pelvic thrusts, ejaculation), which allow copulation to be achieved. And reinforcement processes also remain, associated with body hairy skin and the erogenous zones, which are at the origin of the reiteration of stimulation activities of the body and especially of the genital zones.

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

It appears that the various primordial factors are relatively independent of each other and can be modified or disappear, without necessarily compromising reproduction. In these cases, one observes that the reproductive behavior develops according to the characteristics of the factors which still exist. If seasonal control weakens, the behavior is expressed continuously but with seasonal variations of frequency; if the ***heterosexual discrimination*** of the appropriate partner disappears, the behavior becomes ***bisexual*** (Dulac & Torello, 2003); etc. 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 primordial factors, this species can survive and reproduce.

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

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

In synthesis, in primates and especially in Human, the hormonal and pheromonal innate primordial factors would become secondary, the copulatory sequence would be preserved, and it would be the cognitive and reinforcement factors which would be 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 be the development and the dynamics of the reproductive behavior of Human?

4. Behavioral model in primates and Human.

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

Currently, at least two somatosensory systems are known which are associated with the reinforcement processes. The first one, apparently the most general, is a system located in body hairy skin and probably constituted by fibres with slow conduction, which are not myelinized and which originate in the plexus of the hair roots. This system responds to light touching and projects itself in the limbic areas, which would imply that it is functional in the emotional responses provoked by pleasant physical contacts (Olausson & al., 2002; Wessberg & al., 2003). It may then be responsible for the searching for physical contact and would explain the reason for primates being contact animals. 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). 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 which 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 them 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 would 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* allow the reproduction necessary for the survival of the species. The crucial hypothesis is that *the acquisition of a human behavior allowing reproduction would depend – mainly but indirectly – on the activation of reinforcement processes, provoked by the stimulation of the genital erogenous zones*. Expressed otherwise, *it is mainly the existence of erogenous zones and especially the intense erogeneity of the penis, the clitoris and the vagina which would provoke the discovery and then the repetition of various motor sequences of stimulation of the body and the genitalia, 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 1**).

Emergence of a behavioral dynamics: erotic behavior. The association of two innate biological factors, the processes of reinforcement [1] with the erogenous body zones [2], creates a functional system. This system would be at the origin of the emergence of erotic behavior, characterized by the repetition of the motor sequences of stimulation of the erogenous zones [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 gender*** – would discover the erogenous zones, and, through the medium of the reinforcement processes, would learn to repeat the stimulation of these erogenous zones. Erotic activities would thus be gradually acquired during development, in a few months or several years, according to the learning undergone, the quantity and the quality of the erotic experiences.

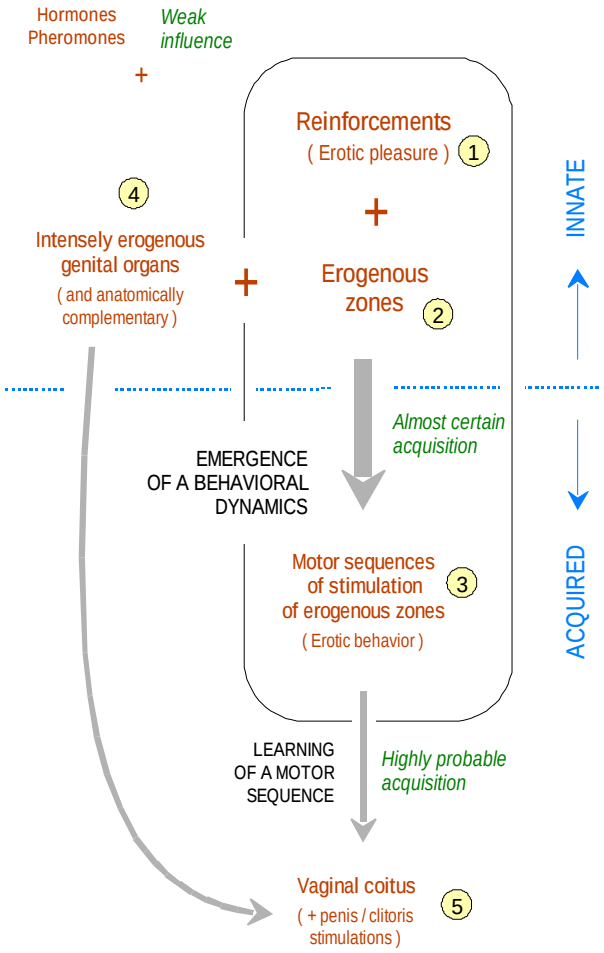

Figure 1: Acquisition of a behavior allowing the reproduction

Learning of a specific motor sequence: vaginal coitus. During erotic behavior, during the search for physical pleasures, the existence of complementary genitals (penis and vagina) having highly erogenous zones [4] would be a characteristic which would induce a high probability that vaginal coitus becomes one of the preferred erotic practices [5] (**Figure 1**, part [4] and [5]).

The fact that the stimulation of the genitals may generally provoke highly intense erotic pleasure, including orgasm, would be one of the main factors facilitating the acquisition and repetition of vaginal coitus. This characteristic would lead erotic activities to be *mainly centered on the genitals*, thus increasing the probability of discovery of *several genital activities*, among which vaginal coitus. Moreover, curiosity, the search for novelty and cognitive capacities would also be factors increasing the probability of the discovery of 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.

It should be noted that in this model, if fertilizing vaginal coitus is practised, 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 primordial factors, this activity is (fortunately) one of the erotic activities which brings most pleasure.

In the following section we will present ethological, clinical and experimental data which 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 going to present only the main animal and human data which permit us to assess this model.

To note that the recent work of Anders Agmo: "Functional and Dysfunctional Sexual Behavior" (2007), presents analyses of a very great number of experimental data which 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 ethological, ethnological and clinical knowledge the data already in existence which would corroborate or refute the model. Our neurobiological hypothesis of the functional preponderance 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 ethologic data, we will limit ourselves to the *pan paniscus* chimpanzee (Bonobos), which is the animal species closest to Human, both at the genetic and the cognitive and behavioral levels. It is the most corticalized animal species, therefore the most appropriate to test the hypothesis, but, contrary to Human, it is difficult to invalidate the behavioral observations by reasoning that its sexuality could be "denatured" by the influence of culture.

To summarise the essentials, the sexuality of the captive or wild Bonobos is continuous throughout the year and begins towards the age of one year, that is to say well before puberty. These prepubescent activities account for almost 1/4 of all sexual activities, the activities of the teenagers represent approximately half, and that of the adults a little more than a quarter. The sexual activities are ***bisexual*** (approximately 1/3 of activities are homosexual and 2/3 heterosexual, but never exclusively homosexual or heterosexual), and one observes many nonreproductive activities: masturbation, use of objects, mutual masturbation, kissing, oro-genital activities, in groups, etc. It is noticed that these nonreproductive activities account for approximately 3/4 of all the sexual activities (Hashimoto, 1997; De Waal, 1993, 1990).

In conclusion, one observes that the sexuality of the Bonobos 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 preponderance of the "reinforcement / erogenous zones" system in the sexuality of the hominoïd primates.

Furthermore, the sexuality of the Bonobos demonstrates that the evolution of the prototypical heterosexual reproductive behavior in 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 gender – 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 (Allgeier & Allgeier, 1992; Brenot, 2004), in handbooks of sexuality (Comfort, 1992; Remes, 2004) or in the great classics of erotic literature (for example the Ars amatoria of Ovid or the Kama Sutra of Vatsayana). These data suggest, both 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 it remains of it in Human) and the acquired erotic behavior. *The erotic activity is acquired and develops on*

the basis of the new or preserved erogenous zones, and no longer has any connection with reproduction, whereas the sexual reflexes which permit the innate achievement of the final sequences of copulation (erection, ejaculation …) always exist but are no longer integrated in the 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 transformations of the nervous system during evolution in Human, genuine heterosexual reproductive behavior of the first mammals no longer exists, but rather *modified behavior* of which *the goal is body and erogenous zones stimulation* has replaced this. Reproduction is nevertheless preserved, because of the intense erogeneity of the penis/clitoris which favors genital activities, including the vaginal coitus which is indispensable to fertilization.

It would even be possible to speak about *erotic behavior*, insofar as the reinforcements (perceived consciously as a sensation of erotic pleasure) would 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 would be organized around a specific purpose: obtaining erotic sensations, of which, especially, orgasmic pleasure.

Besides, with regard to the main erogenous zones (genital, anal, oral and pectoral in woman), a remarkable characteristic is that they are constituted by muco-cutaneous tissue and that they correspond to the openings of the organism which are involved in the entries and exits of matters. These data would 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, eating behavior, 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 presence of the primary erogenous zones at the level of the main openings 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 allow 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 remarkable 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 functional deterioration of the vomeronasal system and the weakening of the hormonal and pheromonal effects as being functional characteristics which optimize reproductive behavior. On the contrary, it would seem that a real heterosexual reproductive behavior exists in rodents, relatively optimized, but of which certain factors of optimization (seasonal control, estrus, recognition of the heterosexual partner…) would have been lost or weakened through the hazardous process of the evolution of mammals. What is also remarkable is that in Human the function of reproduction does not seem to be achieved by a biological organization whose goal is 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 which has a different goal.

What main objections can one raise to this behavioral model (**Figure 1**), based on the hypothesis of the functional preponderance of the system of "reinforcement / erogenous zones"?

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. Nevertheless, one observes that almost all the primates have bisexual activities (Wallen & Parsons, 1997), in particular the chimpanzees *pan paniscus* (Bonobo) (De Waal, 1993), that in sexually liberal societies children and teenagers have bisexual activities (Ford & Beach, 1965; Malinowski, 1929; Diamond, 2004), and that apparently in all the ancient warrior societies, before the advent of the current religions which are unfavorable to sexuality, generalized bisexual practices existed (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 often also rejected by homosexuals, that bisexuality does not exist on the level of practices and cultural values (Rodriguez-Rust, 2002), and that it is thus extremely difficult to live in a bisexual way (Evans, 2003). In order 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 codes of masculinity. 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 a 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 would apparently be the existence of an innate sexual orientation, revealed among homosexuals, and whose origin would be due to the anatomical and functional characteristics of the median preoptic area (Levay, 1991; Savic & al., 2005; Berglund & al., 2006). 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 model supposes only the preponderance of the erotic reinforcement process. The effects of hormones and pheromones can exist, *but would be weaker*.

Finally, the last main objection would be that such a behavior, *the majority of whose activities do not allow reproduction*, would not be adaptive, and would probably be eliminated during evolution by the mechanisms of natural selection. 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 would be necessary to move from the idea that everything that is not optimized is impossible in evolutionary terms, to the idea that everything that survives – *no matter in what 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, 1993, 1990; Hashimoto, 1997; Vasey & Duckworth, 2006), seem to be good examples which show 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 in order to confirm this behavioral model, and to clarify the importance and the respective role of the three factors which seem to be determining in the development of human sexuation and sexuality: sex hormones, reinforcement processes and cognitive processes. This first study allows us to show that this hypothesis of the preponderance of the "reinforcement process / erogenous zones" system is plausible, and that the study of reward systems and the somatosensory system in the emergence and dynamics of human behaviors is an area of research to develop.

7. General 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…), at the origin of the reproductive behavior of the lower mammals were modified during evolution. In the most developed mammals, the hormonal and pheromonal factors would have become marginal whereas the reinforcement processes and the emotional and cognitive factors would have become preponderant. Apparently, it is always the same factors which are at the origin of reproductive behavior among all the mammals, but, as the *characteristics* and the *relative importance* of these factors were modified during evolution, *the behavioral dynamics would be different*.

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

It seems, in Human, that innate *heterosexual reproductive behavior* no longer exists, but, 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, would induce the *learning* of many auto- hetero- homo- and bisexual activities, among which, indirectly, the vaginal coitus sequence crucial for reproduction. Thus Human reproduction, however fundamental to the survival of the species, would paradoxically be only an almost fortuitous consequence of the search for physical pleasures.

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