

Human sexual behavior: reproductive behavior or erotic behavior?

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Figure 1: Genito-genital rubbing
Hominids have many bisexual erotic activities unrelated to reproduction.
Genito-genital rubbing between two females. This frequent daily activity ends with orgasm.
How can we explain this sexual activity which is homosexual and unrelated to reproduction?
(Bonobos, photo Franz Lanting)

Abstract

What factors are at the origin of sexual behavior? What are the major differences between human sexuality and that of other mammals?

The synthesis of the neurobiological, ethological and ethnological data, enables to distinguish two types of sexual behavior in mammals. The reproductive behavior, centered on copulation, is typical of the simplest mammals. This behavior, "hardwired" in the brain, is controlled by hormones, pheromones and innate sexual reflexes. But during the evolution from rodents to humans, the influence of hormones and pheromones decreases, while the influence of reinforcement and cognition increases. Freed from hormonal constraints, sexual activities can exist in many situations that no longer relate to reproduction. The reinforcements, perceived as intense erotic sensations, would become the major factor in sexual activities. In hominids, the behavior that enables reproduction would become an "erotic behavior", characterized by the stimulation of the body and the erogenous zones, as well as by the maximization of pleasure.

This article presents a systematic and detailed comparison, summarized in a summary table, of the main neurobiological and behavioral key differences between these two sexual behaviors.

Key words

Sexual behavior, erotic behavior, reproductive behavior, reward, erogenous zones, pleasure, bisexuality, humans.

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Introduction

Since the beginning of modern sexology, with Krafft-Ebing, the purpose of human sexuality was reproduction. The existence of a "sexual instinct" was indisputable. Indeed, the perpetuation of the human race is not left to chance nor to the whim of individuals: a natural instinct guarantees it, and it imperiously, irresistibly demands satisfaction» (Krafft-Ebing, 1882).

In contrast to this innatist model, based on animal studies, models specific to humans have been developed (see eg Hardy, 1964). These models are based primarily on theories of social learning or conditioning (Pavlov, Skinner, Bandura, Gagnon ...).

Currently, thanks to the development of neuroscience, new data confirm that hominids' sexuality, and especially humans', is very different from that of lower mammals. It is now possible to explain the main mechanisms, to clarify what is "instinctual" and what is acquired, and to contrast point to point all the fundamental differences between the "reproductive behavior" of the simplest mammals and the "erotic behavior" of hominids (see Figure 2).

Figure 2 : "Reproductive behavior" versus "Erotic behavior"

To understand the numerous data currently available relating to human beings' sexuality, it is necessary to change the system of reference. We must, as formerly in cosmology, make a Copernican revolution: *it is no longer REPRODUCTION that is central to human sexuality, but PLEASURE.*

Due to publication constraints, this article presents only the main factors of sexual behaviors, only the crucial differences and not the numerous similarities, as well as only the most recent and the most major reference studies. Of course, many other factors are involved, but their role is less decisive. The reader is referred to complementary work for more detailed explanations.

"Reproductive behavior" VS "Erotic behavior"

What are the particular characteristics which suggest, in mammals, the existence of two types of sexual behavior?

To a remarkable extent, recent studies have shown that rodents' and hominids' sexual behavior depended on different neurobiological processes, which enables to explain the differences in their behavior.

More precisely, at a behavioral level, when we observe the sexual behavior of the simplest mammals (rodents, felines, canines, sheep, horses ...), we notice that the crucial sequence which enables fertilization (i.e.: copulation) is stereotypical: the female is in a position of lordosis or remains motionless, while the male mounts her from behind, penetrates into her, then makes pelvic thrusts until ejaculation. Furthermore, the main part of this sexual behavior appears to be organized around the vaginal intercourse, which enables fertilization. At a neurobiological level, innate and crucial processes, which explain the stereotyping of copulation, have been discovered: in particular *genuine pheromones for sexual behavior* (Roberts et al., 2010; Haga et al., 2010) and the lordosis mechanism, which is the key sequence of copulation (Pfaff, Schwartz-Giblin, MacCarthy, & Kow, 1994; Kow et al., 2007). For all these reasons, which will be detailed later in this article, this behavior corresponds to a "reproductive behavior".

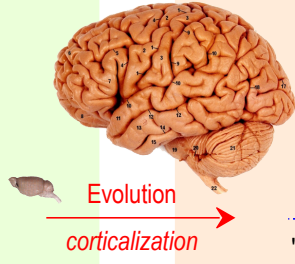
On the other hand, when we observe the sexual behavior of hominoid primates, especially that of human beings, we notice a variety of activities around several areas of the body: sensual caresses, oral-oral, oral-genital, genital-genital or anal-genital activities... *This sexual behavior of hominids is very different from that of the lower mammals* (Bagemihl, 2000), and rather seems to correspond to a behavior of stimulation of erogenous zones, *in order to obtain erotic pleasure.* At the neurobiological level, were also discovered innate and crucial processes which explain the erogenous zones, the erotic reinforcements (Agmo, 2007) and pleasure (Kringelbach & Berridge, 2009). For all these reasons, this behavior appears as being rather an "erotic behavior".

The evolution from the "reproductive behavior" of the simplest mammals to the "erotic behavior" of hominids is gradual, and it is due to the mammalian brain's evolution. *It is still the same factors which intervene, but their importance is not the same any more:* decline of hormonal control (Keverne, Martel, & Nevison, 1996; Signoret, 2006), impaired olfaction (Swaney & Keverne, 2009; Zhang & Webb, 2003), dominance of erotic reinforcements (Agmo, 2007), corticalization and development of cognition.

In order to highlight properly the neurobiological and behavioral differences, the comparisons below are focused on the extremes: rodents, the simplest and most studied mammals, and the human being, the most corticalized mammal.

Figure 2 : Sexual behaviors of mammals
 "reproductive behavior"
 versus "erotic behavior"

		Reproductive behavior	Erotic behavior
PHYLOGENESIS	Representative species	Lower mammals Rodent	Hominoid primates Homo sapiens
	Effects of evolution	Optimisation by natural selection	"Tinkering of evolution" (cf. F. Jacob)
NEUROBIOLOGY	Innate neurobiological factors	HORMONES PHEROMONES Sexual reflexes Reinforcement Cognition	Hormones Pheromones Sexual reflexes REINFORCEMENT COGNITION
	Hormones Neuromediators	Sexual hormones (testosterone)	Endogenous opioids Dopamine
	Innate and crucial structures	Neural circuitry of lordosis (♀) Neural circuitry of pelvic thrusts (♂)	Neural circuitry of reward + penis / clitoris
	Innate and fundamental signals	Olfactif signal <i>triggered by</i> sexual pheromones	Somatosensorial signal <i>triggered by</i> mechanical stimulation of erogenous zones
	Motivation	Pheromones <i>innate</i>	Erotique pleasure (Reinforcement) <i>acquired</i>
	Sexual orientation	Heterosexuality <i>innate</i>	Sexual preferences <i>acquired</i>
	Cognitive processes	[secondary role]	Culture <i>Values, Beliefs, Prohibitions ...</i>
BEHAVIOR	Crucial behavior	Vaginal coitus with ejaculation <i>to obtain fecundation</i>	Stimulation of the most erogenous zones (<i>particularly penis / clitoris</i>) <i>to obtain orgasm</i>
	Modalities of realization	One male and one female	One or several person(s)
	Variability of behavior	Low variability (<i>variations around vaginal coitus</i>)	High variability (<i>anything that enables the erotic stimulation of erogenous zones</i>)
	Purpose of behavior	Reproduction of the species	Maximization of erotic pleasure (<i>reproduction is an indirect consequence of erotic activities</i>)
FUNCTIONAL ANALYSIS	Innate biological organization	" Instinct " (<i>specific hardwired neural circuitry controlling reproductive behavior</i>)	Reinforcement + erogenous zones (<i>induce the learning of erotic activities mainly by operant conditioning</i>)
	Behavioral dynamics	Genuine reproductive behavior, innate	Erotic behavior, acquired <i>potentially pan-sexual</i>



Phylogenesis

Representative species

The most representative species of the "reproductive behavior" are the mammals which have the least developed brain structure, and whose behavior is dependent on hormones and pheromones. Rodents, the best known small mammals, are used as example.

For the "erotic behavior", the most representative species are the most corticalized mammals, that is to say, dolphins and hominids (gorillas, orangutans, chimpanzees, humans). The human species would be the most representative.

Effects of evolution

The "reproductive behavior" seems to have been optimized by natural selection.

On the other hand, the "erotic behavior" of hominids, which results from the decline of hormonal control (Keverne et al., 1996; Signoret, 2006) and from the alteration of olfaction (Swaney et al., 2009; Liman, 2006; Zhang et al., 2003), is not optimized for reproduction. This behavior seems to be the result of the action of several evolutionary factors: *natural selection*, *sexual selection*, but also *chance* (Jacob, 1977; Jacob, 1981; Gould, 2002; Kupiec & Sonigo, 2000), which explains that living organisms are not fully optimized and not perfect. Nevertheless, this lesser optimization seems to have been compensated with adaptive advantages (Bailey & Zuk, 2009): enhancing of social relationships (Neumann, 2009), appeasement of conflicts, reconciliation (De Waal, 1990) ...

It is worth noting that at present the theory of evolution cannot satisfactorily explain some crucial evolutionary phenomena (Denton, 1988). The hypotheses concerning the evolution of sexual behavior should be reconsidered according to the future developments of knowledge.

Neurobiological level

Innate neurobiological factors

What are the most basic innate and primordial neurobiological factors at the origin of sexual behaviors?

A continuum between nature and nurture exists in all mammals. Many factors result from the interaction between the organism and the environment, but some are completely innate or acquired (Kobayakawa et al., 2007; Moncho-Bogani, Lanuza, Hernandez, Novejarque, & Martinez-Garcia, 2002; Schaal et al., 2003).

In adulthood, behaviors are controlled by many factors. But only some innate and specific factors are at the origin of their development. One of the main problems of behavioral research is that many factors are acquired because of the mammalian brain's great learning capacity, and these acquired factors are often consequences and not causes of the behavior. For this reason, it is absolutely crucial to identify precisely the innate factors, that depend on specific neurobiological processes (Kippin, Cain, & Pfaus, 2003), because it is they who are the origin of fundamental behaviors.

It is also crucial to identify the primordial factors, that is to say the most major factors *that act before the others*, because they determine the development of behaviors in a very particular direction. For example, the *darcin* pheromone of the male mouse stimulates in an innate way the vomeronasal organ of all the females. But as soon as a female has detected the *darcin* of a male, the pheromone provokes in this female the learning of this male's specific olfactory characteristics (Roberts et al., 2010). Before this event, the female could react in an innate way to all males. After this event, the female has learned to respond preferentially to a single male. The *darcin* is here an innate and primordial factor which conditions females' future sexual reactions. Without accurate and detailed identification of these critical factors, it is difficult to understand sexual behaviors.

At present, neuroscience research has identified numerous innate and primordial factors, instinctual as well as physiological or autonomous, which can participate directly and indirectly in the realization of sexual behavior:

- **Hormones** (melatonin and sex hormones) exert a global and major control over the sexual behavior.
- **Pheromones**, which are animals' main communication signals, permits, among others, to trigger sexual arousal and recognition of a partner of the opposite sex.
- **Sexual reflexes** (lordosis, erection, pelvic thrusts, ejaculation, reflex ovulation during intercourse ...) enable the motor execution of the final part of sexual behavior (copulation and vaginal intercourse), and optimize fertilization.

- **Rewards / reinforcements**, primordial factors of many behaviors, permit various learning which optimize realization of reproductive behavior

- and, the last innate factor, which has a secondary role in lower mammals, **cognition**.

It is observed that these biological factors are *all* at work in *all* mammals. But from rodents to humans, *their relative importance changes during evolution*. The main changes between rodents and hominids concern hormones and pheromones, the influence of which decreases, as well as reinforcement and cognition, the influence of which increases. And this modification in the key factors' *relative importance* would explain the modification in sexual behavior dynamics (Wunsch, 2010).

The vole is a well known example of structural modification which causes changes in behavior. The modification of the cerebral localization of oxytocin receptors modifies the expression of maternal and sexual attachment. The mountain vole has oxytocin receptors mainly in the lateral septum and shows a minimal attachment, whereas the prairie vole, which presents a significant sexual and maternal attachment, has oxytocin receptors in several structures (nucleus accumbens, prelimbic cortex, lateral amygdala and median nuclei of the thalamus) (Young & Wang, 2004; Insel, Young, & Wang, 1997). Moreover, just a change in the expression of a single gene can profoundly alter this attachment behaviour (Lim et al., 2004; Young, Nilsen, Waymire, MacGregor, & Insel, 1999). We notice in these examples that a small structural modification leads to significant behavioral modification. These examples, as well as others (Beyer, Hoffman, & Gonzalez-Flores, 2007), suggests that the important differences between the brains of rodents and that of hominids should entail significant behavioral differences.

Hormones and neuromediators

What are the main hormones and neuromediators that control the innate and primordial factors of sexual behavior?

In lower mammals, hormones are a major factor of reproductive behavior. They exert numerous organizational and activational effects: sexual differentiation of the body in male and in female, development of the penis and the clitoris, activation of sexual behavior at puberty, control of pheromones and sexual reflexes, modification of the sensory thresholds, etc. (Simerly, 2002; Welsh, MacLeod, Walker, Smith, & Sharpe, 2010; Gandelman, 1983; Remage-Healey & Bass, 2006).

These effects exist in all mammals, but some have been modified during evolution, as the cortical development progresses. In fact, « man appears as the term of an evolution where the part taken by the central nervous system becomes dominant, whereas the hormonal signal, while remaining present and active, loses of its importance to be only optional. » (Signoret, 2006).

The most modified effect during evolution is temporal control. This control is exerted at a seasonal level (by melatonin), at a pubertal level (by testosterone) and at an estrous level (by estrogens). Thanks to this temporal control, in most species of lower mammals, reproduction behavior takes place only at the right season, at the period of the body's reproductive maturity, and at the period of gamete maturity. But in humans, seasonal control has virtually disappeared: sexual activity continues throughout the year and only a minor effect of the seasons on sexual behavior is observed in the Nordic countries (Aleandri, Spina, & Morini, 1996; Pandi-Perumal et al., 2006). Estrous control is weakened: women can have sexual activities throughout the cycle, although there is still a weak hormonal effect during the fertility period (Wilcox et al., 2004). Pubertal hormones are no longer decisive in initiation of sexual behavior: both in chimpanzees (Hashimoto, 1997; De Waal, 1990) and in Man (Malinowski, 1929; Suggs, 1966; Ford & Beach, 1965; Marshall & Suggs, 1971; Henry & Henry, 1974; Diamond, 2004; Martinson, 1994), if the cultural context allows it, sexual activities begin from the first years of life.

Another factor modified during evolution seems to be **Reinforcements / Rewards**. Reinforcements have a secondary role in lower mammals, because they are under the strict control of hormones (Ferris et al., 2005). In hominids, although there remains a hormonal effect, it is weak (Dreher et al., 2007). Freed from hormonal control, reinforcements seem to become the major factor of learning erotic behavior (Agmo, 2007). They are constantly active throughout the year and can be activated in numerous situations unrelated to reproduction (for example during masturbation (Holstege et al., 2003)). The main neuromediators of reinforcements seem to be endogenous opioids, endogenous cannabinoids and dopamine (Kringelbach et al., 2009).

At a molecular level, the lesser influence of hormones on temporal control could be explained quite simply, for example by a mutation of a key enzyme (NO synthase (Du & Hull, 1999)), which would make it independent from testosterone.

It is worth noting that even if their importance decreases for certain functions, *sex hormones remain absolutely necessary*. For example, a minimal rate of 2,5 ng / ml of testosterone is indispensable in man (Giuliano, Tostain, & Rossi, 2004). **But hormones are not sufficient**. Indeed, if testosterone is the hormone of sexual behavior, how does it act on sexual motivation? How exactly does it induce the motivation to copulate with a partner of the opposite sex? Where does it act? Does it activate innate knowledge, representations or motor patterns of vaginal intercourse? How does testosterone act on the motor activities? How does testosterone provoke for example kissing, fellatio, or more fundamental, vaginal intercourse? On what motor centres (medullary, mesencephalic...) does it act to provoke and control the anilingus? To accurately answer all these questions, one notices that on top of hormones, another factor is needed. And all the data presented in this article show that it is the rewards, associated with the erogenous zones, that originate motivation and the learning of the various human erotic activities (see especially the sections "Crucial and innate structures" and "Motivation").

It is also worth noting that if the cultural context prohibits or prevents infantile and / or adolescent erotic activities, the "reinforcement" factor's action is toned down, and erotic behavior development then depends more on the "hormonal" factor. For example, masturbation appears at about 3-4 years old in liberal environments (Yates, 1990; Suggs, 1966), but only at the period of puberty (Bancroft, 2008) in a less favorable cultural context.

In conclusion, in lower mammals, hormones (melatonin, but especially sex hormones) are a major factor and control reproductive behavior. But during the evolution towards hominids, the temporal control exerted by hormones has virtually disappeared, and erotic reinforcements have become continuously active.

And these two capital modifications would have a major impact on sexual behavior.

Crucial and innate structures

What are the innate and crucial biological structures, that control the key sequences of reproductive behavior, that is to say lordosis in females and coitus in males?

In the female of many species of lower mammals, the most fundamental motor sequence, that is absolutely necessary for copulation, is immobilization and/or lordosis. In short, lordosis is a universal motor sequence in mammals, which develops only in female (Kow et al., 2007). This complex reflex depends on the ventromedial hypothalamus' estrogen and is active only during estrus (Spiteri et al., 2010; Kow & Pfaff, 1998). This reflex is facilitated or disinhibited by male pheromones, which are detected by the vomeronasal organ (Haga et al., 2010). Finally, when the male mounts the female, the mechanical somatosensory stimuli trigger lordosis (Pfaff et al., 1994) and the vaginal stimuli of copulation increase the lordotic response (Gonzalez-Flores et al., 2007). What is remarkable, is that there are innate neural structures that control all the parameters of this crucial motor sequence, *so that it is executed only while ovules are mature, and when the male mounts the female* (see overview diagram and synthesis in Breedlove, Rosenzweig, & Watson, 2007, fig. 12.5).

In males, the main motor and autonomous structures of copulation are not as well identified. Nevertheless, erection (Giuliano & Rampin, 2004), intromission (Meisel & Sachs, 1994), pelvic thrusts (Morali et al., 2003; Hart, 1968; Comarr & Gunderson, 1975) and ejaculation (Allard, Truitt, McKenna, & Coolen, 2005; Coolen, 2005) are also innate reflexes.

We thus notice that the terminal and crucial phase of reproductive behavior, i.e: copulation, depends on innate reflexes. Remarkably, the autonomous and motor sequences of copulation correspond point to point with innate neurobiological organizations, *exclusively designed to achieve vaginal intercourse and fertilization*.

However, these innate motor reflexes do not explain the main motor characteristic of human beings' sexual behavior, which is the stimulation of erogenous zones. The most noteworthy fact that suggests a major *qualitative* change (and not quantitative) of sexual activities motor control, is that lordosis, *which is absolutely essential to lower mammals' realization of reproductive behavior, becomes useless and no longer plays any role in human sexual behavior. We notice moreover that when sexual stimuli occur, women's neurobiological processes no longer activate the immobilization of the body and the position of lordosis*.

We notice that sexual reflexes still exist in hominids, but *they have become independent from pheromonal and hormonal control. Most can be triggered at any time, in many situations which no longer have any relation to reproduction* (for example erection and ejaculation during masturbation).

Moreover, There is a system of reinforcement / reward (Olds & Milner, 1954), with a sexual component (Crawford, Holloway, & Domjan, 1993;

Caggiula, 1970; Caggiula & Hoebel, 1966), which enables learning. To simplify, all types of learning already exist in lower mammals: non-associative (habituation, sensitization (Dewsbury, 1981; Bailey, Anderson, & Schillo, 2005)), associative (effective and respondent conditioning (Pfaus, Kippin, & Centeno, 2001)), primary cognitive (motor skills, latent, insight), and rewards (Parada, Chamas, Censi, Coria-Avila, & Pfaus, 2010; Tenk, Wilson, Zhang, Pitchers, & Coolen, 2009; Camacho, Portillo, Quintero-Enriquez, & Paredes, 2009). In hominids, There is also specific learning: social learning (imitation, vicarious). All these types of learning enable sexual learning, and reinforcements / rewards seem to become directly involved in erotic learning through *association and reward*, as well as indirectly in the other types of learning (Kolb & Whishaw, 2006). At present, the existence of the numerous sexual learning is proved (Woodson, 2002), but all the details of the neurobiological processes which intervene in this learning are not exactly known. In outline, the reward / reinforcement system seems to be made up of two complementary systems (Berridge, Robinson, & Aldridge, 2009): a hedonic system especially opioidergic, localized mainly in the ventral pallidum (Smith, Tindell, Aldridge, & Berridge, 2009) and the nucleus accumbens regions (Pitchers et al., 2010b), with structures ("hot spots" (Pecina & Berridge, 2005)) specialized in the homeostatic regulation of the sensation of pleasure (Smith & Berridge, 2007; Tindell, Smith, Berridge, & Aldridge, 2009; Mahler, Smith, & Berridge, 2007); and a dopaminergic motivational system, localized mainly in the region of the ventral tegmental area. This system of reward / reinforcement seems to be similar in all mammals (Berridge & Kringelbach, 2008), *but continually active in hominids* (see the section "Hormones and neuromediators").

Furthermore, there are erogenous zones (Winkelmann, 1959), and the main erogenous zones are the penis and the clitoris (Masters & Johnson, 1980). What is remarkable, is that the functional system made up of reinforcements / rewards associated with the erogenous zones *can explain all the human activities of erogenous zone stimulation*, as well as the observed preference for genital stimulations (Agmo, 2007; Wunsch, 2007). In addition, sexual reinforcements seem to be perceived at a conscious level as sensations of intense pleasure (Kringelbach et al., 2009), which is why human beings would feel subjectively erotic pleasure as being the purpose of sexual activity.

The clinical data resulting from the pathology of spina bifida are very interesting to show the importance of the "reinforcements + erogenous zones" system. Spina bifida is mainly characterized by a vertebral malformation, entailing the crushing of the spinal cord between vertebrae or by the cerebrospinal liquid. In some cases the neurological alteration provokes an absence of sensitivity of the genital region. Unlike the accidental medullary sections, these affected persons have never felt genital somatosensory sensations throughout their life. One then observe that the patients do not masturbate and are not interested in this type of activity. Furthermore, the genital orgasm is absent. Vaginal sexual intercourse, when the pathology has not altered sexual reflexes, is had only in a voluntary way with the intent to procreate. We thus observe that erotic activity is absent from the erogenous zones which do not transmit somatosensory signals to the brain. Nevertheless, patients perceive and look for sensations of an erotic type ("shivers or exceptional sensations"; "feeling of hot flushes"; para-orgasm) provoked by the mechanical stimulation of the upper part of the body (Soulier, 2001; Decter et al., 1997; Lassmann, Garibay, Melchionni, Pasquariello, Jr., & Snyder, III, 2007; Dorner, 1977; Overgoor et al., 2006). It is thus observed that sexual activity gets organized around the preserved or new erogenous zones, which transmit erotic somatosensory signals to the brain. What is remarkable is that a *total dissociation* between reproductive behavior and erotic behavior is observed. *The erotic activity is acquired and developed from the preserved or new erogenous zones and has no longer a connection with reproduction, whereas sexual reflexes that enable the innate realization of the final sequences of copulation (erection, pelvic thrusts, ejaculation ...) sometimes exist but are no longer included in the erotic behavior*.

In conclusion, on a motor level, in lower mammals copulation depends on innate sexual reflexes (lordosis, pelvic thrusts ...), whereas among hominids, erotic activities would depend on the functional "reward / erogenous zones" system.

Primordial and innate signals

What are the innate and primordial sexual signals that initiate sexual behavior?

In lower mammals, the primordial signals are pheromones (see a complete overview of the current data in Keller & Bakker, 2009). To summarize and simplify, the *genuine* pheromones of sexual behavior recently identified (Roberts et al., 2010; Haga et al., 2010) produce the following processes: a specific pheromone (Darcin, ESP1, androstenone...) of the opposite-sex partner is detected even at a very low concentration (Leinders-

Zufall et al., 2000) by specific receptors (V2Rp5, V1rb2...), in general by the vomeronasal organ (Martinez-Ricos, Agustin-Pavon, Lanuza, & Martinez-Garcia, 2008), then information is transmitted to the brain where it increases the state of excitability (Pfaff, Ribeiro, Matthews, & Kow, 2008) and induces to remember the partner's characteristics (Roberts et al., 2010). The pheromonal signal is transmitted to the reward system which activates sexual conditionings (Moncho-Bogani, Martinez-Garcia, Novejarque, & Lanuza, 2005), as well as to the hypothalamus which controls lordosis (Haga et al., 2010) and regulates sex hormones (Boehm, Zou, & Buck, 2005; Yoon, Enquist, & Dulac, 2005).

It is worth noting that the main olfactory system is necessary (Keller, Douhard, Baum, & Bakker, 2006), that it also detects pheromones (Liberles & Buck, 2006; Keller, Baum, Brock, Brennan, & Bakker, 2009; Boehm et al., 2005), but that the vomeronasal organ seems to be more primordial (Grus & Zhang, 2008; Brennan & Kendrick, 2006), because its innate hardwiring initiates crucial learning (Martinez-Garcia et al., 2009; Ramm, Cheetham, & Hurst, 2008). Although variations exist from one species to another, overall, the main events are similar. These signals and processes also exist in certain large mammals, like the elephant, with a well-developed vomeronasal organ and very dependent on olfactory signals (Rasmussen, Lazar, & Greenwood, 2003; Rasmussen, Lee, Roelofs, Zhang, & Daves, Jr., 1996).

In summary, basically, thanks to pheromones, the females and the males are excited and attracted to one another (Stowers, Holy, Meister, Dulac, & Koentges, 2002; Dulac & Torello, 2003), memory and conditioning are activated, and copulation can begin.

In addition, specific and systematic olfactory behaviors corroborate the importance of olfaction: constant smelling, repeated investigation of the anogenital region, territorial scent marking (Brennan & Zufall, 2006); elephants disperse urine with their tail and suck it up with their trunk (Rasmussen et al., 2003); etc.

Moreover, pheromones have a global and major role in lower mammals' reproduction: acceleration of puberty (Vandenbergh, 1969), regulation of estrus (Whitten, 1957; Lee & Boot, 1955), pregnancy block (Bruce, 1959), assessment of the partner (Hurst, 2009), etc. Thus, it is not a coincidence if pheromones are the innate and primordial signals of reproductive behavior.

But in the Old World primates (Catarrhines), the vomeronasal organ genes are altered (Zhang et al., 2003; Young, Massa, Hsu, & Trask, 2010; Young & Trask, 2007), as well as certain genes of the main olfactory system coding for pheromones (Young et al., 2010). For these reasons, pheromonal information becomes secondary (Swaney et al., 2009).

Nevertheless, potential human pheromones (androstenol, androstadienone ...), perceived by the principal olfactory system (Savic, Heden-Blomqvist, & Berglund, 2009; Frasnelli, Lundstrom, Boyle, Katsarkas, & Jones-Gotman, 2010), have been identified (Savic & Berglund, 2010; Berglund, Lindstrom, & Savic, 2006; Savic, Berglund, & Lindstrom, 2005). But they are not perceived by everyone (Keller, Zhuang, Chi, Vosshall, & Matsunami, 2007), and their effects seem to be especially physiological (McClintock, 1971), because the behavioral effects sometimes observed (Jacob, Garcia, Hayreh, & McClintock, 2002; Grosser, Monti-Bloch, Jennings-White, & Berliner, 2000) are weak (Hays, 2003; Foidart, Legros, & Balthazart, 1994). Lastly, 60% of the genes in humans' sense of smell are pseudogenes (Gilad, Man, Paabo, & Lancet, 2003).

These alterations of several types of olfactory genes are not isolated facts. Indeed, a general evolutionary trend is noticed: chemical senses (olfaction and taste), yet so fundamental in animals (Wyatt, 2009; Brennan et al., 2006; Ferrero & Liberles, 2010), lose their importance in primates (Liman, 2006).

If the olfactory sexual signals become secondary, then what would the primordial sexual signals be in hominids?

The somatosensory signals, *provoked by a mechanical stimulation of the erogenous zones*, seem to become the main initial signals triggering sexual reflexes, sexual excitement, sexual reinforcements, then sexual motivation and sexual activities (Agmo, 2007).

Indeed, at birth, several types of events may activate the first erotic reinforcements (Martinson, 1994; Constantine & Martinson, 1981): parental care, with breast-feeding, grooming, physical affection, etc. (for example, one notes that the infant is sometimes in erection when he is breast-fed by his mother); or sexual contacts with other children during social and sexual games (daily in societies that allow child sexuality (Malinowski, 1929; Suggs, 1966; Marshall et al., 1971; Diamond, 2004; Henry et al., 1974)); and especially self-stimulation of genitals or masturbation. It is worth noting that the anatomical arrangement of arms and hands is extremely convenient for self-stimulation (difficult to be any better!). Thus, except if adults actively prevent the child from touching his genitals, self-stimulation takes place from the first months after birth. And as soon as the child has understood and *learnt* that the

intense pleasure results from genital stimulations, he is very motivated to repeat these activities.

We thus notice that with all these possibilities, and in particular with self-stimulation, there are always erotic stimulations from the first months of life. *The context of development makes this learning almost obligatory.* Except from cultural prohibitions, there are early erotic reinforcements and *learning erotic activities is almost certain.*

Furthermore, and especially, in non-human hominids, where there are no cultural prohibitions and where juvenile sexuality is sociosexual, these first stimulations are numerous and take place from the first year after birth (Bagemihl, 2000; Ford et al., 1965).

Finally, it is worth noting that the first stimulations and erotic signals may exist from the fetal period. Indeed, the vasocongestion of genitalia apparently exists from the 12th week of gestation (Pedreira, Yamasaki, & Czeresnia, 2001) and erection has been observed from the 23rd week (Shirozu et al., 1995; Sherer, Eggers, & Woods, Jr., 1990). Towards the end of gestation, 75% of these erections are associated with phases similar to REM sleep (Koyanagi, Horimoto, & Nakano, 1991), suggesting that the relations between the brain and the erectile reflex are already well developed. In this period genital stimulations appear which look like the masturbation (Meizner, 1987; Broussin & Brenot, 1995), and some cases of behavioral reactions which suggest orgasm were observed (Giorgi & Siccaldi, 1996; Broussin & Brenot, 1996).

In conclusion, in lower mammals, the innate and primordial signal of reproductive behavior is olfactory (pheromone detected by the olfactory system), while in hominids, the innate and primordial signal at the origin of erotic activities would be mainly somatosensory (mechanical stimulation of erogenous zones).

Motivation

What are the innate and primordial factors involved in the development of sexual motivation?

In rodents, by simplifying, it is generally a pheromone contained in urine and perceived by the vomeronasal organ which triggers the initial sexual motivation. The olfactory signal is transmitted in various areas of the brain, including the reward system (Ubeda-Banon et al., 2008; Lanuza et al., 2008; Martinez-Garcia et al., 2009; Moncho-Bogani et al., 2005; Moncho-Bogani et al., 2002) which is a major factor of motivations. Next, the somatosensory effects of copulation cause the attachment to the partner (Young et al., 2004), but especially also activate the reward system (Paredes, 2009; Oldenburger, Everitt, & de Jonge, 1992; Paredes & Alonso, 1997).

The sexual rewards, controlled by estrogens in the female (Sakuma, 2008), depend on endogenous opioids (Agmo & Berenfeld, 1990; Agmo & Gomez, 1993) rather than dopamine (Martinez-Hernandez, Lanuza, & Martinez-Garcia, 2006; Paredes & Agmo, 2004). All these data suggest that the innate sexual signals, olfactory and somatosensory, activate the hedonic part ("liking" (Berridge et al., 2009)) of the reward system and provoke various learning. Sexual motivation ("wanting") seems to result mainly from this initial learning.

So, basically, after the sexually naive animal has realized several copulations, various signals (visual, auditory, gustatory, etc.) become, by conditioning, motivational sexual signals which can trigger and influence subsequent copulations (Agmo, 1999; Woodson, 2002). Reproductive behavior can then be realized despite the absence of some innate signals (such as sex pheromones) that are crucial for the sexually naive animal (Meredith, 1991; Balthazart & Fabre-Nys, 2001). Then gradually as sexual experience and concomitant learning increase, different motor sequences are executed more efficiently, different signals become sexually motivating, and reproductive behavior becomes mature and optimized.

Thus, it is noticed that sexual motivation, initially triggered by a pheromone, becomes gradually a more cognitive phenomenon, by memorization, conditioning and integration of all the activities, the sensations and the signals concomitant to sexual situations (Hernandez-Gonzalez, Guevara, & Agmo, 2008).

Reinforcements have a secondary role in lower mammals, because they are under the strict control of hormones (Ferris et al., 2005; Sakuma, 2008). But what is remarkable, it is that the initial sexual reinforcements are generally triggered by an innate structure (vomeronasal organ) which can only detect a specific olfactory signal (sexual pheromone, such as *darcin*). *This neurobiological organization means that the initial sexual reinforcement must be activated by a congener of the opposite sex.* That way, the development and acquisition of a more cognitive and more global sexual motivation is determined in an innate way towards a congener of the opposite sex. The pheromone triggers a sequence of events, including attachment to the partner

of the opposite sex (Young et al., 2004) and memorization of several characteristics of this partner (Roberts et al., 2010), which lead to the *learning* of a heterosexual motivation.

On the other hand, in hominids, the temporal hormonal control weakens (see the section "Hormones and neuromediators"), the chemical senses (olfaction and taste) lose their importance (Liman, 2006), and the vomeronasal organ is no longer functional (see the section "Innate and primordial signals"). But the somatosensory effects of copulation, reinforcing, still exist.

What would the primordial factors of sexual motivation be in hominids then?

The initial signal of the development of erotic motivation seems to become somatosensory, and be the mechanical stimulation of erogenous zones. It is erotic activity which seems to originate erotic motivation (Agmo, 2007; Yates, 2004; Plaud & Martini, 1999). Except for the initial signal, where somatosensory reinforcements replace pheromones, the processes consecutive to the initiation seem to be similar to those of lower mammals: sexual motivation seems to gradually become a more cognitive phenomenon, by memorization, conditioning and integration of all the activities, the sensations and the signals concomitant to sexual situations. Then the sociocultural values and norms also seem to be integrated, hence ending in a complex sexual motivation, made up of multiple sensory, emotional and cognitive signals, internal as well as external, and inhibitory or excitatory (Boul, Hallam-Jones, & Wylie, 2009; Toates, 2009; Hardy, 1964).

But what is extremely remarkable, is that the initial reinforcements are triggered by an innate structure (erogenous zones) that responds to a *nonspecific* somatosensory signal (mechanical stimulations). And it is the element responsible for the mechanical stimulation (persons, animals, objects...) that can be the object of erotic conditioning. Contrary to lower mammals, erotic reinforcements are no longer under hormonal control, but are always active. *This neurobiological organization means that the initial erotic reinforcement can be activated by numerous elements, different from the congener of the opposite sex.* In this way, the development and acquisition of a more cognitive and more global erotic motivation is determined in an innate way towards potentially numerous elements of the environment. Mechanical stimulation can trigger a chain of events, among which the attachment to the stimulating element and the memorization of several characteristics of this element, which end in the learning of an erotic motivation which can be very diverse (hetero-, homo-, bi-, poly-sexual, etc.).

In conclusion, in lower mammals, the innate and essential factor at the origin of the development of sexual motivation is olfactory (pheromone detected by the olfactory system), whereas in hominids, the innate and essential signal at the origin of the development of erotic motivation seems mainly to be somatosensory (mechanical stimulation of erogenous zones).

Sexual orientation

What are the innate and primordial structures and biological signals, which are at the origin of sexual orientation?

In lower mammals, as already indicated, it is pheromones which enable the choice of the partner (Johansson & Jones, 2007), and which provoke the reciprocal attraction of the male and female (Roberts et al., 2010; Keller et al., 2009). *The pheromonal signal is the key factor of sexual orientation, and this orientation is, in an innate way, heterosexual.*

The importance and the simplicity of this pheromonal mechanism is even more obvious for example in insects: all the males are attracted by the pheromones of all the females, and vice versa. By genetically manipulating the pheromones, one can choose the sexual attraction of the males: either heterosexual or homosexual (Ferveur et al., 1997). But this simple mechanism which produces the sexual orientation no longer seems to exist or is weakened in hominids, because the chemical senses (smell and taste) lose their importance (see the section "Primordial and innate signals"), and the vomeronasal organ is no longer functional (Liman, 2006). In rodents, experimental alteration of the vomeronasal system would induce bisexual copulations (Stowers et al., 2002; but see Pankevich, Cherry, & Baum, 2006; and Kimchi, Xu, & Dulac, 2007). But in hominids, one observes more than bisexual copulation. One observes varied erotic activities, a whole continuum of bisexuality, as well as preferred partners: certain females prefer certain males, and vice versa (Bagemihl, 2000; Wallen & Parsons, 1997). In humans, there are also sexual preferences for the physical appearance, size of breasts, penis shape, hair color, the genre and number of partner(s), the positions and erotic activities, the use of certain sexual toys, etc.

It is also necessary to be able to explain the activities which are unexplainable by a mechanism of male-female attraction and orientation, such as for example the sexuality with animals, which is common and regarded as

"normal" in some societies (Ford et al., 1965). Because what is remarkable, is that when humans live with animals, when there is a physical and emotional proximity, and when there are no prohibitions or no cultural stigmatization, then the probability of observing this behavior is very high (Miletsky, 2002; Kinsey, Pomeroy, & Martin, 1948). It is worth noting that the study of this behavior is not a "praise for bestiality", but corresponds to the necessity of taking into account all the existing facts, whether they are frequent or marginal, glorified or depreciated, so that the elaborated scientific models are neither partial, nor biased.

It is worth noting finally that a biological mechanism of heterosexual orientation is not essential. The Bonobos chimpanzees clearly demonstrate that the existence of a genuine bisexuality, with in addition many erotic activities without any connection with fertilization (De Waal, 1990; Bagemihl, 2000), allows nevertheless reproduction and survival of the species.

For all these reasons, rather than an innate "sexual orientation", which would no longer exist or would be weakened, it seems necessary to speak about acquired "sexual preferences". The learning of "sexual preferences" would depend on another neurobiological dynamic, characterized by a combination of several factors: mainly erotic reinforcements and cultural context, secondarily the residual pheromone and hormone effects, then all other types of learning (social, cognitive...), and finally various more minor factors such as visual attraction for some types of faces (Langlois, Roggman, & Musselman, 1994), or the preferences for youthful characteristics, perhaps waist/hip ratio, width of shoulders, etc. (LeVay & Baldwin, 2009). It is worth noting that sexual preferences seem to be formed in a way similar to dietary, auditive or olfactive preferences, and the "preferenciation" does not seem to be a particular characteristic of human sexuality, but a general psychological phenomenon.

As it has already been pointed out, erotic reinforcements seem to be the principal factor originating hominids' erotic activities (Agmo, 2007; Yates, 2004). This means that human erotic activities are learned, and learned especially by conditioning (more precisely, mainly by operant conditioning with a primary sexual reinforcement). Sexual conditioning already exist in lower mammals (Pfaus et al., 2001; Crawford et al., 1993; Woodson, 2002). But this erotic conditioning is controlled by hormones and pheromones and can be expressed only during heterosexual copulation. On the other hand, in hominids, *they have become independent of pheromonal and hormonal control, and they can be activated at any time, in many situations which no longer relate to reproduction* (for example during masturbation, or during erotic activities between people of the same sex). It is this major characteristic which seems to explain the learning diversity of erotic behavior and the formation of sexual preferences: freed of pheromonal and hormonal constraints, the initial factor which triggers erotic reinforcement and conditioning is the mechanical stimulation of the erogenous zones. And it is the element responsible for erotic mechanical stimulation (people, animals, objects...) who will be the object of erotic conditioning. Of course, conditioning is not automatic, but depends on the context. It is noted that it is mainly the *quantity* and the *quality* of erotic experience (Agmo, 2007), *whatever it might be*, which seems to originate sexual preferences (Bell, Weinberg, & Hammersmith, 1981; Van Wyk & Geist, 1984; Yates, 2004; Plaud et al., 1999).

The cultural context, which results indirectly from cognitive activity, is another major factor in preference formation, whether they are eating, clothing or sexual. For example, in the Occident, people are conditioned to be disgusted by annelids or insects, in spite of their gustatory and nutritional interests (DeFoliart, 1992). Whereas in other societies, people are ready to walk during one day to find palm tree's worms for example, and when they eat them, one observes on their face all the signs of pleasure and satisfaction. For sexuality, in every society there are "sexual scripts" (Gagnon, 2008) which indicate what is valued or disapproved. Hence, in every culture, people live specific sexual situations and thus learn sexual and cultural conditioning which are specific to their society. And it is observed that for the majority of people in a social group, the sexually preferred objects are in conformity with the scripts of their culture.

For example, if there is a very strong valorization of the heterosexual couple and a strong homophobia, the probability is high that the majority, even the quasi totality of young people learn heterosexual scripts. They will then have mainly heterosexed beliefs, heterosexual experiences (and thus heterosexual reinforcements/rewards), which will favor the development of heterosexual preferences (Bell et al., 1981; Van Wyk et al., 1984). Heterosexuality can also become dominant with a weak homophobia, provided that the access to heterosexuality is extremely easy. It is the case for example for Trobrianders, where homosexuality is moderately ridiculed while for heterosexual activities « all the customs and rules, all the codes of conduct authorize the Trobrianders to merely go straight to the point, very simply »

(Malinowski, 1929). On the other hand, in Antique Greek society where women had an inferior social position to men, the most desirable love, the "celestial love", was homosexual (Plato, 2001; Plutarch, 1957). Heterosexuality was depreciated, the wives being used to have a legitimate descent and a faithful guardian to the home (Veyne, 2005). This cultural context created concrete situations (women secluded in the gynaeceum) and particular psychological values (the love between men is highly desirable) which favored homosexual activities (and thus homosexual reinforcements/rewards), which thus favored the development of homosexual preferences. More rigorously, a German study evaluated the influence of cultural change on sexual preferences. In Hamburg in 1970, during the years of sexual liberalization, even if homosexuality was not valued, 18 % of teenagers had homosexual activities (Sigusch & Schmidt, 1973). In 1990, with AIDS and the cultural changes, they were no more than 2 % (Sigusch, 2004). This confirms the major role of culture. But above all, *sexual preferences are not limited to the homosexuality-heterosexuality opposition, but concern all the aspects of sexuality*. Sexual reinforcements are also involved in preference formation for the age of the erotic partner (Santtila et al., 2010). Besides, in many traditional societies, genital activities are preferred, kissing is not practiced and anal activities cause disgust. These sexual aversions and preferences are in conformity with cultural beliefs and conditioning: the mouth, with teeth, is designed for eating, and the rectum contains disgusting excrements. In other societies there are sexual preferences for women having multiple rings around the neck or for men having tobacco juice running out by a labial slit, whereas the Western models are not considered sexually exciting (Allgeier & Allgeier, 1988). Intercultural comparisons reveal that the continuum of aversions and preferences for the various types of sexual activities (self-, bi-, hetero-, homo-, poly-sexual, oral, genital, anal, with animals or objects, etc.) depends mainly on the cultural context.

It is worth noting that in societies where certain forms of sexuality or erotic activities are not practiced, there is often in a formal or implicit way cultural restrictions. In order to understand the major effect of the pressure of conformity and cultural context, one can give as example clothing social norms. Although there are no laws or no formal prohibitions and people are *a priori* "free", it is observed that almost the totality of men never wear clothes for women. All men conform to the implicit codes of masculinity (Connell, 1993). This example, relatively close to the field of sexuality while depending on no biological factor, allows to understand the power of dominant social norms.

Biological, genetic and hormonal factors also have an influence on sexual preferences (Rahman & Wilson, 2003; Bocklandt & Vilain, 2007). It is observed for example that women seem to be more attractive for men during the ovulation phase (Miller, Tybur, & Jordan, 2007; but see Pawlowski, 1999). There are also effects which would favor preferences for homosexual activities: hormonal effects, which can be natural or pathological (prenatal stress, adrenal hyperplasia, medicines...), of masculinization or feminization of the body and of certain brain structures (Savic & Lindstrom, 2008; Berglund et al., 2006; Savic et al., 2005; LeVay, 1991; but see Ciumas, Linden, & Savic, 2009), as well as other indirect and poorly understood effects, perhaps by the immune system (Blanchard, 2004) or cognition (Williams & Pleil, 2008). As for pheromones, via the main olfactory system (Savic et al., 2010; Savic et al., 2009), they still seem to have an influence (Grammer, Fink, & Neave, 2005): for example they could induce a preference for partners in better physical condition (Thornhill & Gangestad, 1999) or belonging to a different major histocompatibility complex (Jacob, McClintock, Zelano, & Ober, 2002; Wedekind, Seebeck, Bettens, & Paepke, 1995). Moreover, axillary molecules seem to favor preferences for heterosexual activities (McCoy & Pitino, 2002; Cutler, Friedmann, & McCoy, 1998; but see Winman, 2004; and Wysocki & Preti, 1998).

Nevertheless, overall, the pheromonal and olfactory effects are weak (Hays, 2003; Foidart et al., 1994). In synthesis, the most probable dynamics would be that the various biological variables indirectly induce a succession of physiological, psychological then social events which interact with the cultural context, thus leading to sexual preferences particular to each individual (Bem, 2000).

Among all these factors, it is worth noting the importance and the impact of reinforcements, since already in rodents they can modify the innate properties of the other factors. For example the cadaverine molecule, which is a repulsive odor, becomes appetitive after being associated with sexual activities (Pfaus et al., 2001).

The existence of several factors interacting in the sexual preferences is well highlighted in old world primates (catarrhines). The visual sexual signal of sexual skin is supposed to have replaced the loss of the olfactory signals (Zhang et al., 2003). This visual signal, by its size and its red color, is sufficient

to cause masturbation in baboons (Girolami & Bielert, 1987). In chimpanzees *Pan paniscus* (Bonobos), there is therefore several biological signals (hormones, pheromones, sexual skin (Dixson, 2009), somatosensory reinforcements ...) involved in sexual preferences. And yet one observes many types of erotic activities without relation with fertilization, and all Bonobos have bisexual activities, but with more heterosexual activities (approximately 60%) than homosexual (Bagemihl, 2000). These observations suggest that the factors of heterosexual attraction have a lesser influence than erotic reinforcements, but that their effects exist and increase the share of heterosexual activities of approximately 10 % on average, with more important differences for certain individuals.

It is worth noting that the signal of sexual skin is apparently learnt and seems to result in fact from erotic reinforcements, since Dixson (2009) obtained the same behavioral reactions by sexual conditioning with a glove. In a more general way, there does not seem to exist a visual sexual signal which is innate. Moreover in birds, where *visual information controlling behaviors* is in general more important than in mammals (but see Balthazart & Taziaux, 2009), this visual information is *not innate, but acquired*. And these acquisitions, by the *imprinting* phenomenon (Lorenz, 1935; Heinroth, 1911), do not exist in humans because imprinting depends mainly on the hyperstriatum's activity (Bateson, Rose, & Horn, 1973), a structure absent in the mammalian brain. Imprinting is not a phenomenon which can be directly extrapolated to mammals.

It is also worth noting that the various factors intervening in the formation of sexual preferences are not all known with precision. Complementary research is necessary to evaluate the relative importance of each factor and especially the modalities of their interactions. Nevertheless all the available data suggest the existence of a *multifactorial* dynamic, with several major factors. And the somatosensory reinforcements seem to have a primordial role (Agmo, 2007; Yates, 2004; Wunsch, 2007).

From all these data, one can deduce that for each society (which always have social and cultural codes different from other societies) and for each individual (who always has a different physiology and experience to other people), the influence of each of the biological and cultural factors changes. Hence, in each society and for each person, there is a singular interaction of all these factors, which modifies the erotic activities' profile (hetero-, bi-, homo-, poly-, self-sexuality, oral, genital, anal, with objects, etc.). Thus, in adulthood, each person has acquired a unique sexual profile, but overall in accordance with the customs of its culture.

In conclusion, in lower mammals, pheromones are the key factor of heterosexual orientation. In hominids, there is rather *sexual preferences*, which are acquired during erotic experiences, from a *combination of several factors*. The remaining effects of hormones and pheromones, visual attractions and all the other biological and cultural factors, weak, seem to combine with the powerful effects of conditioning and learning. Sexual preferences, singular and unique to each person, would continue to evolve throughout life.

Cognition

In lower mammals, cognition plays a secondary role in reproductive behavior. On the other hand, during evolution towards hominids, because of the extreme corticalization of the brain, cognition becomes a major factor.

Cognitive processes (categorization, planning, memory, reasoning, symbolization, forming representations...) are the most complex and most elaborate activities of the nervous system. The cognitive processes depend on the neocortex, the most recent and most developed structure (76 %) of the brain. For these reasons, cognition exerts a great influence on behaviors.

The processes of information processing influence sexuality on several levels (Wunsch & Brenot, 2005b):

- First, it is cognitive activity which actually makes it possible for humans to imagine the concept of "sexuality", i.e. a subjective regrouping of various elements (behaviors, affects, psychic states...) in an abstract and single unit which is called "sexuality". More precisely, the concept of "sexuality" corresponds to the denomination of a subjective regrouping of behaviors, psychic states and various elements in an abstract and single unit which is thought as a specific entity, having, essentially, common properties which radically distinguish it from other entities which are for example "feeding", "violence" or "spirituality". The cognitive processes thus allow the creation of abstract and symbolic entities, additional but nonessential to concrete "sexual" activities. Indeed, in most simple sexed animals, "sexual" activities are carried out without any consciousness of their nature.

– Secondly, the cognitive processes induce the psychological “sexualization”¹ of each person: certain elements are referred to as “sexual” (genitals, breasts, kissing with the tongue, sometimes nudity...) and others are designated as “nonsexual”.

More precisely, the cognitive processes influence the “sexualization” of the subject’s subjective world by attributing certain objects - and not others - to what has been conceptualized as “sexuality”, and rarely from objective criteria (for example, depending on the society, caressing breasts or oral kissing can be, or not, considered as “sexual”). These objects, which have become “sexual”, are opposed to those which are not. The “sexual” and the “nonsexual” are subjectively perceived as being radically distinct, and the “sexual” has specific and particular properties that the “nonsexual” does not have. This assignment of behaviors in a particular entity changes considerably the meaning and impact of acts. And one observes that what is considered as “sexual” organizes and determines actions and judgments, even some parts each individual’ life.

– Thirdly and finally, the cognitive processes make “sexuality” more complex by associating and combining the so-called “sexual” elements with other abstract elements: categories, judgment of values, ethics, morals, duty, prohibitions, laws...

For example, the cognitive processes are at the origin of forming the categories, among others, of “man” and “woman”, of “hetero-sexuality” and “homo-sexuality”, of “oral”, “anal” or “vaginal” activity, of “beautiful” or “ugly”, of “good” and “evil”... Then, by combining these categories, “homo-sexuality” can be associated for example with “abnormal”, “hetero-sexuality” with “good” (Tin, 2008; Katz, 1995) and kissing with “beautiful”... But many other categories and combinations can exist.

Erotic activities, which are simple and pleasant motor actions, thus become complex by adding meaning (Bozon, 1999), values, cultural scripts (Gagnon, 2008), beliefs and symbols.

Then all these values, beliefs, prohibitions and symbols will retroact ad infinitum, as much on the erotic activities as on the “sexual” representations, to modify them and integrate them into new models and new social codes.

What is extremely remarkable, it is that the values and the cognitive representations related to the notion of “sexuality” are cultural and subjective constructions which can be completely independent and distinct from biological reality, even completely erroneous. Even in this case, one observes that they have a major influence, in particular on erotic behavior, and that they can give it, in “good” or in “evil”, a social and psychological importance which exceeds by far the simple feeling of intense pleasure that it provides.

Behavioral level

Crucial behavior

What are the crucial sexual behaviors, which correspond exactly to the motor activity produced by the innate biological organization?

In lower mammals, the specific hardwiring of the lordosis motor sequence determines, when the female is in estrus and when she perceives male pheromones, the triggering of the lordotic reflex by tactile stimulations of the flanks during the mount. In male, the specific hardwiring of the pelvic thrusts and intromission motor sequences determine the triggering of the vaginal intercourse sequence as soon as the male mounts the female. The neurobiological organization, coupled with the strict pheromonal and hormonal control, can *a priori* only lead to heterosexual copulation.

In hominids, the “reinforcement associated with erogenous zones” functional system determines motor activities of stimulation of the erogenous zones. The penis and the clitoris, which have the same embryological origin and similar erotic responses (Martin-Alguacil, Schober, Sengelaub, Pfaff, & Shelley, 2008), are the most erogenous organs of the body (Masters et al., 1980). This characteristic means that the penis and the clitoris are the most stimulated erogenous zones. The vagina should also be one of the most stimulated zones, because of its functional relation with the clitoris (Buisson,

Foldes, Jannini, & Mimoun, 2010; Foldes & Buisson, 2009; O’Connell & DeLancey, 2005; Shafik, El, & Shafik, 2008). And it is what is observed in ecological situations as well as in experimental situations. The analysis of erotic activities indicates that people preferentially practice activities « of penis penetration for the men (anal or vaginal intercourse, receiving a fellatio) and of clitoris or vagina stimulation among women (vaginal intercourse and cunnilingus, and being masturbated) » (Wunsch, 2007).

Erotic genital activities are already observed in non-hominids primates (Vasey & Duckworth, 2006). But what is extremely remarkable in hominids, is that the motor sexual reflexes, however innate and specifically designed for reproduction, no longer have crucial roles in the erotic activities. We notice that they are generally replaced by acquired motor activities which make it possible to obtain more intense pleasure. For example, chimpanzees *Pan paniscus* (Bonobos) have many bisexual and non-reproductive sexual activities. Among these, the genito-genital rubbing between two females, during face to face embracing position, is a good example of purely erotic activity, without innate motor reflexes and without relation with reproduction (see Figure 1). This homosexual activity, frequent (approximately once every two hours), exists in females of all ages, and represents approximately one third of all sexual activities (homo- and heterosexual). The clitoris of the bonobo is prominent and well developed; during sexual arousal, it doubles in size. Clitoral penetration has sometimes been observed between two females during genito-genital rubbing. At the time of insertion, the female often modifies the usual movement of lateral friction for vertical pushes of penetration (Bagemihl, 2000). What is remarkable is that the usual movement of lateral friction is not an innate motor activity, and especially that the crucial reflex of lordosis is not practiced by any of the females. Moreover, the facial expressions, vocalizations and genital engorgement indicate that females chimpanzees experience intense pleasure – and probably orgasm – during these homosexual interactions (Bagemihl, 2000). It thus appears that obtaining sexual reinforcements, by means of mechanical stimulations of the most erogenous zones, seems to be the main purpose of Bonobos’ sexual activities. And one can make similar observations in humans: in kissing, reciprocal masturbation or oro-genital activities, no motor sexual reflex is used. *And as already indicated, what is extremely remarkable is that lordosis – which is nevertheless in lower mammals the fundamental and specific reflex of the female – no longer plays a role and becomes useless.*

In conclusion, in lower mammals, innate copulation is the crucial sequence of reproductive behavior. On the other hand, in hominids, the crucial behavior making it possible to obtain erotic reinforcements is the acquired mechanical stimulation of the most erogenous zones of the body (penis/clitoris, vagina).

Modalities of realization

What are the modalities of sexual activities’ realization, which correspond most to the way innate biological organization functions?

In lower mammals, erection, lordosis which exposes the vaginal opening specially for intromission and pelvic thrusts, ejaculation, as well as pheromones which attract the female towards the male and the male towards the female, are characteristics specifically designed for the realization of vaginal coitus between a female and a male.

In hominids, the stimulation of the erogenous zones to obtain erotic and orgasmic pleasure can be realized alone (masturbation), by two, or by several persons. And it is observed, since masturbation is a very banal activity, practiced by approximately 90% of young men and 60% of young women (Langis & Germain, 2009), and the couple is the dominating model of many societies. Moreover, when the cultural context allows it, one observes sexual activities by group, such as the banquets of Antiquity (Partridge, 2002).

Variability of behavior

What is the variability of sexual activities, according to the innate biological organization?

In lower mammals, the neurobiological organization specific to heterosexual copulation, coupled with the strict pheromonal and hormonal control, can generate only a stereotypical behavior, and thus only a low variability of sexual activities.

On the other hand, in hominids, variability is very high, since the stimulation of the erogenous zones can be obtained by various means (hand, tongue, penis, sex toys ...), in various positions (missionary, doggy style, upright...), and by various combinations of partners (alone, by two, in group, with a woman or a man, even with animals...).

Furthermore, in humans, the behavioral and psychic erotic variability is multiplied by the cognitive abilities. The intellect, only limited by its capacity of imagination, originates uncountable sexual fantasies whose primary function is

¹ “Sexualization” is a different phenomenon to “sexuation”. “Sexuation” corresponds to the forming of a sexed individual: 1) on a physiological level (male/female sexual differentiation), and 2) on a psychological level (female/male gender identity). “Sexualization” corresponds to the learning of sexuality: 1) on a behavioral level (learning sexual activities and the emotions caused by these activities), and 2) on a psychological level (learning the concept of “sexuality” and attribution of this sexual concept to objects, actions or situations). It is worth noting that erotic activities, which are primarily motor acts, can be realized independently of the cognitive level (psychic sexuation (gender identity) and psychological sexualization). It is in fact the case in all animals, which carry out all their sexual activities without needing to know that they are male or female and that their activities are “sexual”.

to increase excitement and pleasure, whether it be romantic or erotic (Langis et al., 2009).

Purpose of behavior

What is the purpose of sexual activities, which ensues from the innate biological organization's functioning?

In lower mammals, with temporal hormonal control, with recognition of the partner of opposed sex thanks to pheromones, with motor neurobiological organization specific for copulation, and with ejaculation in the vagina at the ovule's period of maturity, one notices an innate behavioral organization which brings the spermatozoa near the ovules. This behavior leads to fertilization, and its purpose is thus the reproduction of the species.

However, in hominids, the "reinforcement associated with erogenous zones" system leads to motor activities of mechanical stimulation of the most erogenous zones of the body. Physiologically, these erotic stimulations of the penis, the clitoris and the vagina end in orgasm, which is the paroxysm of pleasure (Masters et al., 1980). The purpose of this erotic behavior thus seems to be obtaining maximal pleasure. And it is what is observed as much in ecological situations as in experimental situations. The analysis of erotic activities indicates that people practice the activities « which bring the most intense stimulations at the most erogenous body zones (penis/clitoris, vagina) » (Wunsch, 2007). Moreover, it is observed that people seek specific techniques which will make it possible to maximize even more the erotic and orgasmic feelings (see for example Bodansky & Bodansky, 2002; Taylor, 2002). And if the context permits, the maximization of erotic pleasure is realized by the summation of several types of pleasures, like in the banquets of Antiquity, common and culturally accepted, which were a synthesis of all the intellectual and physical pleasures (Partridge, 2002; Salles, 2004).

As for reproduction, essential to the survival of the species, it is here an indirect consequence of the erotic behavior, insofar as the research of maximizing pleasure induces the development of a majority of activities stimulating the genitals. Reproductive vaginal coitus would thus not be practiced because of an "instinct" of reproduction, but because it is one of the activities which brings the most pleasure (Wunsch, 2007).

It is worth noting that if erotic pleasure appears as the major purpose, it is not the only motive for sexuality. Positive emotions (love, complicity, tenderness...), the quality of the relation with the partner and the need to be loved are also very important (Wunsch, 2007). Moreover, if sexuality is exploited, the reasons for erotic activity can then be very diverse: material profits, to keep one's partner, even revenge... (Meston & Buss, 2007).

In conclusion, in lower mammals, the finality of sexual behavior is reproduction of the species. However, in hominids, the finality of erotic behavior would mainly be the maximization of erotic and orgasmic pleasure.

Functional Analysis

What would the main conclusions be which could be formulated from the functional analysis of the sexual behaviors' innate biological organization?

In the simplest mammals, basically, one observes a succession of innate processes which lead to heterosexual copulation. Hormones control sexual behavior, so that it is carried out at the favorable season as well as at the period of maturity of the organism and the gametes (Fiske, 2004; Sisk & Foster, 2004). Then males and females emit pheromones which attract one another (Roberts et al., 2010). The olfactory stimuli of the male immobilize the female and facilitate its lordosis. Finally, when the male mount the female and when the animals are in physical contact, the physical stimuli provoked by each action constitute the release stimuli of the following reflex action (Balthazart et al., 2001): lordosis (Kow et al., 2007), intromission and pelvic thrusts (Meisel et al., 1994; Contreras & Agmo, 1993), ejaculation (Allard et al., 2005) and release of the ovule (Spies, Pau, & Yang, 1997; More, 2006).

Even if some variations exist from one species to another (Morali et al., 2003), and even if there is only a "partial instinct", that is to say that all the capacities necessary to sexual behavior are not innate (Wunsch & Brenot, 2004; Wunsch, 2007:p.13-43; Cooke, Chowanadisai, & Breedlove, 2000; Spvak, Quadagno, & Knoepfel, 1973; Gruendel & Arnold, 1969; Turner, Davenport, & Rogers, 1969; Missakian, 1969; Ward, 1992; Kendrick, Hinton, Atkins, Haupt, & Skinner, 1998; Moore, 1992), it is noticed nevertheless that there is a *true hardwired reproductive behavior* in lower mammals, the finality of which is the survival of the species.

On the other hand, in hominids, the weakening of temporal hormonal control and the deterioration of the olfactory treatment of pheromones have modified the neurobiological control of sexual behavior. Emancipated from hormonal control, the erotic reinforcements have become continuously active and dominating, and seem to originate the activities of erogenous zones stimulation.

But furthermore, it seems that it is the whole body which participates in the development of erotic behavior. Indeed, 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 the hairy skin of the body. It is probably constituted by fibres with slow conduction, which are not myelinated and originating in the plexus of the hair roots. These fibers respond to light touch and project into the limbic areas, suggesting that nonpainful physical contacts, like caresses, would generate positive and pleasant emotions (Olausson et al., 2002; Wessberg, Olausson, Fernstrom, & Vallbo, 2003; Olausson, Wessberg, Morrison, McGlone, & Vallbo, 2008). This system may then be responsible for searching physical contact and explains the reason for primates being contact animals. The second system, more specific, is that of the erogenous zones. These zones are constituted by mucocutaneous 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 (Winkelman, 1959; Cold & Taylor, 1999). 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.

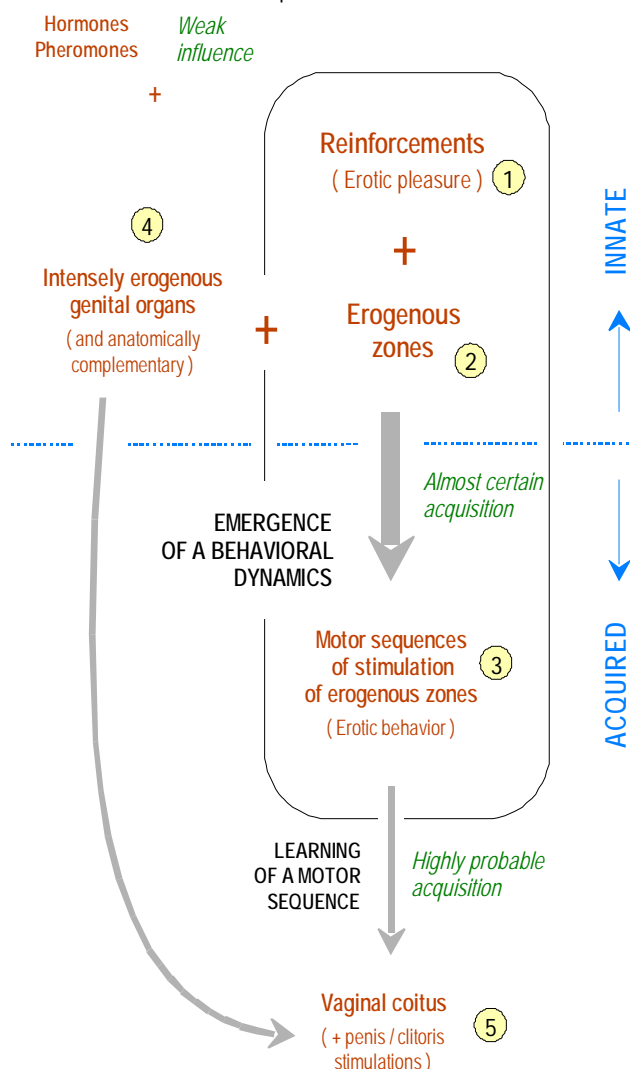


Figure 3: Human behavioral model

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 originates the emergence of erotic behavior, characterized by the repetition of the motor sequences of erogenous zones' stimulation [3].

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 [4] would be a characteristic which would induce a high probability that vaginal coitus becomes one of the preferred erotic practices [5].

One thus notices the existence of a neurobiological organization of *somatosensory reinforcements*, which concerns almost the whole body. This organization should thus induce stimulation activities of all the body, with a gradation from areas providing pleasurable sensations (head, chest...), then erotic (lips...) and until intensely erotic and orgasmic (penis, clitoris and vagina). This neurobiological organization would imply, *whatever the environmental context*, that each person would obligatorily discover, very early in its development, the hedonic nature of body stimulations. They would then try to repeat these pleasant situations, and, except particular events, the activities of body stimulations should end up being focused on the most erogenous zones. The functional analysis suggests that within this specific neurobiological organization, *the penis/clitoris appears as an attractor*, enabling the erotic activities' focus on, among others, vaginal coitus which allows fertilization (see Figure 3). The results of a preliminary experimentation seem to corroborate this model (Wunsch, 2007).

Besides, if there is no sexual instinct in hominids (Wunsch et al., 2004; Wunsch, 2007:p.13-43), and if stimulation of the body and the erogenous zones depends mainly on rewards, then it means that human erotic behavior is learnt, and learnt essentially by operant conditioning with a sexual primary reinforcer (Agmo, 2007).

If this model is overall exact, that would mean that through erotic conditioning many neutral stimuli could become sexual. *Theoretically*, these dynamics correspond to a *potential pan-sexuality*, that is to say that almost everything, through conditioning, can potentially acquire an erotic value. It is suggested for example in conditioning experiments made to understand the origin of fetishism (Rachman, 1966). But this great *potentiality* of human sexuality is especially observed concretely in the various human societies: from chastity to orgies, through sexuality with other animal species, most of the sexual possibilities exist or have existed (Ford et al., 1965; Marshall et al., 1971; Kinsey et al., 1948; Partridge, 2002; Cantarella, 2002; Salles, 2004; Miletsky, 2002).

Moreover, in this model, vaginal coitus is realized in an indirect way. This means that the fundamental function of reproduction is realized in humans by a biological organization, the purpose of which is not reproduction. One could thus observe a beginning of dissociation between sexuality and reproduction, a

dissociation which would become total with contraception and artificial reproduction.

Lastly, the evolution of mammals' sexual behavior suggests, even if animal experimentation is fundamental to understand the working of the nervous system, that it would be advisable not to directly extrapolate the experimental results obtained on lower mammals to the human being.

In conclusion, in lower mammals, one notices an innate *instinctual* biological organization, which produces a behavioral dynamic corresponding to a *true behavior of reproduction*. On the other hand, in hominids, the innate "reinforcement associated with erogenous zones" biological organization would originate learning an erotic behavior which would *potentially* be pan-sexual.

Implications of the "erotic" model

What are the implications of the existence of an erotic behavior specific to hominids?

The main implication would be the necessity of revising the current reference model of human sexuality, the one which is presented in recent specialized works (see LeVay et al., 2009; Langis et al., 2009; Westheimer & Lopater, 2005). Because this model of reference was elaborated, from 19th to 20th century, from old sexological theories (see for example Krafft-Ebing, 1882) and from the Freudian psycho-analytical theory, which, although currently questioned (Grunbaum, 1985; Meyer, 2010), is still influential in France and Argentina. But above all, this model was elaborated from psychological and sociological studies which primarily reflect *the cultural morals and customs used in the West*, and from scientific data resulting mainly from ethological or neurobiological studies of *the reproductive behavior of birds or of lower mammals*.

Figure 4 presents the main differences between the current model and the new model of human sexuality.

Figure 4 : Comparison between paradigms of human sexuality		Old paradigm based on reproductive behavior & psycho-analytical theories	New paradigm based on erotic behavior
PSYCHOLOGY	Psychic motivation	Sexual drive innate	Erotic motivation acquired
ONTOGENESIS	Development	Long duration : > 15 years (maturation after puberty) Particular sexual development, different from the other developments Cognition is dominant	Short duration : < 5 years (maturation at about 3-4 years) Sexual development similar to the other developments Emotion is dominant
PATHOLOGY	Referent normality / disorder health / disease	Deviation from reproductive fonction - Between individuals of the same sex - Nonreproductive activities (<i>oral-genital, anal, masturbation, ...</i>) - Between prepubertal individuals - Between different races/species	Deviation from hedonic fonction (or dysfunction of the reinforcement processes) - Excess of reinforcements = Hyper-sexuality - Lack of reinforcements = Hypo-, a- sexuality - Dysfonctionnement = Sexual addiction - Dyshedonia by : 1) Negative emotional states 2) Ignorance, or Dysfunctional beliefs

Psychological level - Psychic motivation

What would the innate or primordial factors originating sexual motivation in humans be?

The sex drive (or motivation, or urge...) was often thought as innate. For Krafft-Ebing, it resulted from instinct (Krafft-Ebing, 1882), for Freud from libido, (but the latter also resulted from instinct (Freud, 1998)). At present, it would result for certain authors either from pheromones (Nicoli & Nicoli, 1995; Vincent, 2004), or, for many neurobiologists, especially from genes or from hormones (Pfaff, Arnold, Etgen, Fahrback, & Rubin, 2009).

In the erotic model, psychic motivation, mainly *learned*, seems to come from the integration of many factors (see fig. 11.1 in Langis et al., 2009), but erotic reinforcements would be the initial and major factor (see sections "Motivation" and "Sexual preferences").

Ontogenesis - Development

What would the key characteristics of human sexual behavior's development be?

The current model of human sexuality supposes a long and complex duration of development. About fifteen year is needed to reach physiological maturation, at puberty, then some additional years are necessary to reach psychological maturation. Moreover, developmental phenomena seem to exist, which are specific to sexual development (maturation of sexuality thanks to puberty, psycho-emotional sexual stages, resolution of Oedipus or castration "complexes"...), and cognitive maturation seems to be necessary for an adult expression of sexuality.

But what is this model's validity? Are the scientific results of studies on fish, birds or rodents able to be directly extrapolated to humans? Do the psychological and sociological surveys describe the reality of human sexuality, or are they valid only for the time and the society from which they come? Would Bancroft (2008) or Larsson & Svedin (2002) studies on sexuality's development have given the same results if they had been carried out in societies very different from Western societies: for example in the extremely repressive Irish community of Inis Beag (Messenger, 1971), in Marquesan in Oceania (Suggs, 1966), or in Pilagás in Argentina, where « Absolutely no prohibition is placed on child sexual activity », which explains why « sex is a strong and constant interest of Pilagá children »? (Henry et al., 1974). Would the recent large surveys (Laumann, Gagnon, Michael, & Michaels, 1994; Bajos, Bozon, Beltzer, & CSF team, 2008) have reached the same conclusions if they had been led in the India of the Kama-Sutra, in the Greco-Roman Antiquity of bisexuality (Cantarella, 2002) and banquets (Salles, 2004; Partridge, 2002), or in the societies where sexuality with animals is culturally accepted? (Ford et al., 1965; Miletsky, 2002)

Contrary to the current models, puberty seems to correspond primarily to the reproductive apparatus' physiological maturation. Erotic behavior could develop from the maturation of the motor system, at about 2-3 years old, well before puberty's hormonal and pheromonal effects (see sections "Hormones and neuromediators" and "Innate signals"). And erotic activity would be the main factor at the origin of developing erotic behavior, then erotic emotions, and finally the so-called "sexual" representations.

Indeed, the brain is partly structured by information coming from the sensory systems. Experimentally, by inverting the cortical projections of the visual system towards the auditory system, one observes that the auditory areas present activities of the visual type, which demonstrates an "instructive" effect of the sensations on the cortex development (Sur & Rubenstein, 2005). Thus, in a way similar to the development of the other capacities or behaviors (sensoriality, motricity, language...), the concrete erotic activities and the sensory effects of these activities seem to be an important factor of sexual development (Yates, 2004).

Furthermore, emotions and cognition would not be initiating factors of the development of erotic behavior. On the contrary, it seems the erotic activities and sensations structure the emotions and cognitions.

In synthesis, the development of erotic behavior and sexuality would mainly be influenced by internal emotional factors (the emotional effects of the erotic activities and sensations) and external emotional factors (the emotional actions and reactions of others).

More precisely concerning the external emotional factors, during their development, the child then the teenager receives from people around them messages about sexuality. These social interactions generate emotions and affects which are going to shape their future adult sexuality. For example, angry parents may punish (humiliation) and slap (pain) a child caught in homosexual play. An adolescent, with a friend who manifests their attention

and love, may feel tenderness, complicity and intense pleasure, feel a romantic love and be proud of their performance...

Messages about sexuality, *variable according to social and cultural contexts*, induce more intellectualized emotions and affects, like guilt or self-image. For example, an adolescent can perceive themselves as "normal" because he/she knows that their heterosexual activities are valued by the people around them and by their culture. In some societies, a young woman may feel intense guilt because she is not a virgin before her marriage and thus she has "sullied" the honor of her family ...

From birth to adulthood, all these thousands of particular emotional experiences shape, *by emotional conditioning*, the emotional reactions of each person in the face of erotic activities and sexuality.

As for the cognitive activities, under the influence of the cultural context and the emotional experiences, they will be at the origin of developing more or less complex intellectual constructs (beliefs, rules, morals...), which then will retroact on the erotic activities (obligations, prohibitions, taboos...) (see the section "Cognition").

Pathology - Health/disease referent

What would the reference models be which would make it possible to distinguish sexual normality from pathology?

Since the beginning of modern sexology in the nineteenth century, the assessment of human sexual normality was based on the models of animal sexuality and the instinct of reproduction. Even if these referents were not always stated clearly, the function of reproduction made it possible to distinguish normality from sexual pathology. Any deviation from this normality, that is to say all activities which did not allow reproduction (masturbation; sodomy; oral-genital activities, or between prepubertal individuals, or of the same sex or of different races/species...) were pathological (Krafft-Ebing, 1882). And this model is still influential nowadays (Wolpe, 2004).

In the new model, the hedonic function, or more precisely the reinforcement processes, would be the referent of normality. That is to say that probably minimal erotic reinforcements development and/or activity would lead to a state of hypo-, even of a-sexuality, whereas on the contrary maximal reinforcements development and/or activity would induce hypersexuality. An example of weak development of erotic processes would be the primary anorgasmia of women who did not have sufficient autoerotic activities during childhood (Zwang, 1998). An extreme example of absence of development and/or activity of erotic reinforcements would be the women of the So tribe, in Uganda, who have painful sexual intercourse only to have children (Allgeier et al., 1988). At the other end of the continuum, an extreme example of hypersexuality are the young children having lived intense sexual activities. Their erotism is so developed that sexuality becomes « a central, organizing principle in their development » (Yates, 1990; Yates, 1987). Lastly, an example of erotic reinforcements dysfunction would be sexual addiction or dependence (Reynaud, 2005; Southern, 2008), which would correspond to a relatively similar dynamic to addictions to drugs (Frohman, Pitchers, Balfour, & Coolen, 2010; Frohmader, Wiskerke, Wise, Lehman, & Coolen, 2010; Pitchers et al., 2010a), with probably abnormal biological characteristics of the reward system (mutation of an enzyme, impairments of receptor regulation, abnormal development of neural connections ... (for an example, see Salomon, Lanteri, Glowinski, & Tassin, 2006)).

Other sexuality disorders or problems (sexual dysfunctions, STI, conjugopathy, sexual violence...) seem to depend on nonsexual factors (organic diseases, aggression, asociality, lack of sex education...) and could be resolved only by taking into account their real causes and not by actions centered on the erotic behavior (Wunsch & Brenot, 2005a; Wunsch et al., 2005b).

In particular, in this model where the main part of human sexuality is learnt, the majority of sexual disorders would result from a difficulty to express, live and feel sexual pleasure and sexual well-being (dyshedonia). These disorders would come either, on the emotional level, from conditioning, inhibitions and negative emotional states (vaginismus, disgust, aggression, guilt, shame, fear of failure...), or, on the cognitive level, from ignorance or dysfunctional beliefs (erroneous body representations, stereotypes, idealization...). The role of sex education to prevent sexual disorders appears here as crucial (Beltran, 2007).

Conclusion

In synthesis of all these data and analyzes presented in this article, one notes during evolution a gradual transfer of the control of sexual behavior: from olfactory signals to somatosensory signals, as well as from hormones and pheromones to reinforcements and cognition.

The genuine "reproductive behavior" of the simplest mammals, mainly *innate*, seem to *gradually* become in hominids an *acquired* "erotic behavior", which could, *potentially*, be of a very great variability.

This *multifactorial* model, where the importance of the various biological factors is variable according to the species, would make it possible to explain the variations of mammals' sexual behaviors. For the human being, the model of "erotic behavior" would be *the least bad model which is possible to offer today* and which would make it possible to explain all the diversity of sexualities observed, both in History and in the various human societies.

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