Sexual attractiveness: a comparative approach of morphological, behavioral neurophysiological signaling in women and nonhuman primate females

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This comprehensive review focuses on comparative data in nonhuman primates and humans in relation to signaling secondary sex characteristics (SSC), sexual behavior, and neurophysiology of sexuality during the female cycle. Obviously, sexual activities of primates are not limited to specific cycle phases. In higher evolved primate species no distinction can be drawn between sexual interactions as a prerequisite for reproduction or as a pleasurable tool. However, cyclic depended changes of body morphology and behavior, such as feeding, risk taking, mood changes, are documented for both groups. Neurophysiologically, homologous brain areas, sex steroids and receptor compartments are involved in mediating sexual and pleasure during all cycle stages. The interaction between the subcortical reward system and the social brain network and its projection to the prefrontal cortex are of importance. The advertising of SSC indicate analogous strategies between human one male social units and multifemale-multimale groups in nonhuman primates. Women do advertise SSC permanently after the onset of puberty. In contrast, some nonhuman primate species express attractive signals during specific cycle stages and prolong them beyond fertile periods. The physiological and morphological nature of primate SSC and their flexibility of expression in relation to their information content for males will be discussed during different cycle periods for both groups. Because of permanent sexual attractiveness in humans the use of clothes as a specific eye catcher to advertise SSC in relation to biological function will be illustrated. The latter is suggested to be an example of culture-biology adaptation in human sexual behavior.
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This comprehensive review focuses on comparative data in nonhuman primates and humans in relation to signaling secondary sex characteristics (SSC), sexual behavior, and neurophysiology of sexuality during the female cycle. Obviously, sexual activities of primates are not limited to specific cycle phases. In higher evolved primate species no distinction can be drawn between sexual interactions as a prerequisite for reproduction or as a pleasurable tool. However, cyclic depended changes of body morphology and behavior, such as feeding, risk taking, mood changes, are documented for both groups. Neurophysiologically, homologous brain areas, sex steroids and receptor compartments are involved in mediating sexual and pleasure during all cycle stages. The interaction between the subcortical reward system and the social brain network and its projection to the prefrontal cortex are of importance. The advertising of SSC indicate analogous strategies between human one male social units and multifemale-multimale groups in nonhuman primates. Women do advertise SSC permanently after the onset of puberty. In contrast, some nonhuman primate species express attractive signals during specific cycle stages and prolong them beyond fertile periods. The physiological and morphological nature of primate SSC and their flexibility of expression in relation to their information content for males will be discussed during different cycle periods for both groups. Because of permanent sexual attractiveness in humans the use of clothes as a specific eye catcher to advertise SSC in relation to biological function will be illustrated. The latter is suggested to be an example of culture-biology adaptation in human sexual behavior.
Female ovarian cycles are well investigated among mammalian species. During the last decades, research on endocrine mechanisms in relation to behavioral expression rates during different cycle stages provided a picture of functional aspects concerning reproductive strategies in mammalian species. Sexual activities involve complex interactions between neuroendocrine mechanisms in relation to neurotransmitter activities to modulate behavior. Such neurophysiological processes are only partially well understood in primates.

For most mammals, sexual activities are limited to peri-ovulatory cycle periods of females. These periods are characterized by elevated estrogen concentrations leading to ovulation followed by an increase of progesterone secretions permitting the implantation of the egg into the uterus tissue. In general, sexual activity is correlated with estrogen increase and is reduced by elevated progesterone levels. The period of displayed sexual behavior is called estrus. Only during that time per definition females receive males.

The probably best investigated female sexual behavior in terms of physiological and neurobiological aspects seems to be the lordosis reflex in rodents. This is a posture were females allow male intromission. Short before ovulation males approach their mating partners and mount them. This sensory interaction enables the lordosis reflex, which is controlled by the sex steroids estradiol and progesterone. The behavioral aspect of this reflex is regulated by subcortical hypothalamic brain structures, such as the ventromedial nucleus and the periaqueductal gray, where ovarian hormones find acting sites to facilitate it (Flanagan-Cato, 2011; Uphouse, 2013).

Even an – at first glance – very simple sexual behavior such as lordosis seems to be underlined by a complex neurobiological system of interacting circuits and neurochemistry. The mentioned interaction between males and females do correspond to a paradigm pointed out by Beach (1976). Females advertise their sexual readiness to males by being sexual attractive followed by
proceptivity (behavioral signals to males such as solicitation to copulate), and by receptivity (copulatory behavior with subsequent ejaculation to fertilize females). These sequences of sexual interactions are related to hormonal changes during the female cycle and serve ultimately the process of reproduction. It was believed that the Beach paradigm belongs more or less to all nonhuman mammalian species, indicating that these strict biological components of sexual interaction does not relate to humans. Although, scientists suggested that humans do not limit their sexual behavior to specific cycle stages and corresponding hormone fluctuations in contrast to other mammals. This was undermined by the uniqueness of permanent visible stimuli of SSC, such as the breasts and waist-to-hip ratio. The latter and the “freie wille” were thought to be the indicator that sexual interactions and the feeling of lust are unique for humans and have nothing to do with reproductive behavior per se. This belongs to a paradigm, which still confronts biologists and Darwinists today. Many people in industrialized countries do believe that evolutionary processes analyzed for mammals are not acting anymore for humans. Most of them are convinced that humans recently develop decoupled from evolution without natural selection processes along a self-created cultural axis. It is a misconception that the patterns of modern humans have evolved by natural selection during the Pleistocene and stopped after settling and farming (10,000 years ago) as pointed out by Dyson (2007). However, in line with recent research cultural and genetic evolution seem to closely interact in co-evolutionary processes (Richerson et al., 2010). Natural selection is still active on changing traits in contemporary humans (Byars et al., 2009) by effecting adaptations through culture - gene co-evolution, which may act much faster as previously thought (Field et al., 2016). The goal of this work is to characterize functional similarities between humans and nonhuman primates on hormones secretions, neurophysiological subcortical organization and behavior in relation to SSC expression rates during the cycle.
2. Survey methodology

Literature search was carried out by using several databases, such as web of science core collection, web of science all databases, scopus, pubmed, google scholar, research gate or simply searching google. Search strategy for publication databases consisted of chapter specific key words, combinations of chapter specific key words plus relevant institutions with or without known authors. The google survey was different because governmental published data were researched in specific available and known health protection agency web pages. Not available free publications were directly requested from authors or requested from the E-journal service provided by the library of the University of Vienna.

3. Hormones, Behavior and SSC

It is well known that nonhuman primates sexual interactions do not follow completely the paradigm of sex hormone induced estrus, rather sexual behavior is shown throughout all cycle stages (see also Table 1).

During the female’s ovarian cycle, sex steroids are regulated by the release of the pituitary gland peptides follicle-stimulating hormone (FSH) and luteinizing hormone (LH). FSH stimulates the growth of the sex cells, the ovarian follicles; LH in high concentrations induces ovulation in Graafian follicles that have been primed with FSH. Data on rhesus macaques show that preovulatory LH and FSH peaks effect estradiol peaks and thus represent important prerequisites for a successful ovulation (Dixson 1998, pp. 316). More than forty years ago, Dixson et al. (1973) reported not only a peri-ovulatory increase of estradiol for primates, but a similar peak of the androgen testosterone as well. Later, Nadler et al. (1985) were able to show an association of estradiol and testosterone concentrations during the mid-cycle phase and maximum swelling size in the common chimpanzee. Moreover, mid-cycle estradiol and testosterone peaks of chimpanzees are comparable to women (Morris et al., 1987).
3.1. Nonhuman primates

Females of many nonhuman primate species develop sexually attractive signals during their cycle. It is thought that such SSC are attractive for males. The most prominent signals are coloration and/or perineal swelling expressions. The coloration and degree of anogenital swelling size may affect the vulva area, the clitoris, to some extend the circumanal region, even to the area around the ischial callosities (Dixson, 1983). Moreover, it can individually vary among females in a group. Their expression rate is controlled by the sex steroids estradiol and progesterone. Estradiol causes the enlargement of swellings via transferring water into the intercellular tissue and an increased blood flow cause more intensive coloration. After ovulation, the luteal steroid progesterone detacts swellings (Wildt et al., 1977). Both, the intensity of coloration and swelling expression rates are most exaggerated during the periovulatory period (Wallner et al., 2011; Möhle et al., 2005). These periods are corroborated with highest copulation frequencies, where the probability of fertilization is increased as well. However, studies on Barbary macaques indicate that sexual interactions are not limited to peri-ovulatory periods and are therefore, displayed independently of the probability of fertilization, e.g., pregnant females with perineal swelling expressions copulate during non-sexual periods (Küster and Paul, 1984). Moreover, periodic or rhythmic volume and/or color fluctuations, which can be expressed before and after peri-ovulatory are often corroborated with low sex hormone secretion rates and with sexual orientated behavior. Under such conditions females show sexual solicitation behavior and copulations (Brauch et al., 2007). A comparison between non-lactating and lactating individuals in Japanese macaques revealed more intensive red coloration and copulations (with and without ejaculations) for non-lactating individuals during sexually active periods. However, sexual interactions were not diminished in sexually significant unattractive lactating individuals, although their sex steroid production was significantly decreased compared to non-lactating
individuals. These individuals showed slightly changes in coloration intensities and were also engaged in ejaculatory and non-ejaculatory copulations (Wallner et al., 2011). More confusing in biological terms seems to be the expression of SSC and its relation to socio-sexual behavior in Tibetan macaques: Females of this species express both SSC, changes in coloration intensities and perineal swellings. However, the functional aspect of these signals is still unclear in this species. There is uncertainty regarding the extent of these SSC and the display of sexual behavior in the context of advertising fertility. Primatologists did not observe any typical behavior associated with estrus periods. In addition, females copulate outside the mating season when these sex characters are not obviously expressed compared to the mating season (Li et al., 2005; Li et al., 2007). Non-reproductive copulations were not observed for pregnant or lactating individuals and were limited to adolescent males. The authors note (Li et al., 2007) it often happened after social conflicts where females approached males, and solicited copulations.

Even ovariectomy does not inhibit sexual interactions in Old and New World monkeys. In stumptail (Baum et al., 1978) and rhesus macaques (Chambers and Phoenix 1987) females show receptivity, and in the common marmoset (Kendrick & Dixson, 1984) males still perform high copulation frequencies with ovariectomized females. Baboon females with removed ovaries hardly draw the attention of single housed males when placed in visual, olfactory, and auditory contact (Girolami & Bielert, 1987). However, if the same females were provided with large artificial swellings, the males became sexually aroused and masturbated. Masturbation per se seems to be an interesting sexual phenomenon among primates. Dixson discusses auto-eroticism in this context (Dixson p 139ff, 1998). Self-stimulation of genitalia is nearly exclusively reported for Old World monkeys and apes (Dubuc et al., 2013). This type of behavior is shown under captive, semi-free and wild conditions. Barbary macaque females implanted with contraceptives exhibit perineal swellings during non-sexual periods. Males seemed to be more attracted to
females with enlarged swellings (Wallner et al., 1999). They inspect — tactilely and olfactory — the anogenital region of these individuals and masturbate more frequently in their presence. Almost no mounting behavior was performed, suggesting that visible sexual traits seem to stimulate self-directed sexual behavior in males (Wallner, pers. obs. 1995).

A study on same-sex mounting behavior in Japanese macaque females showed that females were able to self-stimulate vulvar, perineal, and anal (VPA) regions. Besides other genital stimulations techniques, mounters rubbed their VPA on their female partners or mounters stroked their VPA with their own tail (Vasey & Duckworth 2006). Because the VPA region mediates sexual arousal in humans and nonhuman primates, the authors interpret their results as an immediate sexual reward. Such sexual sensation from genitalia activates the mesolimbic brain areas (Georgiadis & Kringelbach, 2012) indicating the perception of pleasure.

The most special socio-sexual behavior in nonhuman primates is displayed by bonobos. Their socio-sexual interactions are significant different compared to other species of the ordo primates. It is described as an individual daily life affair independent of female cycle stages, and therefore, of reproductive aspects. Interestingly and uniquely, it involves a variety of sexual interaction types and includes all age and sex combinations (Manson et al., 1997). Striking are face to face copulations similar to humans and seldom in the ordo of primates. Like other species bonobos also exhibit perineal swellings during their cycle and prolong these signals beyond ovulation periods. According to these observations, most authors agree on non-reproductive functional aspects of socio-sexual interactions in nonhuman primates. Barbary macaque females implanted with contraceptives can develop enlarged swellings and if so they have increased socio-positive interactions with males and experience less agonistic encounters, more intervening behavior (on their behalf) from males and receive increased grooming rates (Wallner et al., 1999; Wallner et al., 2006). These results corroborate with similar findings in intact individuals showing infertile
swelling expressions as well. Female chimpanzees enjoy significantly more social privileges than 
those without swellings. In addition to their increased positive social interactions with males, they 
gain greater access to food resources. Pregnant chimpanzee females use their perineal swellings 
as an advantage marker to transfer from one troop to another without experiencing agonistic male 
behavior (Wallis, 1982; Wallis, 1992). Baboon males look strategically for swollen females when 
entering a new group (Goodall, 1986), affiliate temporally with them and use them as a guise. 
In terms of reproductive success, functional explanations of SSC are more difficult to interpret. 
Pagel (1994) pointed out that large perineal swellings are indicators of the reproductive quality 
and health of a female, insofar that this trait informs the males of the female’s social integration 
and biological fitness. Such signals must be the evolutionary result of intra-sexual female 
competition for males. This reliable indicator hypothesis was confirmed in wild olive baboon 
females exhibiting large swellings during their sexually active phases. These individuals had 
increased socio-positive contact with males and produced more offspring than females with 
smaller swellings (Domp & Pagel, 2001). However, critics of this study were able to show that 
the statistics of the work had major flaws. Subsequent investigation did not show better 
reproductive performance for larger swollen individuals (Setchell et al., 2006; see Fitzpatrick et 
al., 2015). Nevertheless, there are indications that conceiptive swellings are larger than non-
conceptive ones and that males do prefer cycles with increased chance of fertilization (Fitzpatrick 
et al., 2015).

According to coloration in Japanese macaques, non-lactating individuals had more intense red 
coloration, especially at the nipple and hindquarter regions, than those who lactated and all of 
them conceived during the sexual active period (Wallner et al., 2011). In mandrill females 
multiparous individuals had brighter faces (Setchell et al., 2006), which might be a hint of better 
reproductive success. Rhesus macaque males prefer more reddened hindquarters in females, 
whereas females do pay more attention to other females with more intense face coloration,
possibly a hint of female competition (Gerald, et al, 2007.) Japanese macaque males were also more interested in increased red colored faces, respectively in faces with increased color contrast than *vice versa* (Pflüger et al., 2014).

Complective has to be pointed out, that the expressions of female temporarily exaggerated SSC in relation to ovulation are generally linked to multi-male, multi-female polygamous mating systems in nonhuman primates. In contrast, in mating systems consisting of one-male units, polygynous or monogamous systems, swelling expressions for example are fairly low and seem to be less related to advertising female fertility. The ultimate reason for such differences seem to be intrasexual competition for mating partners during peri-ovulatory periods in promiscuous species compared to one-male units. An exception to this is the swelling expression in the white-handed gibbon, a species living under monogamous conditions. Females exhibit relatively large swellings during the cycle but also during pregnancy indicating that these individuals are fertile but males are not able to detect ovulation (Barelli et al., 2007).

3.2 *Women: behavioral and morphological variation*

Women also change frequencies of behaviors during the cycle, which might be directly or indirectly associated with sexual activities. A study by Burleson et al. (2002) investigated allosexual, respectively, autosexual behavior in females with or without a partner under heterosexual or lesbian conditions. Allosexual behavior were increased during the follicular and ovulatory phases in groups living with a partner compared to those without a partner. In comparison to that, frequencies of autosexual behavior were elevated in both groups, heterosexual and lesbian, when living without a partner, during the follicular and ovulatory cycle phases compared to those living with a partner. A longitudinal prospective study on female sexual behavior during five cycle phases, menstrual, postmenstrual, ovulatory, luteal and premenstrual showed peaking sexual activities during ovulation (Harvey, 1987). In this study temperature
charts were used to identify different cycle stages. A more recent investigation measured the
preovulatory LH increase in relation to sexual activities. Women initiated more sexual activities
during the preovulatory LH surge and due to that started to show 3 days before increased sexual
desire and fantasy (Bullivant et al., 2004). Pillsworth et al. (2004) were able to show that sexual
desire was only shown in mated women during the peri-ovulatory phase, and among these
women increased conception probability was corroborated with in-pair sexual desire. However,
the duration of partnership was positively related to sexual desire for extra-pair-relationships
during periods of increased fertility. Another study on sexual fantasies in relation to menstrual
cycle phases in single living women showed increased sexual fantasies during preovulatory
elevated LH secretion rates, but these fantasies decreased after ovulation. During follicular and
peri-ovulatory periods the number of male fantasies increased whereas emotional content
increased during ovulation (Dawson et al., 2012). Moreover, cycle stage seems to play an
important role in being motivated to detect erotic stimuli in art. During the first half of the
menstrual cycle women emphasize more erotic stimuli in paintings compared to the second half
(Rudski et al., 2011).

In so-called male mate preference experiments many studies do not explicitly control for cycle
stages but compare fertile vs luteal phases. During fertile cyclic periods women do prefer in
general men masculinity such as social presence, direct intrasexual competition, lower voices, or
scents associated with body symmetry (Gangestad et al., 2004; Gavar-Apgar, 2008). The
preference of male scents of in relation to symmetric body were positively related to women
estrogen and testosterone levels, but negatively to progesterone. Women with decreased urinary
estrone-3-glucuronide levels concentrations showed stronger cyclic shifts (non-fertile/fertile) in
preferences for masculine voices (Feinberg et al, 2006).
Additionally to behavioral changes, different energetic needs are also observed during the menstrual cycle. Lissner et al. (1988) described two peaks of energy intake during the cycle: one at the mid-follicle and the second at the mid-luteal phase. Especially, during the luteal phase, women do crave for more carbohydrate and fat containing food (Davidsen et al., 2007). From a physiological point of view, such food consumption behavior is of significant relevance because energy is needed to produce the endocrine surges for ovulation and for the successful implantation of fertilized eggs into the uterus tissue. Another study showed that the consumption of sweet food and its preference rating is related to preovulatory phases (Bowen & Grunberg, 1990). A comparative work revealed for rodents less energy intake during ovulation compared to luteal phases. Both, nonhuman primates and humans, however, have increased luteal energy intake compared to follicular phases (Dye & Blundell, 1997). Czaja and Goy (1975) carried out classical studies on food intake under estrogan and progesterone control in rhesus macaques and guinea pigs. In both species, the food intake decreased around the time of ovulation and increased during other cyclic periods. The application of sex hormones in ovariectomized individuals showed a clear downregulation of feeding behavior after estrogen administration. However, the role of administered progesterone is less clear. Ovariectomized individuals did not change their feeding behavior after the application of progesterone in comparison to control individuals in both species.

Finally, research on women has documented that estrogen replacement therapy modulates cognitive behavior and mood (review Shively & Bethea, 2004). The authors mention the work of Voytko (2002), where in ovariectomized young female macaques attention rates decreased but increased after a 14 months estradiol treatment. In humans, the premenstrual syndrome in association with depression is relatively well investigated (e.g., Forrester-Knaus et al., 2011). Interestingly, Shively et al (2002) were able to relate less ovarian function, impaired HPA activity with signs of depression in subordinate macaque females.
3.3 Risk behavior during menstrual cycle.

Sexual interactions are *per se* related to physical risks for both sexes (Wallen & Zehr, 2004). For example, T lymphatic viruses are transmitted in humans and in several species of nonhuman primates (see Junglen et al., 2010). For humans at least it is well known that T lymphatic virus I transmission acts via sexual contact. Probably the most famous sexually transmitted diseases are simian and human immunodeficiency viruses (SIV, HIV). The Centers for Disease Control and Prevention ([https://www.cdc.gov/](https://www.cdc.gov/)) points out for the USA that ages between 15–24 represent 27% of the sexual active population account for 50% of sexually transmitted infections. In their fact sheet of infections, gonorrhea ranks number one with 70% followed by chlamydia (63 %), HPV (49 %), genital herpes (45 %), HIV (26%), and syphilis (20 %). Interestingly some of these pathogens such as chlamydia (*Chlamydia trachomatis*) or syphilis (*Treponema pallidum*) were also detected in captive apes (Rushmore et al., 2015). But from these data it is not apparent whether infections are related to specific cycle stages. According to the mentioned female sexual activities, it can be assumed that the peri-ovulatory period can be judged as risky in relation in women to be young at age. Regarding to the type of infection, women between 15-24 ys seem to be most threatened by chlamydia infections. However, there is not very much research available on wild living nonhuman primates considering sexually transmitted diseases. From an evolutionary point of view, patterns of molecular immune defense genes seem to evolve faster in promiscuity primate species and are positively selected with group size (Wlasiuk and Nachman, 2010). These results indicate a molecular counter strategy to sexually transmitted diseases in the *ordo* of primates and most likely in other mammals. Referring to the evolution of the primate immune system, Nunn et al. (2000) found that white blood cell counts were significantly greater in species where females have more mating partners, indicating the risk of sexually transmitted disease. A more recent publication analyzed the evolution of seminal protein gene semenogelin 2
(SEMG2) in primates, which is responsible for the semen coagulation rate. The results showed that promiscuous species do have increased rates of SEMG2 polymorphism, which results in faster semen coagulation rates. The species with the highest evolution rate is the common chimpanzee. Interestingly, the relationship between rate of evolution of SEMG2 and residual testis size is higher in humans compared to polygynous (orangutan, gorilla) or monogamous (gibbon) species (Dorus et al., 2004). A similar result is shown for the correlation between midpiece sperm volume (the location of mitochondria) and the residual testis size in humans (Anderson & Dixson, 2002). Both results do indicate a selection process for moderate promiscuity in humans. Due to these and former mentioned results women sexual behavior during fertile cycle stages could be related to higher risk behavior especially if the desire is corroborated with extra-pair contact. In this context, the question about the origin of human social systems seems to be relevant because selection against sexually transmitted infections would support extra-pair copulations as mating strategies in humans.

However, the type of risk exposure in relation to cycle stages is related to different evolutionary adaptations in primates. In general, male compete for access to females and females compete intrasexually to become fertilized from genetically high-quality males – and additionally in humans from men with elevated socio-economic status corroborated with investment capacities for offspring (Buss, 2008). The increased injury risk for female baboons, for example, is documented for days high in conception probability (Archie et al., 2014). During that period females suffer more from injuries compared to other cycle stages. Compared to women, promiscuous baboon females signal their peri-ovulatory period by exaggerated swellings. In the different socio-eco-system of humans, women seem to have developed strategies to reduce risky behaviors during fertile cycle periods. During ovulation, women do change their behavior to more non-risky behaviors to avoid sexual assaults (Bröder and Hohmann, 2003). Moreover, when confronted with sexual assault scenarios during their ovulatory period, they increase their
handgrip strength (Patralia and Gallup, 2002). Both examples do illustrate that human females try
to avoid an increased risk of undesired fertilizations.

3.4 Women advertising during different cycle phases.

Do human females differ from other nonhuman primates in advertising their sexual attractiveness
in relation to different cycle stages? Many nonhuman primates do exhibit temporally SSC, which
are supposed to be attractive for males. In these species the expression rate of such signals is
linked to sex steroid secretion rates and is supposed to be most exaggerated during peri-ovulatory
phases. After an ovulatory estrogen surge luteal progesterone concentrations reduce the
expression of attractive traits, such as anogenital swellings or color intensity of specific bare
skin areas (Wallner et al., 2006; Wallner et al., 2011). In contrast to nonhuman primates, women
do have permanent developed SSC like waist-to-hip ratio and breasts. However, there are cyclic
changes of body morphology and physiology in women (reviewed in Farage and MacLean,
2009). Most of these changes are related to physiological parameters such as lipid content of skin,
collagen production, pigmentation, hydration, thermoregulation, functional aspects of the
immune system or changes of water compartments and subcutaneous fat tissue. However, which
of these modifications are related to advertise sexual attractiveness, respectively, are detectable
from conspecifics is unclear.

Possibly the most obvious changes occur in subcutaneous fat regions of the thighs and abdomen
(Perin et al., 1999). In this areas up to 4% increase of fat happens during menstruation and fat is
lowest during the first half (follicular stage) of the cycle. Fowler et al. (1990) detected via
magnetic resonance imaging changes of the female breast volume during the cycle as well.
Between day 16 and 28, which represents more or less the luteal phase the water content
increased by 24%, parenchymal volume by 38%. In comparison, during menstruation
parenchymal volume decreased by 30% as well as water content by 17%. These results present a
dramatic volume change for the breast tissue, which is analogous to changes in anogenital
swellings in nonhuman primates. However, the volume increase in swellings is mediated by
estrogens and is based on a shift of intracellular water into the interstitial tissue, whereas the
volume increase in the breast tissue seems to be mediated by luteal progesterone. Again, it is
unclear whether subcutaneous fat changes during the cycle are temporal SSC, which signal
attractiveness in women. However, there are hints that women try to enhance their sexual
attractiveness during the cycle. A study on more than 300 women revealed relationships between
clothing strategies, sexual motivation, and hormone concentrations (Grammer et al., 2004). Sheer
clothing (material is very light and delicate) and sexual motivation was related, whereas salivary
estradiol concentration were corroborated with skin display and clothing tightness. Due to that,
women do change their consumer behavior significantly during fertile cycle periods. They spend
more time in looking for cosmetics, fashion, ornamental stuff like jewelry, and at least spend
more money in such activities. The authors of this work conclude that these behaviors are
hormonally influenced and express female competition for mating partners (Durante &
Griskevicius, 2016; Durante et al., 2010).

These results indicate that women seem to be implicitly aware of their cycle stage and advertise
their morphological cycle changes of the mentioned body regions such as thighs, abdomen,
breasts via choosing specific clothing types. Obviously, the gait also changes during the cycle and
this is related to different postures, which may again advertise the secondary sex character such
as the waist-to-hip ratio. Gueguen (2012) showed that during the peri-ovulatory cycle phase
women walk slower and this is rated sexier by men. Hence, gait *per se* seems to be a critical
behavior used by women to display and perform physical attractiveness. In this context, clothes
such as high heels are very interesting. This type of shoe enables women to change the lumbar
curvature and the inclination of the pelvis significantly (Smith, 1999). Optically this results in a
369 posture signaling a hollow-back and presenting the waist-to-hip ratio more prominently.
370 Evidently, men recognize it as a supernormal stimulus and associate it with female
371 attractiveness. High heels also do influence the gait of women by reducing stride length and
372 increase the rotation of the hip. Regarding shoe design, high heels may mimic the walking
373 performance of women during peri-ovulatory cycle stages.
374 In conclusion, advertising morphological attractiveness is an important evolutionary trait in the
375 context of sexual interactions in nonhuman promiscuous primates and humans. It is shown for
376 nonhuman primates living in multi-male multi-female systems that cycle induced sexual
377 attractive characters are signaled visibly to inform males about female fertility, respectively,
378 readiness to mate. In humans, these signals seem to be more cryptic, which could be caused by
379 the permanent presence of obvious SSC, a fact that does not allow males to recognize women’s
380 fertility easily. From an evolutionary point of view male perception, for example, of
381 morphological cyclic changing traits could make sense in humans under conditions of a selective
382 adaptive balanced polymorphism in females. This would reduce mating competition among
383 females corroborated with increased male attention to hardly visible cues.

4. Neurophysiology of sexual behavior

385 The multi facets of sexual behavior in humans seemed to be very special among primates at least
386 comparable to bonobos. Who else could write about human sexuality in better ways than the
387 eighteenth century Venetian womanizer Giacomo Casanova, only man is capable of real
388 pleasure, because he is gifted with the power of thought, and he expects the desire, he studied it,
389 he gives and remembers her, if he has enjoyed it. Casanova mentions three important
390 neurobiological pre-requisites for sexual behavior: pleasure, desire, and thought. The expression
391 rate of these qualities seem to be distinctively evolved in the ordo of primates. Due to that, it is
392 suggested that functional aspects in biological reproduction, its endocrine regulation in
combination with the expression of SSC in relation to socio-sexual behaviors in humans and nonhuman primate females are species specific, but not in terms of physiological processes. Pleasure and desire are mainly located in subcortical midbrain structures, which are homologous among primates. However, the representation of processes, respectively, consciousness of sexuality in the brain seem to be more difficult to understand and interpret between different primate species. The phylogenetic increase of neocortical cerebralization seems to be related to neuronal projections’ rates from the midbrain to the neocortex and to different evolutionary processes on how the neocortex has evolved.

The vertebrate brain, per se, has developed several areas, which orchestrate the performance and emotional aspects of sexuality. The main structures of the brain are neural interactive nodes that regulate social decision-making. In this context O’Connell and Hofmann (2011) point out in their comprehensive comparative analysis that brain regions representing the social behavior network and the mesolimbic reward system are of special interest for the sensation of pleasure.

Hypothalamic nuclei of the social behavior network are sexual dimorphic in size. The larger male nucleus of the preoptic area (POA) and the bed nucleus of stria terminalis (BNST) are exposed to testosterone during ontogenetic sensitive periods (Hofman & Swaab, 1989). Such a priming reveals concentration depend androgen receptor fields, which are essential for promoting male reproductive behaviors during adulthood. An important functional aspect of the POA is the integration of external and internal information to facilitate mating behavior and gender identity (Garcia-Falgueras, 2011). Research on female macaques reveals neuronal activity in the ventromedial hypothalamus (VMH) and POA areas during sexual activity (see Dixson, 2012, p 502ff). The sex drive in nonhuman primate individuals is mainly characterized by secreted androgens and estrogens, but in humans it is characterized by androgens for both sexes (Fisher et al., 2006). Beside the role of sex steroids, a dopaminergic influence in the POA on sexual arousal
has been documented (Schober and Pfaff, 2007). The mesolimbic reward system is one of the best investigated brain areas in medicine and biology. Comparative studies on fishes, amphibians, reptiles, and mammals reveal analogous functional neuro-anatomic structures (O’Connell and Hofman, 2012). The monoamine neurotransmitter dopamine and its two class receptor system seem to be one of the key players in these mesolimbic structures to mediate pleasure associated with predictive, motivational, or attentional sensations in relation to learning processes (Berridge and Klingelbach, 2008). The dopaminergic system is linked to the prefrontal cortex to mediate cognitive processes generated subcortically regarding to the mentioned emotional and behavioral categories. In the prefrontal cortex the catechol-o-methyltransferase is responsible to deactivate dopamine (Cumming et al., 1992), whereas the dopamine transporter protein regulates the duration of dopamine receptor activation (Giros & Caron, 1993). Comparative analyses of cortical dopaminergic innervation among humans and nonhuman primates reveal no quantitative differences between chimpanzees, macaques and humans (Raghanti et al., 2008). However, sublaminar patterns of innervation differed in specific areas between humans and the other two species.

The main brain structures of the mesolimbic reward system are the striatum (STR: compulsive behavior), ventral tegmental area (VTA: motivation, reproduction, parental care), medial amygdala (meAMY: aggression reproduction, parental care, social recognition), ventral pallidum (VP: emotional learning, parental behavior), nucleus accumbens (NAcc: emotional learning, impulsivity, motivation, parental care), and the hippocampus (HIP: spatial learning) (behaviors from O’Connell & Hofmann, 2011; Berridge & Kringelbach, 2008). In humans the subcortical cognition and cortical consciousness of pleasure is related to activity rates in the medial orbitofrontal, mid insular, and the anterior cingulate areas (de Araujo et al., 2003). Most of the research on the orbitofrontal cortex is concerned about sensory integration and reward value in
relation to food (Kringelbach, 2005). According to Rilling (2011) the reciprocal behavior of food-sharing among non-relative hunter-gatherer populations do represent important neurobiological aspects of the social evolution in humans. fMRI studies confirmed that the orbitofrontal cortex is activated during reciprocal prosocial interactions as well. Therefore, it is proposed that during the evolution of the primate orbitofrontal cortex in relation to subcortical brain areas, functional aspects of prosocial and sexual reward are of specific importance.

Interestingly, both brain areas, the social behavior network and the reward system, consists of highly interactive nodes and overlapping structures, which represent an integrated evolutionary ancient social decision-making network (O’Connell and Hofmann, 2011).

4.1 Sex steroid hormones and related receptors

As indicated before sex steroids, in particular cerebral estrogen hormone concentrations, modulate significantly female behaviors in relation to mood, cognition, or sexuality during different cycle stages. Its neurophysiological function is related to the expression of estrogen receptors, which occur in two isoforms, ERα and ERβ. The latter mediate subcortical cognition processes between hormonal components and expressed behavior. In situ hybridization in ovariectomized and hysterectomized macaques showed the distribution rate of ERβ mRNAs for subcortical hypothalamic, limbic, and midbrain areas. The administration of estrogens did not alter overall receptor densities, however, progesterone down regulated the receptor signal in specific hypothalamic and hippocampus regions (Gundlah et al., 2000).

However, estradiol effects activity rates of ERα in subcortical areas such as POA and VMH (both areas belong to social behavior system, which coordinates sexual activity and is multi-connected with the reward system) are documented in ewes. Increasing estradiol and reduced progesterone concentrations are related to elevated receptor activity and affects sexual behavior under the
The influence of an LH surge in both areas (Fergani et al., 2014). The mentioned scenario seems to be typical for mammalian mid-cycle stages. Similar results were documented for a macaque species, where estrogen receptor activity was investigated in several brain areas between mated and unmated females. Mated females had significant increased receptor activities in POA and VMH regions compared to unmated ones (Michael et al., 2005). Another primate study focused on the ERα and progesterone receptor density in hypothalamic regions of ovariectomized aged and young rhesus macaque females after long-term estradiol treatment. The hormonal treatment did mimic therapeutic supplements in peri-menopausal women. Surprisingly, old macaque females maintain receptor expression, and long-term estradiol supplementation marginally influenced the receptor density (Naugle et al., 2014).

Furthermore, the impact of estrogen on the central dopaminergic system, respectively, brain reward system is worth mentioning. Clinically, it is evident that menopausal females exhibit more often symptoms of Parkinson and schizophrenia diseases, which are related to decreased dopamine production or transmission rates compared to individuals with cycling estrogen changes. Decreased dopamine release seems to be also related to the development of drug addiction was well. Due to that Lynch et al. (2002) indicated that drug abuse is more likely in males than in females, however, in adolescent individuals this maladaptive behavior seems to be marginally different between the sexes. Self administration of alcohol investigated in rats and vervet monkeys show higher amounts of alcohol for females compared to males. However, in rhesus macaques sex differences are vice versa. The authors further report that short time self-administration of heroin in male and females rats did not differ in their consumption rates. However, extended access to this drug resulted in increased self-administration in females (see Lynch et al., 2002, p 125). According to that, cycling women show a dependence of euphoria on d-amphitamine in relation to behaviors such as liking, wanting, or energy and intellectual
improvements during later follicle periods (Justice and de Wit, 1999). Moreover, estradiol seems to improve subjective feelings of pleasure and feeling “high” in associations with amphetamine (Sofuoglu et al., 1999). But, nicotine withdrawal corroborated with premenstrual symptoms during the late luteal phase (Allen et al., 2000). Due to these results, estradiol obviously decreases the dopamine reuptake and increases therefore dopamine concentration in the synaptic cleft and accelerates the binding rate for dopamine at D1 and D2 receptors, while reducing it for D3 in the mesolimbic reward system (see review Almey et al., 2015). Ultrastructural analyses of estrogen receptors within dopamine terminal regions such as the medial prefrontal cortex localized them in extranuclear sites of neurons and glia with the density majority at axons and terminals (Almey et al. 2014). The described central neuro-circuitry of the reward system including the interplay between the dopaminergic system and estrogenic components seem to play a significant role on females’ decision making as well. An experiment on female rats using an effort discounting task approach with different types of reward: using a liver once individuals received two pellets or using the liver many more times they received 4 pellets. The results showed, that ovariectomized individuals made the decision for the high-reward liver, whereas individuals administered with estradiol selected the low-reward lever. Additionally, the application of ERα agonists, independently of ERβ agonists, resulted in high reward cost/benefit decisions, but simultaneous application of agonists for both receptor types decreased the choice for elevated cost/benefit decisions (Uban et al., 2012).

Estrogen effects on the serotonergic brain system in relation to female behavior, which are modulated by different serotonin concentrations have to be emphasized as well. Replacement of ovarian hormones into the dorsal raphe nuclei region of macaque brains altered the mRNA expression rates of components involved in serotonin metabolism (Pecins-Thompson et al., 1998). The rhombencephalic raphe nuclei complex is the origin of the serotonergic system where
serotonergic fibers project into almost all brain areas (Holloway, 1993). Lower amounts of brain serotonin concentrations are related, for example, to depression, anxiety, and impaired cognition (Wallner & Machatschke, 2009). Application of estrogen with or without progesterone increased tryptophan hydroxylase-I mRNA, but decreased mRNAs of MOA-A and concentrations of the serotonin reuptake transporter. The latter impairs the relocation of serotonin metabolites from the postsynaptic membrane into presynaptic regions. All of these components do effect the metabolism of central serotonin expression rates (Smith et al., 2004). The mentioned elements are key structures to influence e.g., female depression and of course behavioral expression rates during the female cycle.

From these neurophysiological data can be suggested that in particular central estrogen and its related receptor system influences significantly female behavior in a socio-sexual context. Because of the distribution rate and density of receptor fields in subcortical brain areas estrogens influence female primate sexuality, food intake, mood changes, feelings of pleasure, and cognitive domains in relation to its cyclic availability in a significant way.

5. Conclusion

Women share with nonhuman primates subcortical brain areas, which are essential to produce behavioral and physiological effects during different cycle stages. These homologous regions represent evolutionary conservative structures documented in nearly all vertebrates. The interconnected social behavior network and the mesolimbic reward system are responsible for a basic integration of sexual behavior to related reward sensations. Obviously, these sensations are not limited to sexuality, but to food intake (Adams and Epel, 2007) or prosocial interactions (Rilling, 2011) as well. With regard to this, the individual emotional reward will be produced
mainly via the dopaminergic system. Research on rhesus macaques showed two types of
dopamine neurons, one excited by reward-predicting stimuli and the other inhibited by airpuff-
predicting stimuli. However, more neurons do excite by both stimuli (Matsumoto and Hikosaka,
2009). These results document that the dopamine system can differentiate between positive and
negative signals. Therefore, the authors propose two functional dopamine neurons, the airpuff-
inhibited and the airpuff-excited type. They are located in the ventromedial substantia nigra
region and the ventral tegmental area for the airpuff-inhibited, and the dorsolateral substantia
nigra region for the airpuff-excited type (these areas are all part of the reward system). For
mammals, it has to be pointed out, that both the mesolimbic reward and the dopaminergic system
project to the prefrontal cortex, but innervation density of cortical striata differs between humans
and nonhuman primate species (Raghanti et al., 2008). Additionally, the distribution of estradiol
receptors at subcortical and cortical sites suggest that value-orientated signals can be transformed
into distinctive behaviors modulated by estradiol concentrations during different cycle phases.
Such modulations seem to be homologous and are stable in physiological and behavioral
expression rates across species. Due to this, the comparison between obvious ovulation signalling
in some nonhuman Old World primate species and silent ovulation in humans reveals
overwhelming similarities according to functional and emotional aspects (Tab 1). Possibly the
most striking differences between man and other primates is the increased postnatal development
of the neo-cortex in newborns, which is related to parental investment. This fact is associated
with different behavioral strategic decisons in women before fertilization. From an evolutionary
point of view, women have to make sure that prospective spouses are in good physical condition
and willing to show longterm investment for the offspring – physically as well as in terms of
providing essential resources.

To achieve this cooperation between reproducing partners pair-bonding mechanisms
have evolved. However, such social binding should not be confused with monogamous mating
systems. A stepwise evolution of different mating system is suggested for primates. Solitary individuals seem to enter a multi-male, multi-female stage approximately 52 million years ago and derived in pair living and polygynous structures since 16 million years (Shultz et al., 2011). For both, humans and nonhuman primate societies the mongamous system appears in lower frequencies compared to harems or multi-male, multi-female societies. However, it can be assumed that social bonding between the sexes is tighter in one-male units than in multi-male, multi-female structures. Neurophysiologically, these bonds are mediated by the neuropeptides oxytocin and vasopressin, which are produced in hypothalamic magnocellular neurons of the paraventricular and supraoptic nuclei and projects into areas of the mesolimbic reward system, such as amygdala or hippocampus, and into the social behavior network, such as the bed nucleus of stria terminalis or the preoptic area (Meyer-Lindenberg et al., 2011). The projection into both mentioned subcortical brain areas suggests that bonding mechanism are related to sexual activities in relation to emotional positive rewards (Young & Wang, 2004), and moreover, represent evolutionarily relatively old brain areas. Insofar, it is assumed that the neuro-circuits of sexual interaction, positive reward in relation to pair-bonding, were established at least after the evolution of single-male units in humans and nonhuman primates. Due to that the origin of advertising female sexually attractive signals seems to be older and is related to the development of multi-male, multi-female societies.

According to the problem of figuring out valueable partners, human female pre-fertilization partner selection seems to be, in general, timely expensive and therefore, vulnerable to intra-female mating competition. Evidence for the latter are permanently expressed sex characters in women. Packing stored energy – naimly fat reserves, which are needed for succesful ovulation, gestation, and lactation –is transferered into beauty, respectively, sexual attractivenss perceived by males. Therefore, breast and waist-to-hip ratio expressions may signal physical and genetic
fitness via beauty. Under these circumstances permanent sexual attractiveness may allow females elevated periods of decision making without losing the interest from prospective partners. However, permanent signalling can have a counter-productive impact for individuals because men can evaluate the quality of different signals on the mating market. Obviously, regarding the waist-to-hip ratio, it is the interaction with the body mass index, which signals healthiness (Singh, 2002). A intercultural rating experiment of the attractiveness of the waist-to-hip ratio showed a preference in males for a certain range of this signal. Such a variance could be caused by evolutionary forced adaptations to varying ecological environments. However, these studies document that extreme measurements are not preferred. Additionally, the breast morphology, respectively, size in fertile females may enhance the sexual attractiveness of the so called hourglass body shape in women (Dixson 2009, p. 136, ff). From the mentioned studies, it can be suggested that human males do recognize female SSC in size relative to body mass parameters and age (see Havlicek et al. 2015 and commentaries). The emerging question in this context is: Can men perceive female morphological changes of SSC and culture-related behaviors such as using different clothing during different cycle phases? For example (as mentioned in 2.4), the water content and paranchymal tissue volume increase in women during the the luteal period and decreases during menstruation. These outlined numbers seem to be dramatically. But, due to the fact that in most human societies cloth wearing is common it seems highly probable that men are not able to recognize cyclic morphological changes of these signals covered by textiles. In general, it is questionable whether men can detect morphological changes in permanent stable relationships. Men perception rates and the information content of female SSC may result from direct comparisons of shape, size, etc., expressions between women undependent of the cycle stage. Such perceptions of expression ranges may deliver them valuable information about females’ healthy, or fitness. In this context the American College of Radiology classified different mammographic density stages based on fat to parenchymal tissue content in relation to
the risk of developing cancer. In general, a higher proportion of parenchymal tissue compared to fat is related to cancer (type 1, less than 25% of parenchymal tissue; type 2, up to 50%; type 3, up to 75%; type 4, more than 75% parenchymal tissue). This classification shows that the ratio between parenchymal and fat tissue can vary extremely. From these data it can be concluded, first, the fat content of female SSC signals health and additionally provides women and the prospective offspring with vital energy resources, and secondly, men perceive properly the relative size of breasts and waist-to-hip ratios in relation to the body mass index of women for their judgement of women’s health. But, the attractiveness of breast sizes and/or shapes does not indicate necessarily a fitness marker insofar as a significant reduction of fat proportion is related to less available energy resources and to increased health risk. In this context more subtle changes during the cycle of other body areas, such as lipid content of skin, fat content of thighs and abdomen, pigmentations, etc. are presumably not reliably detectable by men, even if they are living in long-term partnerships.

However, as indicated in former paragraphs women do change their behavior in relation to cycle phases as well. Some of these changes are obviously linked to the development of human culture. During peri-ovulatory periods women advertise not only by changing their gait, but also by using sheer clothes in relation to their shopping behavior and food consumption. Especially clothing adapted as a tool to advertise sexual attractiveness could be culturally developed to signal fertility, respectively, ovulation. The reason for such a signaling may lie in the compensation of evolutionary evolved permanent sexual attractiveness in relation to non-visible ovulation in humans. The mentioned temporary advertisement seems to be analogous to cyclic changes of swelling or coloration expression in nonhuman primate females. Functionally, both the morphological changes in nonhuman primates and the behavioral strategies in humans are caused by female intra-sexual competition for valuable mates. Interestingly, neither the morphological changes described in nonhuman primates nor the culturally emphasized behaviors in humans,
such as sheer clothes or high heels, seem to be reliable signals of fertility, ovulation or readiness to mate, because prolonged swellings are expressed during non-fertile cycle periods as well the use of sheer clothes. Possibly, the cultural developed use of specific clothes to enhance and accentuate sexual attractive body areas in women can be judged as culture – biology co-adaptation to highlight permanent attractive SSC in a better way under competing partner market conditions. These issues seem to be very important during the mentioned partner selection processes. In such a scenario the use of specific type of cloths during specific cycle periods allow women to signal SSC temporarily and individually. Therefore, cultural adaptation on clothing patterns may play a significant strategy in sexual advertising by women.

Finally due to the presented arguments, the recent study concludes, female sexual attractiveness of nonhuman primates and humans are signaled by morphological flexible traits, which are not per se related to signal conception probability for males. Traits such as temporal perineal swellings are often expressed beyond fertile periods but may be more reliable to ovulation compared to permanent visible SSC in humans. As mentioned before cultural development in humans lead to wear clothes, which may be counterproductive for signaling subtle cyclic morphological changes of SSC. On the other hand, clothing behavior is used to showcase the expression of SSC outside and during fertile periods. Thus, specific clothes may ultimately function as a tool to increase male preference for females by signaling body conscious of SSC. Such a cultural behavior could be developed to underline youth, health and of course fertility under competitive intra-sexual mating market conditions.

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Table 1 (on next page)

Table 1

Summary of comparative cycle expressions in nonhuman primates and humans
Table 1. Summary of comparative cycle expressions in nonhuman primates and humans

<table>
<thead>
<tr>
<th>Phase</th>
<th>Nonhuman primates</th>
<th>Humans</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peri-ovulatory phase</td>
<td><strong>Hormones</strong>&lt;br&gt; LH, FSH, E&lt;sub&gt;2&lt;/sub&gt;, T↑&lt;br&gt;Morphology of SSC coloration (↑ blood flow), swellings (↑ interstitial water)↑&lt;br&gt;Behavior copulation and solicitation↑</td>
<td>LH, FSH, E&lt;sub&gt;2&lt;/sub&gt;, T↑&lt;br&gt;permanent&lt;br&gt;allo-, autosexuality ↑; in pair sex desire ↑; male fantasies ↑; in long-term partnerships desire for extra-pair relationships ↑; pre-ovulatory: sexual fantasies ↑&lt;br&gt;ovulation: emotions ↑; shopping of cosmetics, ornamental goods, etc. ↑; sheer clothing ↑; slower walking ↑</td>
</tr>
<tr>
<td>Non-fertile sexual activities</td>
<td>copulations happen: during pregnancy swelling ↑&lt;br&gt;with ovarioctomized females outside the mating period artificial swelling - males masturbate homosexual behavior</td>
<td>during all cycle stages</td>
</tr>
<tr>
<td>Advertising SSC</td>
<td>temporarily (swelling, coloration expression) E&lt;sub&gt;2&lt;/sub&gt; facilitates SSC, P retracts it</td>
<td>permanent SSC (waist-to-hip ratio, breasts)</td>
</tr>
<tr>
<td>Cyclic changes of SSC</td>
<td>generally after ovulation SSC are ↓ however, individually SSC are prolonged beyond ovulation</td>
<td>follicle stage: subcutaneous fat of thighs ↓ menstruation: subcutaneous fat of thighs ↑ luteal stage: parenchym, water content breasts ↑ menstruation: parenchym, water content breasts ↓ luteal stage: energy, carbohydrate ↑ pre-ovulatory: sweet food ↑</td>
</tr>
<tr>
<td>Cyclic changes of food intake</td>
<td>luteal stage: energy ↑</td>
<td></td>
</tr>
<tr>
<td>Neurophysiology</td>
<td>social behavior network mesolimbic reward system orchestrate emotional aspects of sexuality androgens ↑ pleasure, attentional sensation, learning ↑; linked to the prefrontal cortex</td>
<td>androgens ↑ specifically, innervation in layer I of area 9, 32 and in infragranular layers involved in high level cognition ↑</td>
</tr>
<tr>
<td>Advertising sexual attractiveness</td>
<td>beyond ovulation</td>
<td>beyond ovulation</td>
</tr>
</tbody>
</table>