

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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10 Abstract

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13 of sexuality during the female cycle. Obviously, sexual activities of primates are not limited to
14 specific cycle phases. In higher evolved primate species no distinction can be drawn between
15 sexual interactions as a prerequisite for reproduction or as a pleasurable tool. However, cyclic
16 depended changes of body morphology and behavior, such as feeding, risk taking, mood changes,
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18 receptor compartments are involved in mediating sexual and pleasure during all cycle stages. The
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20 to the prefrontal cortex are of importance. The advertising of SSC indicate analogous strategies
21 between human one male social units and multifemale-multimale groups in nonhuman primates.
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26 cycle periods for both groups. Because of permanent sexual attractiveness in humans the use of
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28 illustrated. The latter is suggested to be an example of culture-biology adaptation in human
29 sexual behavior.

30 1. Introduction

31 Female ovarian cycles are well investigated among mammalian species. During the last decades,
32 research on endocrine mechanisms in relation to behavioral expression rates during different
33 cycle stages provided a picture of functional aspects concerning reproductive strategies in
34 mammalian species. Sexual activities involve complex interactions between neuroendocrine
35 mechanisms in relation to neurotransmitter activities to modulate behavior. Such
36 neurophysiological processes are only partially well understood in primates.

37 For most mammals, sexual activities are limited to peri-ovulatory cycle periods of females. These
38 periods are characterized by elevated estrogen concentrations leading to ovulation followed by an
39 increase of progesterone secretions permitting the implantation of the egg into the uterus tissue.

40 In general, sexual activity is correlated with estrogen increase and is reduced by elevated
41 progesterone levels. The period of displayed sexual behavior is called estrus. Only during that
42 time per definition females receive males.

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

50 Even an – at first glance – very simple sexual behavior such as lordosis seems to be underlined
51 by a complex neurobiological system of interacting circuits and neurochemistry. The mentioned
52 interaction between males and females do correspond to a paradigm pointed out by Beach (1976).

53 Females advertise their sexual readiness to males by being sexual attractive followed by

54 proceptivity (behavioral signals to males such as solicitation to copulate), and by receptivity
55 (copulatory behavior with subsequent ejaculation to fertilize females).

56 These sequences of sexual interactions are related to hormonal changes during the female cycle
57 and serve ultimately the process of reproduction. It was believed that the Beach paradigm belongs
58 more or less to all nonhuman mammalian species, indicating that these strict biological
59 components of sexual interaction does not relate to humans. Although, scientists suggested that
60 humans do not limit their sexual behavior to specific cycle stages and corresponding hormone
61 fluctuations in contrast to other mammals. This was undermined by the uniqueness of permanent
62 visible stimuli of SSC, such as the breasts and waist-to-hip ratio. The latter and the “*freie wille*”
63 were thought to be the indicator that sexual interactions and the feeling of lust are unique for
64 humans and have nothing to do with reproductive behavior *per se*. This belongs to a paradigm,
65 which still confronts biologists and Darwinists today. Many people in industrialized countries do
66 believe that evolutionary processes analyzed for mammals are not acting anymore for humans.
67 Most of them are convinced that humans recently develop decoupled from evolution without
68 natural selection processes along a self-created cultural axis. It is a misconception that the
69 patterns of modern humans have evolved by natural selection during the Pleistocene and stopped
70 after settling and farming (10.000 years ago) as pointed out by Dyson (2007). However, in line
71 with recent research cultural and genetic evolution seem to closely interact in co-evolutionary
72 processes (Richerson et al., 2010). Natural selection is still active on changing traits in
73 contemporary humans (Byars et al., 2009) by effecting adaptations through culture - gene co-
74 evolution, which may act much faster as previously thought (Field et al., 2016).

75 The goal of this work is to characterize functional similarities between humans and nonhuman
76 primates on hormones secretions, neurophysiological subcortical organization and behavior in
77 relation to SSC expression rates during the cycle.

78 2. Survey methodology

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

87 3. Hormones, Behavior and SSC

88 It is well known that nonhuman primates sexual interactions do not follow completely the
89 paradigm of sex hormone induced estrus, rather sexual behavior is shown throughout all cycle
90 stages (see also Table 1).
91 During the female's ovarian cycle, sex steroids are regulated by the release of the pituitary gland
92 peptides follicle-stimulating hormone (FSH) and luteinizing hormone (LH). FSH stimulates the
93 growth of the sex cells, the ovarian follicles; LH in high concentrations induces ovulation in
94 Graafian follicles that have been primed with FSH. Data on rhesus macaques show that
95 preovulatory LH and FSH peaks effect estradiol peaks and thus represent important prerequisites
96 for a successful ovulation (Dixson 1998, pp. 316). More than forty years ago, **Dixson** et al. (1973)
97 reported not only a peri-ovulatory increase of estradiol for primates, but a similar peak of the
98 androgen testosterone as well. Later, Nadler et al. (1985) were able to show an association of
99 estradiol and testosterone concentrations during the mid-cycle phase and maximum swelling size
100 in the common chimpanzee. Moreover, mid-cycle estradiol and testosterone peaks of
101 chimpanzees are comparable to women (Morris et al., 1987).

102 3.1. Nonhuman primates

103 Females of many nonhuman primate species develop sexually attractive signals during their
104 cycle. It is thought that such SSC are attractive for males. The most prominent signals are
105 coloration and/or perineal swelling expressions. The coloration and degree of anogenital swelling
106 size may affect the vulva area, the clitoris, to some extent the circumanal region, even to the area
107 around the ischial callosities (Dixon, 1983). Moreover, it can individually vary among females
108 in a group. Their expression rate is controlled by the sex steroids estradiol and progesterone.
109 Estradiol causes the enlargement of swellings via transferring water into the intercellular tissue
110 and an increased blood flow cause more intensive coloration. After ovulation, the luteal steroid
111 progesterone detracts swellings (Wildt et al., 1977). Both, the intensity of coloration and swelling
112 expression rates are most exaggerated during the periovulatory period (Wallner et al., 2011;
113 Möhle et al., 2005). These periods are corroborated with highest copulation frequencies, where
114 the probability of fertilization is increased as well. However, studies on Barbary macaques
115 indicate that sexual interactions are not limited to peri-ovulatory periods and are therefore,
116 displayed independently of the probability of fertilization, e.g., pregnant females with perineal
117 swelling expressions copulate during non-sexual periods (Küster and Paul, 1984). Moreover,
118 periodic or rhythmic volume and/or color fluctuations, which can be expressed before and after
119 peri-ovulatory are often corroborated with low sex hormone secretion rates and with sexual
120 orientated behavior. Under such conditions females show sexual solicitation behavior and
121 copulations (Brauch et al., 2007). A comparison between non-lactating and lactating individuals
122 in Japanese macaques revealed more intensive red coloration and copulations (with and without
123 ejaculations) for non-lactating individuals during sexually active periods. However, sexual
124 interactions were not diminished in sexually significant unattractive lactating individuals,
125 although their sex steroid production was significantly decreased compared to non-lactating

126 individuals. These individuals showed slightly changes in coloration intensities and were also
127 engaged in ejaculatory and non-ejaculatory copulations (Wallner et al., 2011). More confusing in
128 biological terms seems to be the expression of SSC and its relation to socio-sexual behavior in
129 Tibetan macaques: Females of this species express both SSC, changes in coloration intensities
130 and perineal swellings. However, the functional aspect of these signals is still unclear in this
131 species. There is uncertainty regarding the extent of these SSC and the display of sexual behavior
132 in the context of advertising fertility. Primatologists did not observe any typical behavior
133 associated with estrus periods. In addition, females copulate outside the mating season when
134 these sex characters are not obviously expressed compared to the mating season (Li et al., 2005;
135 Li et al., 2007). Non-reproductive copulations were not observed for pregnant or lactating
136 individuals and were limited to adolescent males. The authors note (Li et al., 2007) it often
137 happened after social conflicts where females approached males, and solicited copulations.

138 Even ovariectomy does not inhibit sexual interactions in Old and New World monkeys. In
139 stump-tail (Baum et al., 1978) and rhesus macaques (Chambers and Phoenix 1987) females show
140 receptivity, and in the common marmoset (Kendrick & Dixson, 1984) males still perform high
141 copulation frequencies with ovariectomized females. Baboon females with removed ovaries
142 hardly draw the attention of single housed males when placed in visual, olfactory, and auditory
143 contact (Girolami & Bielert, 1987). However, if the same females were provided with large
144 artificial swellings, the males became sexually aroused and masturbated. Masturbation *per se*
145 seems to be an interesting sexual phenomenon among primates. Dixson discusses auto-eroticism
146 in this context (Dixson p 139ff, 1998). Self-stimulation of genitalia is nearly exclusively reported
147 for Old World monkeys and apes (Dubuc et al., 2013). This type of behavior is shown under
148 captive, semi-free and wild conditions. Barbary macaque females implanted with contraceptives
149 exhibit perineal swellings during non-sexual periods. Males seemed to be more attracted to

150 females with enlarged swellings (Wallner et al., 1999). They inspect — tactilely and olfactory —
151 the anogenital region of these individuals and masturbate more frequently in their presence.
152 Almost no mounting behavior was performed, suggesting that visible sexual traits seem to
153 stimulate self-directed sexual behavior in males (Wallner, pers. obs. 1995).

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

161 The most special socio-sexual behavior in nonhuman primates is displayed by bonobos. Their
162 socio-sexual interactions are significant different compared to other species of the ordo primates.
163 It is described as an individual daily life affair independent of female cycle stages, and therefore,
164 of reproductive aspects. Interestingly and uniquely, it involves a variety of sexual interaction
165 types and includes all age and sex combinations (Manson et al., 1997). Striking are face to face
166 copulations similar to humans and seldom in the ordo of primates. Like other species bonobos
167 also exhibit perineal swellings during their cycle and prolong these signals beyond ovulation
168 periods. According to these observations, most authors agree on non-reproductive functional
169 aspects of socio-sexual interactions in nonhuman primates. Barbary macaque females implanted
170 with contraceptives can develop enlarged swellings and if so they have increased socio-positive
171 interactions with males and experience less agonistic encounters, more intervening behavior (on
172 their behalf) from males and receive increased grooming rates (Wallner et al., 1999; Wallner et
173 al., 2006). These results corroborate with similar findings in intact individuals showing infertile

174 swelling expressions as well. Female chimpanzees enjoy significantly more social privileges than
175 those without swellings. In addition to their increased positive social interactions with males, they
176 gain greater access to food resources. Pregnant chimpanzee females use their perineal swellings
177 as an advantage marker to transfer from one troop to another without experiencing agonistic male
178 behavior (Wallis, 1982; Wallis, 1992). Baboon males look strategically for swollen females when
179 entering a new group (Goodall, 1986), affiliate temporally with them and use them as a guise.
180 In terms of reproductive success, functional explanations of SSC are more difficult to interpret.
181 Pagel (1994) pointed out that large perineal swellings are indicators of the reproductive quality
182 and health of a female, insofar that this trait informs the males of the female's social integration
183 and biological fitness. Such signals must be the evolutionary result of intra-sexual female
184 competition for males. This reliable indicator hypothesis was confirmed in wild olive baboon
185 females exhibiting large swellings during their sexually active phases. These individuals had
186 increased socio-positive contact with males and produced more offspring than females with
187 smaller swellings (Domp & Pagel, 2001). However, critics of this study were able to show that
188 the statistics of the work had major flaws. Subsequent investigation did not show better
189 reproductive performance for larger swollen individuals (Setchell et al., 2006; see Fitzpatrick et
190 al., 2015). Nevertheless, there are indications that conceptive swellings are larger than non-
191 conceptive ones and that males do prefer cycles with increased chance of fertilization (Fitzpatrick
192 et al., 2015).

193 According to coloration in Japanese macaques, non-lactating individuals had more intense red
194 coloration, especially at the nipple and hindquarter regions, than those who lactated and all of
195 them conceived during the sexual active period (Wallner et al., 2011). In mandrill females
196 multiparous individuals had brighter faces (Setchell et al., 2006), which might be a hint of better
197 reproductive success. Rhesus macaque males prefer more reddened hindquarters in females,
198 whereas females do pay more attention to other females with more intense face coloration,

199 possibly a hint of female competition (Gerald, et al, 2007.) Japanese macaque males were also
200 more interested in increased red colored faces, respectively in faces with increased color contrast
201 than *vice versa* (Pflüger et al., 2014).

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

212

213 3.2 Women: behavioral and morphological variation

214 Women also change frequencies of behaviors during the cycle, which might be directly or
215 indirectly associated with sexual activities. A study by Burleson et al. (2002) investigated
216 allosexual, respectively, autosexual behavior in females with or without a partner under
217 heterosexual or lesbian conditions. Allosexual behavior were increased during the follicular and
218 ovulatory phases in groups living with a partner compared to those without a partner In
219 comparison to that, frequencies of autosexual behavior were elevated in both groups,
220 heterosexual and lesbian, when living without a partner, during the follicular and ovulatory cycle
221 phases compared to those living with a partner. A longitudinal prospective study on female sexual
222 behavior during five cycle phases, menstrual, postmenstrual, ovulatory, luteal and premenstrual
223 showed peaking sexual activities during ovulation (Harvey , 1987). In this study temperature

224 charts were used to identify different cycle stages. A more recent investigation measured the
225 preovulatory LH increase in relation to sexual activities. Women initiated more sexual activities
226 during the preovulatory LH surge and due to that started to show 3 days before increased sexual
227 desire and fantasy (Bullivant et al., 2004). Pillsworth et al. (2004) were able to show that sexual
228 desire was only shown in mated women during the peri-ovulatory phase, and among these
229 women increased conception probability was corroborated with in-pair sexual desire. However,
230 the duration of partnership was positively related to sexual desire for extra-pair-relationships
231 during periods of increased fertility. Another study on sexual fantasies in relation to menstrual
232 cycle phases in single living women showed increased sexual fantasies during preovulatory
233 elevated LH secretion rates, but these fantasies decreased after ovulation. During follicular and
234 peri-ovulatory periods the number of male fantasies increased whereas emotional content
235 increased during ovulation (Dawson et al., 2012). Moreover, cycle stage seems to play an
236 important role in being motivated to detect erotic stimuli in art. During the first half of the
237 menstrual cycle women emphasize more erotic stimuli in paintings compared to the second half
238 (Rudski et al., 2011).

239 In so-called male mate preference experiments many studies do not explicitly control for cycle
240 stages but compare fertile vs luteal phases. During fertile cyclic periods women do prefer in
241 general men masculinity such as social presence, direct intrasexual competition, lower voices, or
242 scents associated with body symmetry (Gangestad et al., 2004; Gavar-Apgar, 2008). The
243 preference of male scents of in relation to symmetric body were positively related to women
244 estrogen and testosterone levels, but negatively to progesterone. Women with decreased urinary
245 estrone-3-glucuronide levels concentrations showed stronger cyclic shifts (non-fertile/fertile) in
246 preferences for masculine voices (Feinberg et al, 2006).

247 Additionally to behavioral changes ,different energetic needs are also observed during the
248 menstrual cycle. Lissner et al. (1988) described two peaks of energy intake during the cycle: one
249 at the mid-follicle and the second at the mid-luteal phase. Especially, during the luteal phase
250 women do crave for more carbohydrate and fat containing food (Davidsen et al., 2007). From a
251 physiological point of view, such food consumption behavior is of significant relevance because
252 energy is needed to produce the endocrine surges for ovulation and for the successful
253 implantation of fertilized eggs into the uterus tissue. Another study showed that the consumption
254 of sweet food and its preference rating is related to preovulatory phases (Bowen & Grunberg,
255 1990). A comparative work revealed for rodents less energy intake during ovulation compared to
256 luteal phases. Both, nonhuman primates and humans, however, have increased luteal energy
257 intake compared to follicular phases (Dye & Blundell, 1997). Czaja and Goy (1975) carried out
258 classical studies on food intake under estrogen and progesterone control in rhesus macaques and
259 guinea pigs . In both species, the food intake decreased around the time of ovulation and
260 increased during other cyclic periods. The application of sex hormones in ovariectomized
261 individuals showed a clear downregulation of feeding behavior after estrogen administration.
262 However, the role of administered progesterone is less clear. Ovariectomized individuals did not
263 change their feeding behavior after the application of progesterone in comparison to control
264 individuals in both species.

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

272 3.3 Risk behavior during menstrual cycle.

273 Sexual interactions are *per se* related to physical risks for both sexes (Wallen & Zehr, 2004). For
274 example, T lymphatic viruses are transmitted in humans and in several species of nonhuman
275 primates (see Junglen et al., 2010). For humans at least it is well known that T lymphatic virus I
276 transmission acts via sexual contact. Probably the most famous sexually transmitted diseases are
277 simian and human immunodeficiency viruses (SIV, HIV). The Centers for Disease Control and
278 Prevention (<https://www.cdc.gov/>) points out for the USA that ages between 15–24 represent
279 27% of the sexual active population account for 50% of sexually transmitted infections. In their
280 fact sheet of infections, gonorrhea ranks number one with 70% followed by chlamydia (63 %),
281 HPV (49 %), genital herpes (45 %), HIV (26%), and syphilis (20 %). Interestingly some of these
282 pathogens such as chlamydia (*Chlamydia trachomatis*) or syphilis (*Treponema pallidum*) were
283 also detected in captive apes (Rushmore et al., 2015). But from these data it is not apparent
284 whether infections are related to specific cycle stages. According to the mentioned female sexual
285 activities, it can be assumed that the peri-ovulatory period can be judged as risky in relation in
286 women to be young at age. Regarding to the type of infection, women between 15-24 ys seem to
287 be most threatened by chlamydia infections. However, there is not very much research available
288 on wild living nonhuman primates considering sexually transmitted diseases. From an
289 evolutionary point of view, patterns of molecular immune defense genes seem to evolve faster in
290 promiscuity primate species and are positively selected with group size (Wlasiuk and Nachman,
291 2010). These results indicate a molecular counter strategy to sexually transmitted diseases in the
292 *ordo* of primates and most likely in other mammals. Referring to the evolution of the primate
293 immune system, Nunn et al. (2000) found that white blood cell counts were significantly greater
294 in species where females have more mating partners, indicating the risk of sexually transmitted
295 disease. A more recent publication analyzed the evolution of seminal protein gene semenogelin 2

296 (SEMG2) in primates, which is responsible for the semen coagulation rate. The results showed
297 that promiscuous species do have increased rates of SEMG2 polymorphism, which results in
298 faster semen coagulation rates. The species with the highest evolution rate is the common
299 chimpanzee. Interestingly, the relationship between rate of evolution of SEMG2 and residual
300 testis size is higher in humans compared to polygynous (orangutan, gorilla) or monogamous
301 (gibbon) species (Dorus et al., 2004). A similar result is shown for the correlation between
302 midpiece sperm volume (the location of mitochondria) and the residual testis size in humans
303 (Anderson & Dixson, 2002). Both results do indicate a selection process for moderate
304 promiscuity in humans. Due to these and former mentioned results women sexual behavior
305 during fertile cycle stages could be related to higher risk behavior especially if the desire is
306 corroborated with extra-pair contact. In this context, the question about the origin of human
307 social systems seems to be relevant because selection against sexually transmitted infections
308 would support extra-pair copulations as mating strategies in humans.

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

321 handgrip strength (Patralia and Gallup, 2002). Both examples do illustrate that human females try
322 to avoid an increased risk of undesired fertilizations.

323 *3.4 Women advertising during different cycle phases.*

324 Do human females differ from other nonhuman primates in advertising their sexual attractiveness
325 in relation to different cycle stages? Many nonhuman primates do exhibit temporally SSC, which
326 are supposed to be attractive for males. In these species the expression rate of such signals is
327 linked to sex steroid secretion rates and is supposed to be most exaggerated during peri-ovulatory
328 phases. After an ovulatory estrogen surge luteal progesterone concentrations reduce the
329 expressions of attractive traits, such as anogenital swellings or color intensity of specific bare
330 skin areas (Wallner et al., 2006; Wallner et al., 2011). In contrast to nonhuman primates, women
331 do have permanent developed SSC like waist-to-hip ratio and breasts. However, there are cyclic
332 changes of body morphology and physiology in women (reviewed in Farage and MacLean,
333 2009). Most of these changes are related to physiological parameters such as lipid content of skin,
334 collagen production, pigmentation, hydration, thermoregulation, functional aspects of the
335 immune system or changes of water compartments and subcutaneous fat tissue. However, which
336 of these modifications are related to advertise sexual attractiveness, respectively, are detectable
337 from conspecifics is unclear.

338 Possibly the most obvious changes occur in subcutaneous fat regions of the thighs and abdomen
339 (Perin et al., 1999). In this areas up to 4 % increase of fat happens during menstruation and fat is
340 lowest during the first half (follicular stage) of the cycle. Fowler et al. (1990) detected via
341 magnetic resonance imaging changes of the female breast volume during the cycle as well.
342 Between day 16 and 28, which represents more or less the luteal phase the water content
343 increased by 24 %, parenchymal volume by 38 %. In comparison, during menstruation

344 parenchymal volume decreased by 30 % as well as water content by 17 %. These results present a
345 dramatic volume change for the breast tissue, which is analogous to changes in anogenital
346 swellings in nonhuman primates. However, the volume increase in swellings is mediated by
347 estrogens and is based on a shift of intracellular water into the interstitial tissue, whereas the
348 volume increase in the breast tissue seems to be mediated by luteal progesterone. Again, it is
349 unclear whether subcutaneous fat changes during the cycle are temporal SSC, which signal
350 attractiveness in women. However, there are hints that women try to enhance their sexual
351 attractiveness during the cycle. A study on more than 300 women revealed relationships between
352 clothing strategies, sexual motivation, and hormone concentrations (Grammer et al., 2004). Sheer
353 clothing (material is very light and delicate) and sexual motivation was related, whereas salivary
354 estradiol concentration were corroborated with skin display and clothing tightness. Due to that,
355 women do change their consumer behavior significantly during fertile cycle periods. They spend
356 more time in looking for cosmetics, fashion, ornamental stuff like jewelry, and at least spend
357 more money in such activities. The authors of this work conclude that these behaviors are
358 hormonally influenced and express female competition for mating partners (Durante &
359 Griskevicius, 2016; Durante et al., 2010).

360 These results indicate that women seem to be implicitly aware of their cycle stage and advertise
361 their morphological cycle changes of the mentioned body regions such as thighs, abdomen,
362 breasts via choosing specific clothing types. Obviously, the gait also changes during the cycle and
363 this is related to different postures, which may again advertise the secondary sex character such
364 as the waist-to-hip ratio. Gueguen (2012) showed that during the peri-ovulatory cycle phase
365 women walk slower and this is rated sexier by men. Hence, gait *per se* seems to be a critical
366 behavior used by women to display and perform physical attractiveness. In this context, clothes
367 such as high heels are very interesting. This type of shoe enables women to change the lumbar
368 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 mimicry 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.

384 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

393 combination with the expression of SSC in relation to socio-sexual behaviors in humans and
394 nonhuman primate females are species specific, but not in terms of physiological processes.
395 Pleasure and desire are mainly located in subcortical midbrain structures, which are homologous
396 among primates. However, the representation of processes, respectively, consciousness of
397 sexuality in the brain seem to be more difficult to understand and interpret between different
398 primate species. The phylogenetic increase of neocortical cerebralization seems to be related to
399 neuronal projections' rates from the midbrain to the neocortex and to different evolutionary
400 processes on how the neocortex has evolved.

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

406 Hypothalamic nuclei of the social behavior network are sexual dimorphic in size. The larger male
407 nucleus of the preoptic area (POA) and the bed nucleus of stria terminalis (BNST) are exposed to
408 testosterone during ontogenetic sensitive periods (Hofman & Swaab, 1989). Such a priming
409 reveals concentration depend androgen receptor fields, which are essential for promoting male
410 reproductive behaviors during adulthood. An important functional aspect of the POA is the
411 integration of external and internal information to facilitate mating behavior and gender identity
412 (Garcia-Falgueras, 2011). Research on female macaques reveals neuronal activity in the
413 ventromedial hypothalamus (VMH) and POA areas during sexual activity (see Dixson, 2012, p
414 502ff). The sex drive in nonhuman primate individuals is mainly characterized by secreted
415 androgens and estrogens, but in humans it is characterized by androgens for both sexes (Fisher et
416 al., 2006). Beside the role of sex steroids, a dopaminergic influence in the POA on sexual arousal

417 has been documented (Schober and Pfaff, 2007). The mesolimbic reward system is one of the
418 best investigated brain areas in medicine and biology. Comparative studies on fishes, amphibians,
419 reptiles, and mammals reveal analogous functional neuro-anatomic structures (O'Connell and
420 Hofman, 2012). The monoamine neurotransmitter dopamine and its two class receptor system
421 seem to be one of the key players in these mesolimbic structures to mediate pleasure associated
422 with predictive, motivational, or attentional sensations in relation to learning processes (Berridge
423 and Klingelbach, 2008). The dopaminergic system is linked to the prefrontal cortex to mediate
424 cognitive processes generated subcortically regarding to the mentioned emotional and behavioral
425 categories. In the prefrontal cortex the catechol-o-methyltransferase is responsible to deactivate
426 dopamine (Cumming et al., 1992), whereas the dopamine transporter protein regulates the
427 duration of dopamine receptor activation (Giros & Caron, 1993). Comparative analyses of
428 cortical dopaminergic innervation among humans and nonhuman primates reveal no quantitative
429 differences between chimpanzees, macaques and humans (Raghanti et al., 2008). However,
430 sublaminal patterns of innervation differed in specific areas between humans and the other two
431 species.

432 The main brain structures of the mesolimbic reward system are the striatum (STR: compulsive
433 behavior), ventral tegmental area (VTA: motivation, reproduction, parental care), medial
434 amygdala (meAMY: aggression reproduction, parental care, social recognition), ventral pallidum
435 (VP: emotional learning, parental behavior), nucleus accumbens (NAcc: emotional learning,
436 impulsivity, motivation, parental care), and the hippocampus (HIP: spatial learning) (behaviors
437 from O'Connell & Hofmann, 2011; Berridge & Kringelbach, 2008). In humans the subcortical
438 cognition and cortical consciousness of pleasure is related to activity rates in the medial
439 orbitofrontal, mid insular, and the anterior cingulate areas (de Araujo et al., 2003). Most of the
440 research on the orbitofrontal cortex is concerned about sensory integration and reward value in

441 relation to food (Kringelbach, 2005). According to Rilling (2011) the reciprocal behavior of food-
442 sharing among non-relative hunter-gatherer populations do represent important neurobiological
443 aspects of the social evolution in humans. fMRI studies confirmed that the orbitofrontal cortex is
444 activated during reciprocal prosocial interactions as well. Therefore, it is proposed that during the
445 evolution of the primate orbitofrontal cortex in relation to subcortical brain areas, functional
446 aspects of prosocial and sexual reward are of specific importance.

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

450 *4.1 Sex steroid hormones and related receptors*

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

460 However, estradiol effects activity rates of ER α in subcortical areas such as POA and VMH (both
461 areas belong to social behavior system, which coordinates sexual activity and is multi-connected
462 with the reward system) are documented in ewes. Increasing estradiol and reduced progesterone
463 concentrations are related to elevated receptor activity and affects sexual behavior under the

464 influence of an LH surge in both areas (Fergani et al., 2014). The mentioned scenario seems to
465 be typical for mammalian mid-cycle stages. Similar results were documented for a macaque
466 species, where estrogen receptor activity was investigated in several brain areas between mated
467 and unmated females. Mated females had significant increased receptor activities in POA and
468 VMH regions compared to unmated ones (Michael et al., 2005). Another primate study focused
469 on the ER α and progesterone receptor density in hypothalamic regions of ovariectomized aged
470 and young rhesus macaque females after long-term estradiol treatment. The hormonal treatment
471 did mimic therapeutic supplements in peri-menopausal women. Surprisingly, old macaque
472 females maintain receptor expression, and long-term estradiol supplementation marginally
473 influenced the receptor density (Naugle et al., 2014).

474 Furthermore, the impact of estrogen on the central dopaminergic system, respectively, brain
475 reward system is worth mentioning. Clinically, it is evident that menopausal females exhibit more
476 often symptoms of Parkinson and schizophrenia diseases, which are related to decreased
477 dopamine production or transmission rates compared to individuals with cycling estrogen
478 changes. Decreased dopamine release seems to be also related to the development of drug
479 addiction as well. Due to that Lynch et al. (2002) indicated that drug abuse is more likely in
480 males than in females, however, in adolescent individuals this maladaptive behavior seems to be
481 marginally different between the sexes. Self administration of alcohol investigated in rats and
482 vervet monkeys show higher amounts of alcohol for females compared to males. However, in
483 rhesus macaques sex differences are vice versa. The authors further report that short time self-
484 administration of heroin in male and female rats did not differ in their consumption rates.
485 However, extended access to this drug resulted in increased self-administration in females (see
486 Lynch et al., 2002, p 125). According to that, cycling women show a dependence of euphoria on
487 *d*-amphetamine in relation to behaviors such as liking, wanting, or energy and intellectual

488 improvements during later follicle periods (Justice and de Wit, 1999). Moreover, estradiol seems
489 to improve subjective feelings of pleasure and feeling “high” in associations with amphetamine
490 (Sofuoglu et al., 1999). But, nicotine withdrawal corroborated with premenstrual symptoms
491 during the late luteal phase (Allen et al., 2000). Due to these results, estradiol obviously decreases
492 the dopamine reuptake and increases therefore dopamine concentration in the synaptic cleft and
493 accelerates the binding rate for dopamine at D1 and D2 receptors, while reducing it for D3 in the
494 mesolimbic reward system (see review Almey et al., 2015). Ultrastructural analyses of estrogen
495 receptors within dopamine terminal regions such as the medial prefrontal cortex localized them in
496 extranuclear sites of neurons and glia with the density majority at axons and terminals (Almey et
497 al. 2014). The described central neuro-circuitry of the reward system including the interplay
498 between the dopaminergic system and estrogenic components seem to play a significant role on
499 females’ decision making as well. An experiment on female rats using an effort discounting task
500 approach with different types of reward: using a liver once individuals received two pellets or
501 using the liver many more times they received 4 pellets. The results showed, that ovariectomized
502 individuals made the decision for the high-reward liver, whereas individuals administered with
503 estradiol selected the low-reward lever. Additionally, the application of ER α agonists,
504 independently of ER β agonists, resulted in high reward cost/benefit decisions, but simultaneous
505 application of agonists for both receptor types decreased the choice for elevated cost/benefit
506 decisions (Uban et al., 2012).

507 Estrogen effects on the serotonergic brain system in relation to female behavior, which are
508 modulated by different serotonin concentrations have to be emphasized as well. Replacement of
509 ovarian hormones into the dorsal raphe nuclei region of macaque brains altered the mRNA
510 expression rates of components involved in serotonin metabolism (Pecins-Thompson et al.,
511 1998). The rhombencephalic raphe nuclei complex is the origin of the serotonergic system where

512 serotonergic fibers project into almost all brain areas (Holloway, 1993). Lower amounts of brain
513 serotonin concentrations are related, for example, to depression, anxiety, and impaired cognition
514 (Wallner & Machatschke, 2009). Application of estrogen with or without progesterone increased
515 tryptophan hydroxylase-I mRNA, but decreased mRNAs of MOA-A and concentrations of the
516 serotonin reuptake transporter. The latter impairs the relocation of serotonin metabolites from the
517 postsynaptic membrane into presynaptic regions. All of these components do effect the
518 metabolism of central serotonin expression rates (Smith et al., 2004). The mentioned elements are
519 key structures to influence e.g., female depression and of course behavioral expression rates
520 during the female cycle.

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

526 5. Conclusion

527 Women share with nonhuman primates subcortical brain areas, which are essential to produce
528 behavioral and physiological effects during different cycle stages. These homologous regions
529 represent evolutionary conservative structures documented in nearly all vertebrates. The
530 interconnected social behavior network and the mesolimbic reward system are responsible for a
531 basic integration of sexual behavior to related reward sensations. Obviously, these sensations are
532 not limited to sexuality, but to food intake (Adams and Epel, 2007) or prosocial interactions
533 (Rilling, 2011) as well. With regard to this, the individual emotional reward will be produced

534 mainly via the dopaminergic system. Research on rhesus macaques showed two types of
535 dopamine neurons, one excited by reward-predicting stimuli and the other inhibited by airpuff-
536 predicting stimuli. However, more neurons do excite by both stimuli (Matsumoto and Hikosaka,
537 2009). These results document that the dopamine system can differentiate between positive and
538 negative signals. Therefore, the authors propose two functional dopamine neurons, the airpuff-
539 inhibited and the airpuff-excited type. They are located in the ventromedial substantia nigra
540 region and the ventral tegmental area for the airpuff-inhibited, and the dorsolateral substantia
541 nigra region for the airpuff-excited type (these areas are all part of the reward system). For
542 mammals, it has to be pointed out, that both the mesolimbic reward and the dopaminergic system
543 project to the prefrontal cortex, but innervation density of cortical striata differs between humans
544 and nonhuman primate species (Raghanti et al., 2008). Additionally, the distribution of estradiol
545 receptors at subcortical and cortical sites suggest that value-orientated signals can be transformed
546 into distinctive behaviors modulated by estradiol concentrations during different cycle phases.
547 Such modulations seem to be homologous and are stable in physiological and behavioral
548 expression rates across species. Due to this, the comparison between obvious ovulation signalling
549 in some nonhuman Old World primate species and silent ovulation in humans reveals
550 overwhelming similarities according to functional and emotioal aspects (Tab 1). Possibly the
551 most striking differences between man and other primtes is the increased postnatal development
552 of the neo-cortex in newborns, which is related to parental investment. This fact is associated
553 with different behavioral strategic decesions in women before fertilization. From an evolutionary
554 point of view, women have to make sure that prospective spouses are in good physical condition
555 and willing to show longterm investment for the offspring – physically as well as in terms of
556 providing essential ressources.

557 To achieve this cooperation between reproducing partnerns pair-bonding mechanisms
558 have evolved. However, such social binding should not be confused with monogamous mating

559 systems. A stepwise evolution of different mating system is suggested for primates. Solitary
560 individuals seem to enter a multi-male, multi-female stage approximately 52 million years ago
561 and derived in pair living and polygynous structures since 16 million years (Shultz et al., 2011).
562 For both, humans and nonhuman primate societies the monogamous system appears in lower
563 frequencies compared to harems or multi-male, multi-female societies. However, it can be
564 assumed that social bonding between the sexes is tighter in one-male units than in multi-male,
565 multi-female structures. Neurophysiologically, these bonds are mediated by the neuropeptides
566 oxytocin and vasopressin, which are produced in hypothalamic magnocellular neurons of the
567 paraventricular and supraoptic nuclei and projects into areas of the mesolimbic reward system,
568 such as amygdala or hippocampus, and into the social behavior network, such as the bed nucleus
569 of stria terminalis or the preoptic area (Meyer-Lindenberg et al., 2011). The projection into both
570 mentioned subcortical brain areas suggests that bonding mechanism are related to sexual
571 activities in relation to emotional positive rewards (Young & Wang, 2004), and moreover,
572 represent evolutionarily relatively old brain areas. Insofar, it is assumed that the neuro-circuits of
573 sexual interaction, positive reward in relation to pair-bonding, were established at least after the
574 evolution of single-male units in humans and nonhuman primates. Due to that the origin of
575 advertising female sexually attractive signals seems to be older and is related to the development
576 of multi-male, multi-female societies.

577 According to the problem of figuring out valuable partners, human female pre-fertilization
578 partner selection seems to be, in general, timely expensive and therefore, vulnerable to intra-
579 female mating competition. Evidence for the latter are permanently expressed sex characters in
580 women. Packing stored energy – namely fat reserves, which are needed for successful ovulation,
581 gestation, and lactation – is transferred into beauty, respectively, sexual attractiveness perceived
582 by males. Therefore, breast and waist-to-hip ratio expressions may signal physical and genetic

583 fitness via beauty. Under these circumstances permanent sexual attractiveness may allow females
584 elevated periods of decision making without losing the interest from prospective partners.
585 However, permanent signalling can have a counter-productive impact for individuals because
586 men can evaluate the quality of different signals on the mating market. Obviously, regarding the
587 waist-to-hip ratio, it is the interaction with the body mass index, which signals healthiness (Singh,
588 2002). A intercultural rating experiment of the attractiveness of the waiste-to-hip ratio showed a
589 preference in males for a certain range of this signal. Such a variance could be caused by
590 evolutionary forced adaptations to varying ecological environments. However, these studies
591 document that extreme measurements are not preferred. Additionally, the breast morphology,
592 respectively, size in fertile females may enhance the sexual attractiveness of the so called
593 hourglass body shap in women (s Dixson 2009, p. 136, ff). From the mentioned studies, it can be
594 suggested that human males do recognize female SSC in size relative to body mass parameters
595 and age (see Havlicek et al. 2015 and commentaries). The emerging question in this context is:
596 Can men perceive female morphological changes of SSC and culture-related behaviors such as
597 using different clothing during different cycle phases? For example (as mentioned in 2.4), the
598 water content and parachemal tissue volume increase in women during the the luteal period and
599 decreases during menstruation. These outlined numbers seem to be dramatically. But, due to the
600 fact that in most human societies cloth wearing is common it seems highly probable that men are
601 not able to recoginze cyclic morphological changes of these signals covered by textiles. In
602 general, it is questionalble whether men can detect morphological changes in permant stable
603 relationsshps. Men perception rates and the information content of female SSC may result from
604 direct compariosn of shape, size, etc., expressions between women undipendent of the cycle
605 stage. Such perceptions of expression ranges may deliver them valuable information about
606 femals' healthy, or fitness . In this context the American College of Radiology classified
607 different mammographic density stages based on fat to parenchymal tissue content in relation to

608 the risk of developing cancer. In general, a higher proportion of parenchymal tissue compared to
609 fat is related to cancer (type 1, less than 25 % of parenchymal tissue; type 2, up to 50 %; type 3,
610 up to 75 %; type 4, more than 75 % parenchymal tissue). This classification shows that the ratio
611 between parenchymal and fat tissue can vary extremely. From these data it can be concluded,
612 first, the fat content of female SSC signals health and additionally provides women and the
613 prospective offspring with vital energy resources, and secondly, men percept properly the relative
614 size of breasts and waist-to-hip ratios in relation to the body mass index of women for their
615 judgement of women's health. But, the attractiveness of breast sizes and/or shapes does not
616 indicate necessarily a fitness marker insofar as a significant reduction of fat proportion is related
617 to less available energy resources and to increased health risk. In this context more subtle changes
618 during the cycle of other body areas, such as lipid content of skin, fat content of thighs and
619 abdomen, pigmentations, etc. are presumably not reliably detectable by men, even if they are
620 living in long-term partnerships.

621 However, as indicated in former paragraphs women do change their behavior in relation to cycle
622 phases as well. Some of these changes are obviously linked to the development of human culture.
623 During peri-ovulatory periods women advertise not only by changing their gait, but also by using
624 sheer clothes in relation to their shopping behavior and food consumption. Especially clothing
625 adapted as a tool to advertise sexual attractiveness could be culturally developed to signal
626 fertility, respectively, ovulation. The reason for such a signaling may lie in the compensation of
627 evolutionary evolved permanent sexual attractiveness in relation to non-visible ovulation in
628 humans. The mentioned temporary advertisement seems to be analogous to cyclic changes of
629 swelling or coloration expression in nonhuman primate females. Functionally, both the
630 morphological changes in nonhuman primates and the behavioral strategies in humans are caused
631 by female intra-sexual competition for valuable mates. Interestingly, neither the morphological
632 changes described in nonhuman primates nor the culturally emphasized behaviors in humans,

633 such as sheer clothes or high heels, seem to be reliable signals of fertility, ovulation or readiness
634 to mate, because prolonged swellings are expressed during non-fertile cycle periods as well the
635 use of sheer clothes . Possibly, the cultural developed use of specific clothes to enhance and
636 accentuate sexual attractive body areas in women can be judged as culture – biology co-
637 adaptation to highlight permanent attractive SSC in a better way under competing partner market
638 conditions. These issues seem to be very important during the mentioned partner selection
639 processes. In such a scenario the use of specific type of cloths during specific cycle periods allow
640 women to signale SSC temporarily and individually. Therefore, cultural adaptation on clothing
641 patterns may play a significant stratetgy in sexual advertising by women.

642 Finally due to the presented arguments, the recent study concludes, female sexual attractiveness
643 of nonhuman primates and humans are signaled by morphological flexible traits, which are not
644 per se related to signal conception probability for males. Traits such as temporal perineal
645 swellings are often expressed beyond fertile periods but may be more reliable to ovulation
646 compared to permanent visible SSC in humans. As mentioned before cultural development in
647 humans lead to wear clothes, which may be counterproductive for signaling subtle cyclic
648 morphological changes of SSC. On the other hand, clothing behavior is used to showcase the
649 expression of SSC outside and during fertile periods. Thus, specific clothes may ultimately
650 function as a tool to increase male preference for females by signaling body conscios of SSC.
651 Such a cultural behavior could be developed to underline youth, health and of course fertility
652 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

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