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### **Topography of Human Erogenous Zones**

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**Abstract** Touching is a powerful means for eliciting sexual arousal. Here, we establish the topographical organization of bodily regions triggering sexual arousal in humans. A total of 704 participants were shown images of same and opposite sex bodies and asked to color the bodily regions whose touching they or members of the opposite sex would experience as sexually arousing while masturbating or having sex with a partner. Resulting erogenous zone maps (EZMs) revealed that the whole body was sensitive to sexual touching, with erogenous hotspots consisting of genitals, breasts, and anus. The EZM area was larger while having sex with a partner versus while masturbating, and was also dependent on sexual desire and heterosexual and homosexual interest levels. We conclude that tactile stimulation of practically all bodily regions may trigger sexual arousal. Extension of the erogenous zones while having sex with a partner may reflect the role of touching in maintenance of reproductive pair bonds.

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#### Introduction

Touching is a powerful means for eliciting sexual arousal, and both affectionate caress from one's partner and self-stimulation of the genitals are capable of triggering arousal responses. Sexual arousal promotes sexual behavior via peripheral and central physiological as well as emotional and motivational mechanisms (Janssen, 2011). Although human sexual arousal may be triggered by visual and auditory cues, they are also driven by tactile stimulation of the genitals (Steers, 2000; Walen & Roth, 1987). This presumably results from initial sensory projections from the external genitalia relaying multiple sensory qualities to sensory thalamus, periaqueductal grey matter, and hypothalamic sites governing sexual functions (Dean & Lue, 2005; Hubscher & Johnson, 2003; Martin-Alguacil, Schober, Kow, & Pfaff, 2006), as well as from further interactions between these relay centers and the somatosensory cortical (S1) sites representing the genitals and the neural circuitry governing arousal and reward processing (Georgiadis et al., 2006; Georgiadis, Reinders, Paans, Renken, & Kortekaas, 2009; Komisaruk & Whipple, 2005). Consequently, genital stimulation, either by a partner or by oneself, is a common sexual behavior of humans.

Yet, paradoxically, tactile stimulation of bodily regions with no apparent connection to the genitals, such as breasts and nipples, has also been found to trigger sexual arousal (Levin & Meston, 2006; Turnbull, Lovett, Chaldecott, & Lucas, 2014) and consequently human partners also caress each other's bodies in regions outside the genitals during sexual interaction. Together with genitals, such regions are often called *erogenous zones* due to their capability of triggering sexual arousal. Even though tactile and nociceptive sensitivity of different bodily regions is well understood (Ackerley, Carlsson, Wester, Olausson, & Backlund Wasling, 2014; Mancini et al., 2014), the quantitative topographical layout as well as functions of human erogenous zones has remained unresolved. Furthermore, the functional role of the arousal-triggering properties of the non-genital areas is poorly understood. If sexual touching serves only a general arousal modulating function, touching patterns could be hypothesized to be focused on the genitals and be concordant during masturbation and while having sex with a partner because touching genitals triggers the most powerful arousal responses (Turnbull et al., 2014). However, if touching the partner's body during sexual interaction also serves functions unrelated to sexual arousal, it could be hypothesized that the touching patterns are different when having sex with a partner versus masturbating. Indeed, humans (Jones & Yarbrough, 1985; Willis & Briggs, 1992) and non-human primates use touching for maintaining social relations (Dunbar, 2010); thus, it is possible that partners having sex could extend caresses also to each others' non-genital regions to promote long-term pair bonding in addition to triggering and maintaining sexual arousal.

Furthermore, sex differences in human erogenous zones have remained underspecified and, in addition to trivial differences stemming from anatomy, the capability of tactile stimulation of different bodily regions in triggering sexual arousal in males and females is not well understood. Finally, touching a partner may trigger and maintain their sexual arousal, thus preparing the partner physically for copulation and promoting sexual behavior. Sexual compatibility with the partner contributes significantly to sexual satisfaction and motivation (Hurlbert, Apt, Hurlbert, & Pierce, 2000). On the other hand, poor communication regarding sexual matters also plays a key role in sexual dissatisfaction (Purnine & Carey, 1997) and is prevalent among couples where the female partner has orgasmic problems (Kelly, Strassberg, & Turner, 2006). It is, therefore, of

#### Table 1 Participant characteristics

interest to find out whether men's and women's perception of each other's erogenous zones correspond.

In the present study, we reveal a high-resolution spatial topography of human erogenous zones and their relation to tactile and nociceptive sensitivity using a novel computer-based self-report tool. Participants were shown nude own-sex bodies and were asked to color the regions whose touching they experience as sexually arousing when they are masturbating or having sex with a partner. This resulted in erogenous zones maps (EZMs). To tap knowledge regarding opposite sex EZMs, participants also repeated the tasks with opposite sex bodies.

#### Method

#### Participants

A total of 704 Finnish volunteers (528 females,  $M_{age} = 26$  years,  $SD_{age} = 6.5$ ; see Table 1 for details) participated in the study and completed the online questionnaires. Participants were recruited from university email lists and social media, and the study was described as an investigation on sexual touching on different bodily regions. An independent sample of 88 volunteers (24 males,  $M_{age} = 26$  years) participated in a control experiment mapping tactile and nociceptive sensitivity of different bodily regions. Participants were not compensated and none were excluded from the sample. Because methodologically comparable studies do not exist, formal a priori power analyses were not possible. Thus, the sample (targeted 700 responses) size was based on our previous related work on mapping emotional sensations in the body (Nummenmaa, Glerean, Hari, & Hietanen, 2014).

	Males $(n = 176)$		Females $(n = 528)$		<i>p</i> value
	М	SD	M	SD	
Age (years)	28.05	8.26	25.11	5.56	***
Married (%)	35.00		27.00		
Cohabiting (%)	20.00		26.00		
In relationship (%)	29.00		36.00		
Not in relationship (%)	16.00		11.00		
Exercise (h/week)	3.03	2.12	3.23	2.23	
Physical attractiveness (1-10)	6.90	1.36	6.90	1.51	
Sexual attractiveness (1-10)	6.39	1.68	6.66	1.70	
Relationship satisfaction (1-7)	3.81	2.92	4.29	2.78	*
Sexual desire (1–9)	5.53	1.35	5.16	1.39	**
Sexual activity (1–9)	4.03	1.10	3.76	1.02	**
Sell Homosexuality (1–7.5)	0.42	0.97	0.78	0.94	**
Sell Heterosexuality (1–7.5)	3.23	1.22	2.85	1.00	***

\*\*\* p < .001; \*\* p < .01; \* p < .05 in two-sample *t*-test between males and females

#### Measures

#### Background Information and Questionnaires

After providing online informed consent, participants provided background information (age, sex, education, relationship status, weight and height, and weekly hours spent on physical exercise) as well as evaluated how physically and sexually attractive they considered themselves (1-10). Female participants also reported the phase of their menstrual cycle (in days since the last menstruation began). Next, they completed the following questionnaires: Sell Assessment of Sexual Orientation (Sell, 1996), Derogatis Sexual Functioning Inventory (Derogatis, 1978), and Relationship Questionnaire (Bartholomew & Horowitz, 1991). The Sell questionnaire provides continuous, orthogonal estimates of heterosexual and homosexual drive. The Derogatis Inventory indexes actual and desired frequency of sexual behaviors, including caressing, sexual fantasies, masturbation, and oral, anal, and vaginal sex. The Relationship Questionnaire measures the perceived quality, closeness, and emotional intensity of the current intimate relationship averaged into one global score.

#### Mapping the Erogenous Zones

EZMs were acquired online with the emBODY instrument (Nummenmaa et al., 2014; http://emotion.nbe.aalto.fi/software; see also Hietanen, Glerean, Hari, & Nummenmaa, in press). In this tool (Fig. 1), participants were shown ventral and dorsal views of bodies of their own sex, and were asked to color on separate trials the regions whose touching they would find sexually arousing while having sex with a partner (whose sex was not specified) and while masturbating. To estimate correspondence between sexspecific erogenous zones and their estimated distribution by the opposite sex, participants were also shown bodies of their opposite sex and this time asked to color the regions whose touching they thought an opposite sex individual would experience as arousing while masturbating or having sex with a partner. These opposite sex EZM data were only used for correlating EZMs across sexes and when comparing the own-sex EZM area to opposite sex's estimated EZM area. All other analyses were restricted to the own-sex EZM data. Paint color was set to red to maximize visibility. Painting was dynamic; thus, successive strokes on a region increased the opacity of the paint, and the diameter of the painting tool was 12

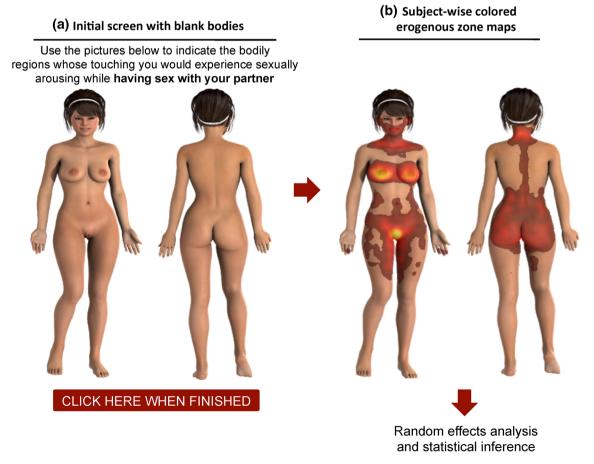


Fig. 1 Data acquisition with the emBODY tool

pixels. Erasing paint was not possible but participants could restart each trial from scratch as many times they wanted. Finished images were stored in matrices where the paint intensity ranged from 0 to 100. Male and female bodies were approximately of similar size in pixels (M = 107,321 px).

To test for the relationship between tactile, nociceptive, and sexual sensitivity of different body regions empirically, an independent sample of 88 volunteers used the emBODY tool to indicate, on separate trials, the tactile and nociceptive sensitivity of their different body regions. The resulting sex-wise mean tactile and nociceptive sensitivity maps were subsequently correlated with the condition-wise EZMs obtained in the main experiment.

#### **Statistical Analysis**

Data were screened manually for anomalous painting behavior (e.g., drawing symbols on bodies or scribbling randomly). In random effects analyses, mass univariate *t*-tests were used on the subject-wise EZMs to compare pixel-wise values for each condition against zero. This resulted in *t*-maps where pixel intensities reflect statistically significant experience of sexual arousal while touching the corresponding bodily region. Finally, False Discovery Rate (FDR) correction with an alpha level of .05 was applied to the statistical maps to control for false positives due to multiple comparisons. EZMs for masturbation versus sex with partner conditions were compared using mass univariate *t*-tests. Pearson correlation coefficients were used for comparing the similarity of male and female erogenous zones reported by male and female participants.

Total area of erogenous zones was computed as the subjectwise proportion of colored pixels; proportional rather than absolute numbers were used to control for a slightly different number of pixels in the male and the female bodies. Separate maps were computed for own-sex masturbation and sex with a partner and opposite sex masturbation and sex with a partner conditions. Subsequently, the effects of participant sex, sexual behavior, and targeted person (male versus female) were analyzed with mixed ANOVAs.

Stepwise linear regression analysis was used to predict the area of subject-wise EZMs in different conditions (masturbating self, having sex with a partner, opposite sex masturbating, and opposite sex having sex with a partner) with participants' age, BMI, marital status, physical and sexual attractiveness, relationship satisfaction, heterosexuality and homosexuality scores (from the Sell scale), as well as estimates of sexual desire and activity.

To characterize in which order participants paid attention to different erogenous zones, we first divided both the dorsal and ventral body surfaces into seven regions of interest (ROIs; Fig. S-2) and log-scaled total painting time into 24 bins. Subsequently, ROI-wise *t*-values were computed for each bin, and subjected to FDR correction.

#### Results

Participant characteristics are shown in Table 1 and correlations between the questionnaire scores in Table S-1. Mean EZMs (Fig. 2 and Video S-1) revealed that, for both males and females, erogenous hotspots were focused not only around the genitals and breasts, but also mouth, buttocks, anus, thighs, and neck were consistently reported to trigger sexually arousing sensations. Practically, the whole body was capable of triggering sexually arousing sensations when touched by a partner, with only lower legs and parts of hands being left out of the maps. Males and females also estimated the opposite sex erogenous zones accurately. Mean intersex correlations for the EZMs (Table 2) were in general high (mean r = 0.78) and responses were most consistent for ventral EZMs "with partner" condition (mean r = 0.95) and least consistent for dorsal EZMs in the masturbation condition (mean r = 0.35).

Correlating the EZMs with the tactile and nociceptive sensitivity maps (Fig. 3) revealed that erogenous zones were more strongly associated with tactile (mean r = 0.64) than with nociceptive (mean r = 0.37) sensitivity maps, p < .001. The correlation between tactile sensitivity maps and EZMs was stronger in the sex with partner condition and smaller for the masturbation condition (Fig. S-1).

The EZMs in Fig. 2 were also indicative of significant differences between masturbation and sex with partner conditions. This was confirmed by subtraction analyses for the EZMs, which revealed that, except for genitals and male anus, all bodily regions were considered to trigger stronger arousal when being touched by a partner versus the participants themselves (Fig. 4).

Analysis of the total EZM area qualified how the total area of erogenous zones was dependent on both participant sex and touch type (Fig. 5). A 2 (Participant sex: male, female)  $\times$  2 (Touch type: masturbation, sex with partner)  $\times 2$  (Target person: female versus male) mixed ANOVA revealed that EZM area was larger when having sex with a partner than when masturbating F(1, 702) = $659.62, p < .001, \eta_p^2 = 0.48$ , and EZM area was also evaluated larger for females versus males, F(1, 702) = 167.89, p < .001,  $\eta_p^2 = 0.10$ . On average, 26% of the female and 22% of male body area were capable of triggering arousal when touched by a partner, whereas corresponding percentages were 6.3 and 4.3 % when masturbating (all ps < .001 for between-conditions comparisons). Moreover, males estimated EZM areas to be larger than females (mean difference 2.64 %), F(1, 702) = 5.84 p = .02,  $\eta_p^2 = 0.008$ . Finally, a threeway interaction between participant sex, sexual behavior, and target person,  $F(1, 702) = 16.36, p < .001, \eta_p^2 = 0.023$ , revealed that males overestimated the female EZM area in the masturbation condition

<sup>&</sup>lt;sup>1</sup> A trivial explanation for these results is that while masturbating an individual cannot touch all of their back. However, the overall pattern of results remains essentially unchanged even when only the ventral surface of the body is considered.

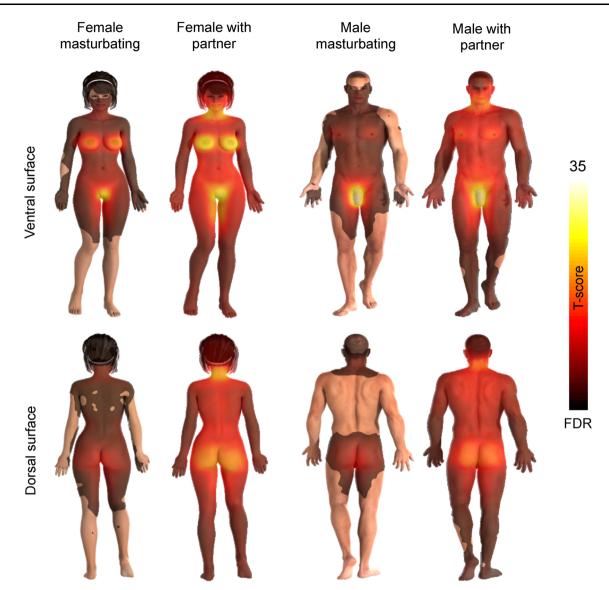


Fig. 2 Maps of human erogenous zones during masturbation and sex with a partner. The data are thresholded at p < .05, FDR corrected. The *color bar* indicates the *t*-statistic range in one sample test

 Table 2
 Pearson correlations between EZMs estimated by male and female participants

Condition	r
Female ventral with partner	0.95
Female dorsal with partner	0.95
Male ventral with partner	0.92
Male dorsal with partner	0.91
Female ventral masturbation	0.85
Male ventral masturbation	0.78
Female dorsal masturbation	0.59
Male dorsal masturbation	0.35

The correlations represent the pixel-wise similarities between averaged, condition-wise EZMs for male and female participants. All shown correlations are significant at p < .05

(p < .05 Bonferroni corrected), whereas male and female estimates of EZM area did not differ in other conditions.

Linear regression analysis (Table 3) revealed that sexual desire, homosexual interest, and heterosexual interest were the strongest predictors of the total EZM area, being significant for both masturbation and sex with a partner conditions. The frequency of sexual activity was negatively associated with EZM area in the masturbation condition. However, the EZM area was insensitive to demographic factors, including age, marital status, and education. Separate analysis restricted to the female sample found no effects of menstrual cycle phase on the EZM area.

Finally, a time series analysis (Fig. S-2) confirmed that across all conditions, participants first attended to the genitals, ventral surface chest, neck, and legs. Other regions were attended to substantially later, yet they nevertheless received attention earlier in

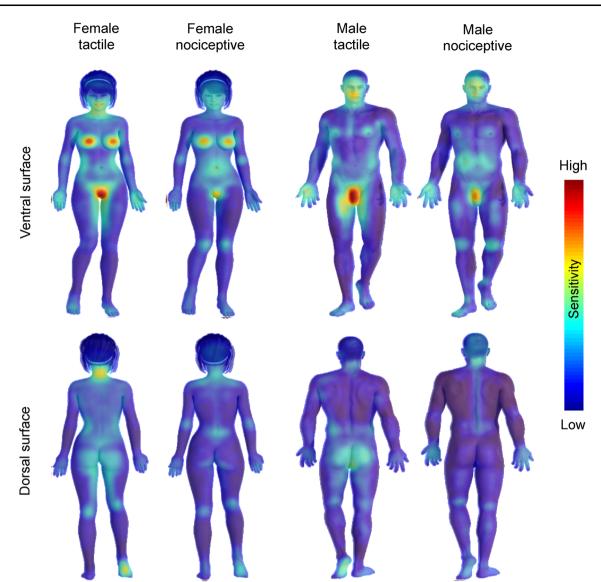


Fig. 3 Mean tactile and nociceptive sensitivity maps for males and females. The data are shown on an arbitrary scale [0, 1] and are square root transformed to better visualize regional variation in the lower tail of the distribution

the sex with a partner versus masturbation condition. Early preference toward genitals was profound in males, whereas females attended to non-genital areas earlier than males.

#### Discussion

Our findings reveal for the first time the sex- and sexual behaviorspecific topographical organization of erogenous zones in humans. We show that the whole skin serves as a somatosensory sexual organ for both males and females, particularly when having sex with a partner. Although the erogenous hotspots were located on core erogenous zones in the genitals, erogenous zones extended to practically everywhere in the body forming a set of extended erogenous regions with second-highest arousal-triggering capability in the breasts and nipples, anus, buttocks, and inner thighs. The total bodily area triggering sexual arousal was significantly smaller during masturbation versus having sex with a partner. Taken together, these findings highlight the importance of tactile sensation of nongenital areas in sexual arousal modulation and suggest that the core and extended erogenous zones may serve different functions in sexual behavior and arousal modulation.

## Maps of Core and Extended Erogenous Zones in Men and Women

Our main finding was that touching practically all areas covered by skin in the body may trigger sexual arousal when touched by partner, with an average of 24 % of the total area body area being capable for triggering sexual arousal upon touch. Males and

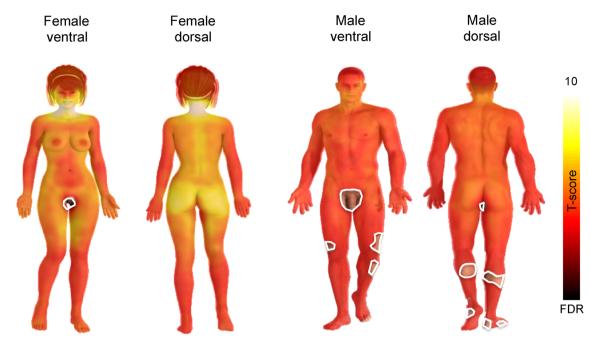
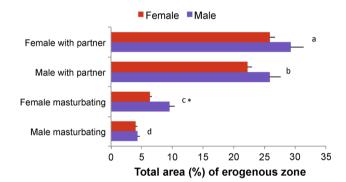


Fig. 4 Subtraction contrasts for the erogenous zones in the partner versus masturbation condition. *White outline* shows regions where the opposite contrast (masturbation vs partner) was significant. The data are



**Fig. 5** Effects of participant sex and touch type (masturbation vs sex with partner) on the total area of erogenous zones in the male and female body averaged across ventral and dorsal surfaces. *Error bars* show standard errors of mean. Touching conditions with *different letters* are significantly different at p < .05, and *asterisks* denote conditions with significant sex differences at p < .05. All multiple comparisons are Bonferroni corrected

females also evaluated each others' EZMs similarly (mean r = 0.79). The total area of erogenous zones was larger in females versus males, indicative of heightened tactile sensitivity to sexual touch. This accords with prior work using vibrotactile (Gescheider, Bolanowski, Hall, Hoffman, & Verrillo, 1994) and nociceptive stimulation (Fillingim & Maixner, 1995), which point toward higher sensitivity in females versus males.

The erogenous hotspots being most consistently associated with sexual arousal and also attended first were focused on genitals. Significant EZM peaks were not only observed in chest, neck, buttocks, anus, and mouth area (see Video S-1 for dynamically thresholded

thresholded at p < .05, FDR corrected. The *color bar* indicates the *t*-statistic range in a paired samples test

t-maps) but also in some other regions such as back, thigh, and shin that have low pain and tactile sensitivity (Ackerley et al., 2014; Mancini et al., 2014). However, correlating EZMs with tactile and nociceptive sensitivity maps highlighted that a region's capability for triggering sexual arousal upon touching was primarily—but not completely—determined by its tactile sensitivity, and that tactile sensitivity across the whole body is exploited only when having sex with a partner.<sup>2</sup>

Nevertheless, the EZMs bore little resemblance to the somatosensory organization of the body in somatosensory cortices (Penfield & Boldrey, 1937; Ruben et al., 2001), with regions whose representation is close to genitals in the S1 not being significantly more prone to trigger sexual arousal than those further apart. Thus, it is unlikely that partial activation of the S1 representation of the genitals by stimulation to adjacent areas would be driving the arousal response (see also Turnbull et al., 2014). However, more complete understanding of the somatotopic organization of male and female genitals and erogenous zones in S1 and SII is needed to understand the role of extragenital regions in triggering sexual arousal.

The EZMs were invariant to demographic factors such as age and education. However, sexual desire as well as homosexual and heterosexual interest emerged as consistent predictors for the total EZM area while masturbating or having sex with a partner,

 $<sup>^2</sup>$  These maps reflect participants' evaluation of tactile and nociceptive sensitivity, rather than true sensory thresholds. However, the maps shown in Fig. 4 agree in general well with prior studies using sparse spatial sampling of tactile sensitivity (Ackerley, Carlsson, Wester, Olausson, & Backlund Wasling, 2014; Mancini et al., 2014).

	F	$R^2$	Sexual desire	Sell HMSX	Sell HESX	Sexual activity
Masturbating	14.59***	8 %	0.11**	0.24***	0.10*	-0.13**
Sex with partner	19.01***	8 %	0.12**	0.20***	0.10*	

**Table 3** Model fits, coefficients of determination (in %), and betas for variables predicting total area (%) of erogenous zones while masturbating and having sex with a partner

\*\*\*p < .001; \*\*p < .01, \*p < .05

suggesting a direct link between sexual drive and the size of the sexually receptive field of the body. These effects accord with the general proposal that sexual attraction toward both same and opposite sex partners is associated with sex drive (Lippa, 2006).

### Sexual and Social Functions of the Extended Erogenous Zones

Although the EZMs for the masturbation condition covered practically all of the body except lower legs, touching was considered as sexually arousing in significantly larger areas while having sex with a partner rather than masturbating (Fig. 4). The only regions more consistently triggering sexual arousal by self-stimulation versus stimulation by partner were the genitals and male anus (but see Schober, Meyer-Bahlburg, & Dolezal, 2009 for opposite findings). Masturbation occurs frequently in both human and nonhuman primates even when opportunities for copulation exist (Ford & Beach, 1951; Oliver & Hyde, 1993) and male masturbation (leading to ejaculation and wasting of sperm) across a variety of species has been proposed to increase sperm fit without increasing the number of sperm in the female tract (Baker & Bellis, 1993). Against this background, different goals of masturbation versus having sex with the partner could explain this difference: Stimulation of the sexually most sensitive regions during masturbation would be an effective way of obtaining sexual release, as no excess energy is wasted on stimulating the sexually less sensitive regions. This however raises the question why the-seemingly less sexually sensitive-areas outside genitals are stimulated during sex with a partner.

The reason for the lack of self-produced tactile stimulation outside the genitals could be that sensation of self-produced touch is simply attenuated. A forward model incorporating motor actions predicts their sensory consequences and leads to sensory attenuation of self-produced tactile stimulation in the somatosensory and insular cortices (see review in Blakemore, Wolpert, & Frith, 2000). Such attenuation may tone down the arousal responses triggered by self-touch, consequently lowering the incentive motivation for extragenital touching during masturbation. While such attenuation for self-stimulation seems to occur almost everywhere in the body, it was markedly absent in the genital region and participants consistently reported higher arousal ratings for touch on genitals in the masturbation versus sex with partner condition. Different forward model attenuation patterns across SI regions representing the genitals versus other bodily regions could explain the heightened sensitivity for self-touching on the genitals, in order to enable self-stimulation potentially increasing reproductive fit (Baker & Bellis, 1993).

However, the forward model attenuation does not explain why humans experience sexual arousal when their partners touch less sexually sensitive bodily regions while having sex together. From the perspective of energy expenditure, it would be beneficial to restrict mutual touching to the genital regions while having sex with a partner as well. A possible explanation is that stimulating these areas by touching promotes non-sexual aspects of partnership, such as pair bonding. Abundant evidence suggests that both humans (Jones & Yarbrough, 1985; Suvilehto, Glerean, Dunbar, Hari, & Nummenmaa, 2015; Willis & Briggs, 1992) and non-human primates use social touching or grooming for reinforcing social structures (Dunbar, 2010). Translational work shows that slow stroking of the hairy (but not glabrous) skin stimulates the slow-conducting unmyelinated c-tactile fibers (CTF), subsequently projecting insular (but not somatosensory) cortices and possibly providing the sensory pathway for emotional and affiliative touching (Loken, Wessberg, Morrison, McGlone, & Olausson, 2009; Olausson et al., 2002). Affiliative touching and stimulation of the CTF may support maintenance and establishment of long-term relationships in humans as well (Dunbar, 2010). In line with this, intimate touching is typically restricted to the closest relationships only (Jones & Yarbrough, 1985; Suvilehto et al., 2015; Willis & Briggs, 1992), and quality and quantity of social touching is positively associated with relationship satisfaction in couples (Hertenstein, Verkamp, Kerestes, & Holmes, 2006). Because c-tactile receptors have not been found in genitalia, it is unlikely this pathway plays a role in triggering of sexual arousal (Liu et al., 2007). We thus propose that touching non-genital regions during sexual interaction with a partner could serve a double function: stimulating the fast-conducting myelinated afferents projecting to S1 and via interaction with thalamic arousal circuits serves to trigger sexual arousal, whereas simultaneous stimulation of the slow-conducting CTFs could promote affiliation and long-term pair bonding between the partners.

#### **Potential Limitations and Future Directions**

It must be noted that our study was based on self-reports; hence, the data may not directly translate to different bodily regions' capabilities in triggering physiological sexual arousal when touched. However, given the consistent association between self-reported and physiologically measured emotional (Lang, 1995) and sexual arousal (Chivers, Seto, Lalumiere, Laan, & Grimbos, 2010), it is feasible to assume that the findings reflect physiological sexual arousal

reasonably accurately. The study participants were recruited from Finland. Even though the biologically based sexual sensitivity of different bodily regions is likely culturally universal, in future, it will be interesting to address what kinds of sexual response-specific plasticity the tactile systems may exhibit in different cultures and sexual preferences. Finally, future studies need to disentangle the sexual sensitivity of specific parts of the genitalia (such as vulva versus clitoris), as this was beyond the spatial resolution of the current study.

#### Conclusions

We conclude that the whole human body supports triggering of sexual arousal by somatosensory stimulation. There is a clear topographical organization of the core and extended zones with differential arousal-triggering capabilities. The core regions show high sensitivity to self-touch during masturbation as well as to external touching while having sex with a partner, yet the extended regions are selectively sensitive to externally produced stimulation. We propose that this selectivity of the extended erogenous zone reflects its role in establishment and maintenance of pair bonds, highlighting the role of somatosensory system and sexual behavior in human social interaction.

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#### **Compliance with Ethical Standards**

Conflict of interest The authors declare no competing financial interests.

#### References

- Ackerley, R., Carlsson, I., Wester, H., Olausson, H., & Backlund Wasling, H. (2014). Touch perceptions across skin sites: Differences between sensitivity, direction discrimination and pleasantness. *Frontiers in Behavioral Neuroscience*, 8, 54. doi:10.3389/fnbeh.2014.00054.
- Baker, R. R., & Bellis, M. A. (1993). Human sperm competition–ejaculate adjustment by males and the function of masturbation. *Animal Behaviour*, 46, 861–885.
- Bartholomew, K., & Horowitz, L. M. (1991). Attachment styles among young adults—A test of a 4-category model. *Journal of Personality and Social Psychology*, 61, 226–244.
- Blakemore, S. J., Wolpert, D., & Frith, C. (2000). Why can't you tickle yourself? *NeuroReport*, 11, R11–R16.
- Chivers, M. L., Seto, M. C., Lalumiere, M. L., Laan, E., & Grimbos, T. (2010). Agreement of self-reported and genital measures of sexual arousal in men and women: A meta-analysis. *Archives of Sexual Behavior*, 39, 5–56.
- Dean, R. C., & Lue, T. F. (2005). Physiology of penile erection and pathophysiology of erectile dysfunction. Urologic Clinics of North America, 32, 379–395.
- Derogatis, L. R. (1978). The DSFI: A multidimensional measure of sexual functioning. *Journal of Sex & Marital Therapy*, 5, 244–281.
- Dunbar, R. I. M. (2010). The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. *Neuroscience* and Biobehavioral Reviews, 34, 260–268.
- Fillingim, R. B., & Maixner, W. (1995). Gender differences in the responses to noxious stimuli. *Pain Forum*, 4, 209–221.

- Ford, C. S., & Beach, F. A. (1951). Patterns of sexual behavior. New York: Harper & Brothers.
- Georgiadis, J. R., Kortekaas, R., Kuipers, R., Nieuwenburg, A., Pruim, J., Reinders, A. A., & Holstege, G. (2006). Regional cerebral blood flow changes associated with clitorally induced orgasm in healthy women. *European Journal of Neuroscience*, 24, 3305–3316.
- Georgiadis, J. R., Reinders, A., Paans, A. M. J., Renken, R., & Kortekaas, R. (2009). Men versus women on sexual brain function: Prominent differences during tactile genital stimulation, but not during orgasm. *Human Brain Mapping*, 30, 3089–3101.
- Gescheider, G. A., Bolanowski, S. J., Hall, K. L., Hoffman, K. E., & Verrillo, R. T. (1994). The effects of aging on information-processing channels in the sense of touch 1. Absolute sensitivity. *Somatosensory and Motor Research*, 11, 345–357.
- Hertenstein, M. J., Verkamp, J. M., Kerestes, A. M., & Holmes, R. M. (2006). The communicative functions of touch in humans, nonhuman primates, and rats: A review and synthesis of the empirical research. *Genetic*, *Social, and General Psychology Monographs*, 132, 5–94.
- Hietanen, J. K., Glerean, E., Hari, R., & Nummenmaa, L. (in press). Bodily maps of emotions across child development. *Developmental Science*. doi:10.1111/desc.12389.
- Hubscher, C. H., & Johnson, R. D. (2003). Responses of thalamic neurons to input from the male genitalia. *Journal of Neurophysiology*, 89, 2–11.
- Hurlbert, D. F., Apt, C., Hurlbert, M. K., & Pierce, A. P. (2000). Sexual compatibility and the sexual desire-motivation relation in females with hypoactive sexual desire disorder. *Behavior Modification*, 24, 325–347.
- Janssen, E. (2011). Sexual arousal in men: A review and conceptual analysis. Hormones and Behavior, 59, 708–716.
- Jones, S. E., & Yarbrough, A. E. (1985). A naturalistic study of the meanings of touch. *Communication Monographs*, 52, 19–56.
- Kelly, M. P., Strassberg, D. S., & Turner, C. M. (2006). Behavioral assessment of couples' communication in female orgasmic disorder. *Journal* of Sex and Marital Therapy, 32, 81–95.
- Komisaruk, B. R., & Whipple, B. (2005). Functional MRI of the brain during orgasm in women. Annual Review of Sex Research, 16, 62–86.
- Lang, P. J. (1995). The emotion probe: Studies of motivation and attention. *American Psychologist*, 50, 372–385.
- Levin, R., & Meston, C. (2006). Nipple/breast stimulation and sexual arousal in young men and women. *Journal of Sexual Medicine*, 3, 450–454.
- Lippa, R. A. (2006). Is high sex drive associated with increased sexual attraction to both sexes? It depends on whether you are male or female. *Psychological Science*, 17, 46–52.
- Liu, Q., Vrontou, S., Rice, F. L., Zylka, M. J., Dong, X., & Anderson, D. J. (2007). Molecular genetic visualization of a rare subset of unmyelinated sensory neurons that may detect gentle touch. *Nature Neuroscience*, 10, 946–948.
- Loken, L. S., Wessberg, J., Morrison, I., McGlone, F., & Olausson, H. (2009). Coding of pleasant touch by unmyelinated afferents in humans. *Nature Neuroscience*, 12, 547–548.
- Mancini, F., Bauleo, A., Cole, J., Lui, F., Porro, C. A., Haggard, P., & Iannetti, G. D. (2014). Whole-body mapping of spatial acuity for pain and touch. *Annals of Neurology*, 75, 917–924.
- Martin-Alguacil, N., Schober, J., Kow, L.-M., & Pfaff, D. (2006). Arousing properties of the vulvar epithelium. *Journal of Urology*, 176, 456–462.
- Nummenmaa, L., Glerean, E., Hari, R., & Hietanen, J. K. (2014). Bodily maps of emotions. Proceedings of the National Academy of Sciences of the United States of America, 111, 646–651.
- Olausson, H., Lamarre, Y., Backlund, H., Morin, C., Wallin, B. G., Starck, G., & Bushnell, M. C. (2002). Unmyelinated tactile afferents signal touch and project to insular cortex. *Nature Neuroscience*, 5, 900–904.
- Oliver, M. B., & Hyde, J. S. (1993). Gender differences in sexuality: A metaanalysis. *Psychological Bulletin*, 114, 29–51.
- Penfield, W., & Boldrey, E. (1937). Somatic motor and sensory representation in the cerebral cortex of man as studied by electrical stimulation. *Brain*, 60, 389–443.

- Purnine, D. M., & Carey, M. P. (1997). Interpersonal communication and sexual adjustment: The roles of understanding and agreement. *Journal* of Consulting and Clinical Psychology, 65, 1017–1025.
- Ruben, J., Schwiemann, J., Deuchert, M., Meyer, R., Krause, T., Curio, G., ... Villringer, A. (2001). Somatotopic organization of human secondary somatosensory cortex. *Cerebral Cortex*, 11, 463–473.
- Schober, J. M., Meyer-Bahlburg, H. F. L., & Dolezal, C. (2009). Self-ratings of genital anatomy, sexual sensitivity and function in men using the Self-Assessment of Genital Anatomy and Sexual Function, Male questionnaire. *BJU International*, 103, 1096–1103.
- Sell, R. L. (1996). The Sell assessment of sexual orientation: Background and scoring. *Journal of Gay, Lesbian, and Bisexual Identity*, 1, 295–310.
- Steers, W. D. (2000). Neural pathways and central sites involved in penile erection neuroanatomy and clinical implications. *Neuroscience and Biobehavioral Reviews*, 24, 507–516.

- Suvilehto, J., Glerean, E., Dunbar, R. I. M., Hari, R., & Nummenmaa, L. (2015). Topography of social touching depends on emotional bonds between humans. *Proceedings of the National Academy of Sciences of the United States of America*, 112, 13811–13816.
- Turnbull, O. H., Lovett, V. E., Chaldecott, J., & Lucas, M. D. (2014). Reports of intimate touch: Erogenous zones and somatosensory cortical organization. *Cortex*, 53, 146–154.
- Walen, S. R., & Roth, D. (1987). A cognitive approach. In J. H. Geer & W. T. O'Donohue (Eds.), *Theories of human sexuality* (pp. 335–362). New York: Plenum Press.
- Willis, F, Jr, & Briggs, L. (1992). Relationship and touch in public settings. Journal of Nonverbal Behavior, 16, 55–63.