Topography of social touching depends on emotional bonds between humans

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Nonhuman primates use social touch for maintenance and reinforcement of social structures, yet the role of social touch in human bonding in different reproductive, affiliative, and kinship-based relationships remains unresolved. Here we reveal quantified, relationship-specific maps of bodily regions where social touch is allowed in a large cross-cultural dataset (N = 1,368 from Finland, France, Italy, Russia, and the United Kingdom). Participants were shown front and back silhouettes of human bodies with a word denoting one member of their social network. They were asked to color, on separate trials, the bodily regions where each individual in their social network would be allowed to touch them. Across all tested cultures, the total bodily area where touching was allowed was linearly dependent (mean r^2 = 0.54) on the emotional bond with the toucher, but independent of when that person was last encountered. Close acquaintances and family members were touched for more reasons than less familiar individuals. The bodily area others are allowed to touch thus represented, in a parametric fashion, the strength of the relationship-specific emotional bond. We propose that the spatial patterns of human social touch reflect an important mechanism supporting the maintenance of social bonds.

touch | social networks | grooming | bonding | emotion

The time primates devote to grooming each other far exceeds the requirements of hygiene. Kinship and the power dynamics of the group determine the amount of grooming devoted to different individuals (1), and grooming relationships are fairly stable over time, predicting aid in times of stress (2). Because such allogrooming follows relationship-specific patterns, it likely serves social functions, such as establishment and maintenance of complex social structures (2) and reduction of tension between individuals (3, 4).

Human social bonds are characterized by mutual positive emotions, such as trust and affection between the dyad, that maintain the individuals' proximity to significant others and modulate interpersonal behavior (5, 6). It is possible that social touch could help maintain the multitude of emotional bonds humans have in all areas of life, ranging from intimate romantic bonds to kinship and friendships. Postnatal skin-to-skin contact indeed promotes mother–infant bonding, and the quantity and quality of social touch are positively associated with relationship satisfaction in adult romantic couples (7). Touching also facilitates confiding via speech (8), and even a brief touch can lead to more positive evaluations of the toucher (9, 10), increased compliance (11), and prosocial behavior, such as more generous tipping in restaurants (12). Behavioral evidence further suggests that human social touch is particularly dependent on the emotional bond between the parties (13): The bodily regions where one may touch different individuals in their social network are relationship-specific (14), with hands and arms being routinely touched by even emotionally distant acquaintances, whereas touching the head, neck, and buttocks is typically restricted to emotionally closer relationships (13, 14).

Altogether, the human and monkey data thus suggest that relationship-specific spatial patterns of social touch are intimately related to the establishment and maintenance of social structures and affective relationships among human adults. As the degree of social touching varies across cultures (15, 16), it however remains unclear whether the relationship between social touch and interpersonal emotional bonds mainly reflects biologically driven bonding or culture-based normative behavior. Here we reveal relationship-specific social touching patterns in humans in a large multicultural sample of 1,368 individuals. We focused on the association between social touching and interpersonal emotional bonds, because such bonds are the best predictors for engaging in social contact with someone and consequently tell the positions of different individuals in one's social network (17).

We first explored the reasons for social touching across different social relationships (experiment 1). We then (in experiments 2 and 3) used a high-resolution self-reporting tool [emBODY (18); *SI Appendix*, Fig. S1] to quantify relationship-specific maps of bodily regions where social touch is allowed. Participants also evaluated how pleasant they would find the touch by different social network members, and they reported when they had last seen each network member. We show that the total bodily area allowed for touching is linearly dependent on the emotional bond with the toucher across a wide range of European cultures (Finland, France, Italy, Russia, and the United Kingdom), with the strength of two individuals' social bond predicting, on average, 54% of the variance in spatial touching patterns.

Significance

Touch is a powerful tool for communicating positive emotions. However, it has remained unknown to what extent social touch would maintain and establish social bonds. We asked a total of 1,368 people from five countries to reveal, using an Internet-based topographical self-reporting tool, those parts of their body that they would allow relatives, friends, and strangers to touch. These body regions formed relationship-specific maps in which the total area was directly related to the strength of the emotional bond between the participant and the touching person. Cultural influences were minor. We suggest that these relation-specific bodily patterns of social touch constitute an important mechanism supporting the maintenance of human social bonds.

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Results

Experiment 1. The subjects had, on average, 14 of the 15 candidate members (SD = 1.9) in their social network. The number of reasons for touching an individual was positively associated with the emotional bonds with them, with emotionally closest individuals being touched for the most reasons (mean $r = 0.81$; $P < 0.01$). Likelihood of touching individuals for different reasons varied (*SI Appendix*, Fig. S2): negative forms of touch (punishing, hurting, scaring) were rare, whereas greeting was the most frequent reason for touching (*SI Appendix*, Table S1). Additionally, frequency of different touch types was relationship-dependent ($\chi^2 \geq 34.72$, $P < 0.05$) for all other reasons expect for ritualistic (greeting and parting) and negative (punishing, hurting, and scaring) touching.

Experiment 2. Participants were shown front and back silhouettes of human bodies with a word denoting one member of their social network. They were asked to color, on separate trials, the bodily regions where each individual in their social network would be allowed to touch them. These subjectwise maps were averaged across subjects to obtain relationship-specific touch-area maps (TAMs; *SI Appendix*, Fig. S1).

TAMs for different social network members were clearly separable. The partner was allowed to touch basically anywhere over the body, closest acquaintances and relatives over the head and upper torso, whereas strangers were restricted to touch only the hands. Taboo zones, where touching was not allowed, included the genitals for extended family and males in family, acquaintances, and strangers, as well as the buttocks for males in extended family, acquaintances, and strangers (Fig. 1). Statistical analysis confirmed the relationship specificity of the TAMs. Both social network layer and strength of emotional bond predicted statistically significantly the "touchability" of head, torso, legs, and feet (Fig. 2); no effects were observed at hands. In general, TAMs were consistent across male and female participants (*SI Appendix*, Fig. S3). The time lapse since last meeting someone was negatively correlated with touchability of most body regions, with a negligible but statistically significant average correlation coefficient ($r = -0.08$). *SI Appendix*, Fig. S4, shows lapse data and emotional-bond ratings for different social-network members.

We next defined touchability index (TI) as the total number of pixels in the body that each candidate individual was allowed to touch the participants. Linear regression analysis revealed that the TI depended linearly on the emotional bond with social-network members across all tested countries (mean $r^2 = 0.54$; Fig. 3). Regression coefficients were also remarkably similar across countries ($P > 0.05$ for differences between β values). However, the mean TI (i.e., the constant term of the regression line) varied across cultures, with the United Kingdom reaching a TI of 0 (no touch allowed) already at emotional bond level of 2, whereas the corresponding value for Finland, France, Italy, and Russia was 0–0.5. Somewhat surprisingly to the Finnish and Italian authors of the present study, Finland had larger TIs than Italy ($P < 0.01$ in Bonferroni-corrected two-sample t tests). Associations between TI and social bond did not depend on subjects' age: $F = 0.09$, $P = 0.77$, $R^2 = 6.46^{-5}$. When data from all five tested countries were analyzed together, the pleasantness of touch also correlated positively with the TI ($r = 0.66$; *SI Appendix*, Table S2). Emotional bond and pleasantness of touch also correlated with each other ($r = 0.77$). However, lapse since last meeting someone was only weakly correlated with TI, bond, or experienced pleasantness of touch.

The association between TI and emotional bond was even stronger in data collapsed over all individuals with similar-strength emotional bonds (i.e., instead of treating different factual network members separately), with the average strength of emotional bond explaining 92% of TI variance across cultures (*SI Appendix*, Fig. S5).

We next ran k-means clustering ($k = 6$) on the TAM data to test whether relationship-dependent touching patterns would similarly depend on the six different a priori layers (family, family of origin, extended family, friends, acquaintances, strangers) of the social network across countries. The six-cluster solution fit the data ($F = 142.2$; $P \approx 10^{-35}$) and corresponded with the a priori social network layers: Social network members from the same layer were generally clustered together across countries, despite some cross-cultural variation (*SI Appendix*, Table S3). As a complementary approach, we calculated Spearman correlation matrix for the TAMs of the whole dataset, as well as separately for each country. When averaged across countries, the TAM-based social network structure

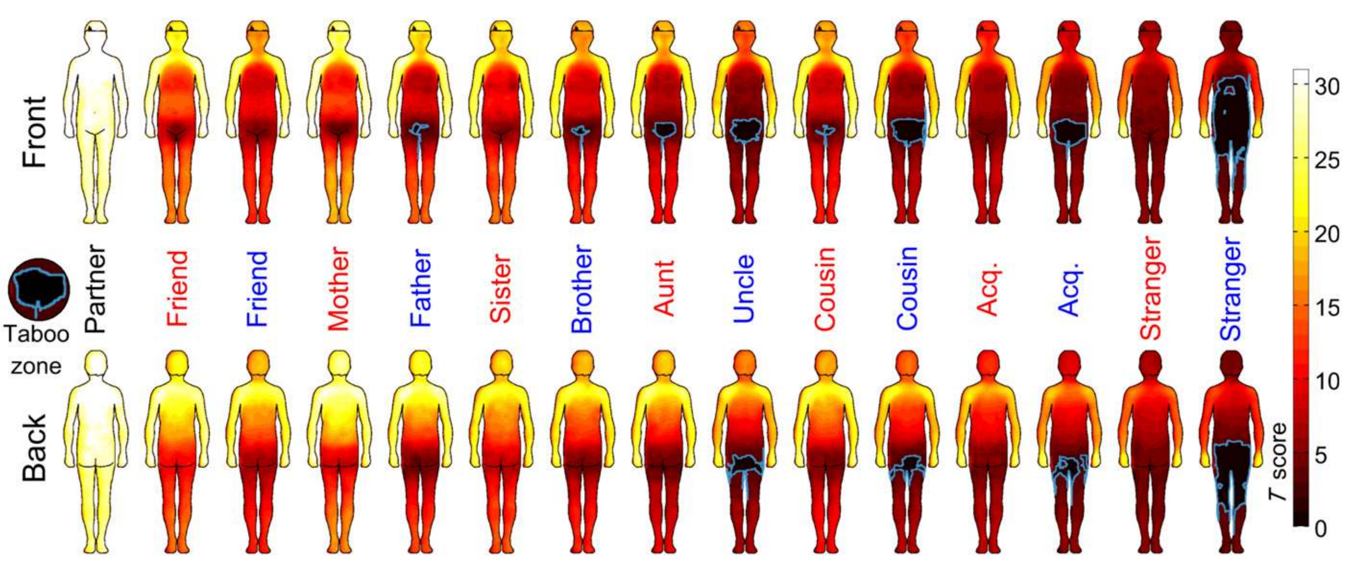

Fig. 1. Relationship-specific TAMs across all studied countries ($N = 1,368$ individuals). The blue-outlined black areas highlight the taboo zones, where a person with that relationship is not allowed to touch. The data are thresholded at $P < 0.05$, FDR-corrected. Color bar indicates the t statistic range. Blue and red labels signify male and female subjects, respectively.

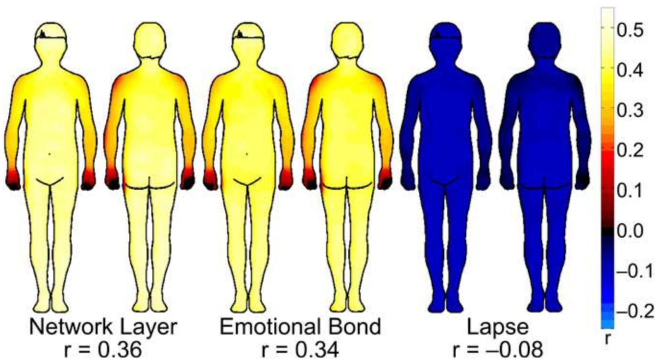

Fig. 2. Associations between touchability and social network layer (*Left*), emotional bond (*Middle*), and lapse since last meeting a person (*Right*). The data are thresholded at $P < 0.05$, FDR corrected. Color bar indicates the r statistic range.

(*SI Appendix*, Fig. S6) accorded with the a priori organization of the social network layers (Mantel correlation statistic with hypothesized network structure $r = 0.45$; $P \approx 10^{-7}$). The same result was obtained when similarity matrices were analyzed separately for each culture (Mantel correlation statistic ≥ 0.3; $P < 0.01$). The TAM-based social network structures (i.e., similarities in touching patterns) were also concordant across cultures (*SI Appendix*, Table S4; Spearman $r \geq 0.79$; $P \sim 10^{-40}$).

Finally, the sex of the participant and the toucher significantly influenced the TIs (Fig. 4). When considering social network members having the same type of social relationship with the participant (e.g., sister vs. brother), females were allowed to touch wider body areas than males. The sex-related TI differences were significant for all male–female pairs of the social network ($P < 0.05$, t test). Accordingly, participants also reported stronger emotional bonds with female than male members of their social networks (*SI Appendix*, Table S5). Moreover, female subjects reported, on average, higher TIs across all members of their social network than males did, with the exception of female acquaintances and female strangers.

Experiment 3. Relationship-dependent variability map of touching allowances (TAMs) correlated significantly ($P < 0.01$) with hedonic ($r = 0.45$), tactile ($r = 0.38$), and nociceptive ($r = 0.21$) sensitivity maps with significantly larger correlation for hedonic vs. tactile or nociceptive sensitivity maps ($P < 0.05$, Fisher test; Fig. 5).

Discussion

In what is, to our knowledge, the largest quantified study on the allowance of social touch on bodily regions, we reveal that interpersonal emotional bonds are associated with spatial patterns for social touch in a culturally universal manner across a broad range of European countries with varying cultural conventions. As expected, emotionally closer individuals in inner layers of the social network were allowed to touch wider bodily areas and for more reasons, whereas touching by strangers was primarily limited to the hands and upper torso. Genitals and buttocks formed clear "taboo zones" that only the emotionally closest individuals were allowed to touch. Frequency of social contact with an individual did not predict the area available for social touch, confirming that the experienced bond between the individuals, rather than mere familiarity, modulates social touching behavior in dyads.

Touch as Means for Social Bonding. Relationship-specific TIs depended linearly on the emotional bond with different individuals in the participants' social networks. Paralleling these findings, we found that social touch was linearly associated with more positive emotional sensations in closer relationships. These effects were observed across a wide range of relationships ranging from romantic partners to distant acquaintances, but they were independent of subjects' age. This result suggests that touch is used for modulating complex large-scale social networks and not only potentially reproductive relationships. Furthermore, the results indicate that the spatial distributions of social touching do not reflect mere categorical structure of an individual's social

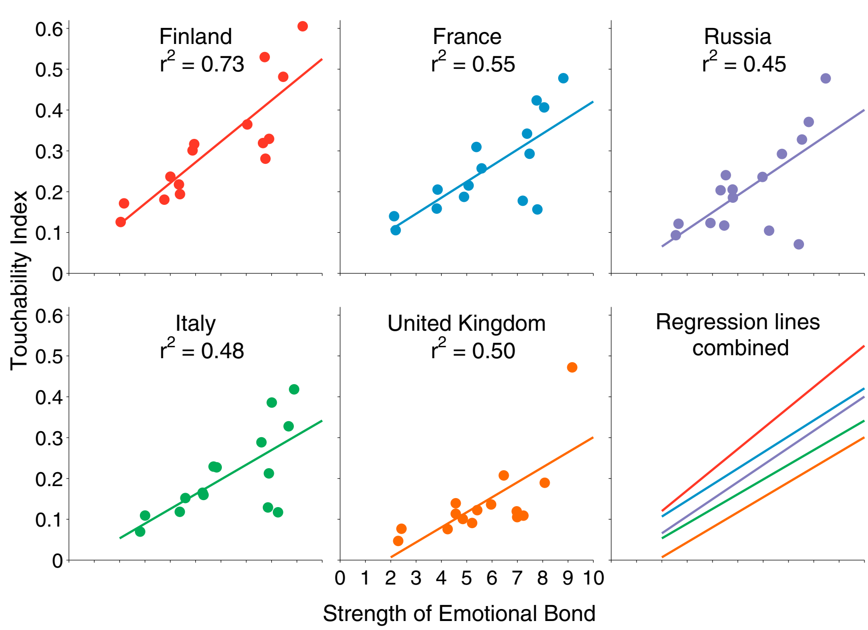

Fig. 3. Least-squares regression lines for TI as a function of emotional bond in the five countries. Data points are averages of each dyadic relationship, i.e., each point denotes one person in the social network of all participants from that country. The final panel shows the countrywise regression lines together to facilitate comparisons.

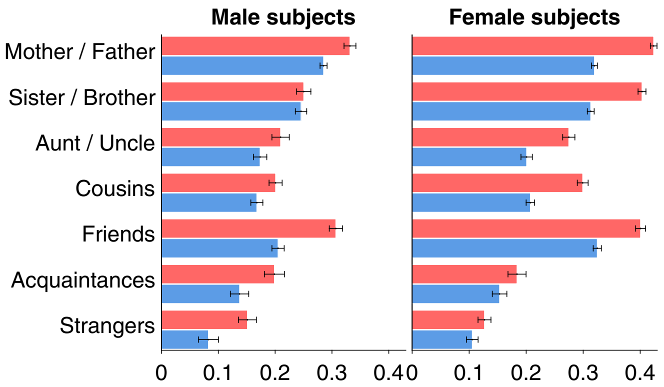

Fig. 4. Sex differences of TI for male (*Left*) and female (*Right*) subjects. Red and blue bars indicate female and male touchers, respectively.

network; rather, they represent the strength of the relationship-specific emotional bonds in a parametric fashion.

Our data from human subjects corroborate work done in non-human primates (2), indicating that relationship-specific social touch is closely related to the maintenance and establishment of social bonds also in humans. Skin is the largest organ and the clearest border between individuals and the world. Already 19-wk-old fetuses touch themselves and anticipate self-oriented touches (19). Skin-to-skin contact is also one of the earliest communication channels promoting attachment between the infant and the caregiver (7). Recent work has revealed a special class of unmyelinated C-tactile afferents that respond selectively to slow pleasurable stroking. Stimulating these fibers activates insular cortex and possibly provides the sensory pathway for emotional and affiliative touching (20, 21). Our results imply that this kind of social touch is interpreted in context-dependent fashion depending on the interaction partner. Such social coding of touch seems to occur at early processing stages in the brain, as recent neuroimaging work has established that the human primary somatosensory cortex is involved in discriminating between interpersonal (22) and physical (23) aspects of social touch.

If variations in social touch would be closely related to the maintenance of social bonds, touching behavior toward an individual should be adaptive while the relationship with a specific individual develops. Even though cross-sectional, the present data provide indirect support for this claim: The participants' partners, generally associated with the largest TIs, have, at some point of the relationship, been strangers (whose TIs are, on average, the lowest) to the participants. The present correlational data cannot, however, be used to infer whether increased social touching leads to stronger emotional bonds or vice versa. They nevertheless suggest that the touching patterns and the encoding of the corresponding hedonic sensations show the necessary plasticity for changing touching behavior under the course of a relationship. Additionally, prior behavioral work suggests a causal role of social touch in modulating affective bonds, showing that touching leads to a more positive evaluation of the toucher (9, 10, 24) and increases prosocial behavior (11, 12, 25, 26). Regulation of the relationship-specific touch patterns could thus be a candidate mechanism in governing the emotional closeness between different individuals in one's social network.

A critical question is why the TAMs are so strongly relationship-dependent. One possibility is that the social relationship between people touching each other moderates the rewarding properties of social touch, which promotes or inhibits touching in different relationships. The TI was indeed positively correlated with the experienced pleasantness of touch, and the more pleasant a touch by an individual was felt, the larger body surface that individual was allowed to touch. Consequently, closer social relationships would allow larger capacity (i.e., total body area allowed for touching) for triggering pleasurable sensations. This hypothesis was corroborated by experiment 3, in which we tested whether the TAMs would depend on the nociceptive, tactile, or hedonic sensitivity of the involved skin sites: Acceptability of social touch was most limited (i.e., most relationship-specific) in regions with the strongest hedonic sensitivity, implying that it is the skin area's capacity to trigger pleasure when touched that likely determines its relationship-specificity for social touch.

Primate studies suggest that the rewarding effects of pleasurable touching and the consequent modulation of anxiety-related behaviors are governed by the endogenous μ-opioid system (27), well known for its role in governing analgesic responses (28) and pleasurable sensations (29). In primates, opioid-receptor antagonists increase the frequency of grooming (27, 30) and grooming solicitations (31) irrespective of the dyadic relationship (32). Consequently, calming effects of endogenously released opioid peptides acting on the μ-opioid receptors during pleasurable social touch could promote the establishment and reinforcement of safe social bonds (e.g., ref. 33). However, other neuropeptides also contribute significantly to the maintenance of social bonds by touching, and, for example, oxytocin is released by social grooming in a relationship-specific manner (34). Future neuropharmacological studies need to address the potentially interacting roles of the opioid and oxytocin systems on human touch and pair bonding.

Is Bonding by Touch Culturally Universal? Relationship-specific TAMs were concordant across the range of tested countries, and the culture-specific TAMs differed mainly with respect to the mean area available for touching. The closeness of different members of a social network, as evaluated from emotional bonds, was also similar across cultures (*SI Appendix*, Table S7). The data, however, suggest that Russians use touch in slightly more conservative patterns than the other cultures, even though their TIs were in the average range, and that subjects from the United Kingdom had the lowest TIs even though the touch patterns—on the basis of TAM clustering—were similar as in the other cultures. Other countries fell between these two extremes.

In all tested cultures, the higher the emotional bond, the larger the bodily area available for touching, with no statistically significant

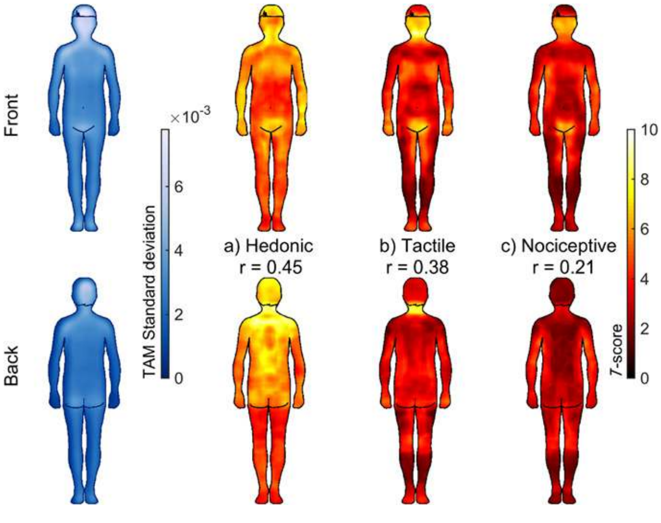

Fig. 5. Relationship-dependent SD maps for touching allowances (*Left*; from experiment 2) and t-maps for hedonic (*A*), tactile (*B*), and nociceptive (*C*) sensitivity from experiment 3. The *r* values show correlations between the relationship-dependent touching-allowance map and each of the sensitivity maps.

differences in the slopes of the regression lines between cultures. TAM-based social networks were concordant, and the social network members clustered consistently across different cultures, which further corroborates the relative consistency of social touch across the studied cultures. However, because of Internet-based data acquisition, the sample comprised relatively young well-educated participants and more female than male subjects. As the connection between emotional bond and TI was similar in the United Kingdom (with equal proportion of male and female subjects with a wide age range) and other countries (with more female subjects and a restricted age range), we contend that our results are not, in general, confounded by sampling bias.

Altogether, the present findings point toward universality and biological basis of the touch-driven bonding behavior, which is, however, modulated by cultural factors: Whereas the primary mechanism for maintaining closeness of social bonds via regulating the spatial patterns of touch (i.e., association with TI and emotional bond) seems biologically determined and minimally influenced by culture, our data suggest that cultural conventions may up- or down-regulate the average magnitude of social touching (15, 16). However, it must be noted that, even though the studied countries reside thousands of kilometers apart and vary significantly with respect to majority languages and cultural conventions, they can still be considered as primarily Western cultures. The present data cannot thus confirm whether the association between touching and social bonding would hold in all possible cultures.

Female, rather than opposite-sex, touch was, in general, evaluated as more pleasant, and it was consequently allowed on larger bodily areas. It is known that females allow themselves to be touched on a larger bodily area than males (see also ref. 35) and that female same-sex touch is allowed without discomfort on most of the body surface. Our findings agree with a number of early behavioral studies outlining females as touching and being touched more often (meta-analysis in ref. 36). The reason for this sex difference remains unclear. Primate studies indicate that female grooming relationships are fairly stable (2) and that relationship quality, serviced by grooming behavior, and longevity in female baboons do not correlate (37). Together, these findings support social touching, as a human equivalent of grooming, as a predominantly feminine-appropriate behavior (38).

Finally, it should be noted that our study was based on self-reports, and thus the data may not directly translate to real-life touching behavior. However, given the general consistency between our results and those stemming from observational research (39), it is feasible to assume that the self reports of the body's regional touching allowances also reflect real-life touching behavior.

Conclusions

We conclude that the emotional bonds between individuals are closely associated with the bodily patterns where social touch is allowed. Such relationship-specific spatial patterns may reflect an important mechanism supporting establishing and maintenance of human social bonds. Altogether our data highlight the central role played by nonverbal intimate interaction involving touch in modulating human social interaction and interpersonal bonds.

Materials and Methods

Participants. Altogether, 91 Finnish volunteers (61 female; mean age 28 y, SD 9 y) participated in experiment 1, and 1,368 volunteers from Finland, France, Italy, Russia, and the United Kingdom participated in experiment 2 (886 female; mean age 37 y, SD 14 y). The subjects in Finland, France, Italy, and Russia were recruited from university email lists and social media. To ensure the generalizability of the experiment, an additional sample was gathered from the United Kingdom by using an incentivized survey-data gathering service (Maximiles). This sample was gathered from 18–65-y-old subjects, with emphasis on a representative age and sex distribution. A total of 76 Finnish volunteers (51 female; mean age 31 y, SD 10 y) participated in experiment 3. *SI Appendix*, Table S6, presents participant characteristics. The ethics boards of Aalto University and University of Oxford approved the study protocols.

Data Acquisition. All measurements were conducted online, and all national participant groups completed the survey using the majority language (Finnish, French, Italian, Russian, and English) of each country. Subjects recruited in the United Kingdom were compensated for their time. Before participating in the actual experiment, all participants completed written informed consent online.

In experiments 1 and 2, participants first provided background information and details regarding members of their social network. They were given a list of candidate members of the different layers of their social network and asked whether they had at least one exemplar of each in their social network. The probed layers were based on widely existing social structures (such as primary family and extended family), and were chosen to include members from the support clique, sympathy group, band, and wider trading networks ("active social network") observed in most individuals (40). The candidate members and their a priori division to layers of the social network, in the order from nearest to furthest, were as follows: family (spouse or significant other, child*), family of origin (mother, father, sister, brother), friends (female and male friend), extended family (aunt, uncle, female and male cousin), acquaintances (female and male acquaintance, under-school-age girl and boy who are not subject's own biological children). If the subjects had multiple persons fitting one category (for example, several brothers), they were instructed to choose one of them and provide all subsequent responses with respect to that person. In addition to the these network members, responses were also gathered from a strangers layer defined as unfamiliar female and male of the subject's own age and unfamiliar under-school-age girl and boy.

Participants reported the sexes (for partners and biological children only) and the ages of each member of their social network. Participants also evaluated their emotional bond with each network member (from 1 representing no emotional bond at all to 10 representing the strongest possible emotional bond) and provided an estimate of how pleasant a touch by each network member would feel (from 1 representing not pleasant at all to 10 representing extremely pleasant). Finally, they reported lapses (times in days) since last meeting these network members. We assumed that subjects would encounter strangers on a daily basis and set "lapse" to zero for strangers. This score served as a proxy for the frequency of communicating with each network member (e.g., ref. 41).

In experiment 1, participants reported reasons for social touch. They were presented with a list of potential reasons for social touch, such as "greeting" or "comforting" (*SI Appendix*, Table S1) and were asked to report whether they would touch each member of their social network for that reason.

In experiment 2, the participants indicated where on their bodies they would allow different members of their social network to touch them. Responses were recorded by using the emBODY tool (18) (*SI Appendix*, Fig. S1; git.becs.aalto.fi/eglerean/embody). Participants were shown front and back silhouettes of a human body and a word denoting one member of their social network. They were asked to paint with a mouse the bodily regions where the indicated member of their social network would be allowed to touch them. Painting was dynamic, and successive strokes on a region increased the opacity of the paint. The diameter of the painting tool was set to 12 pixels. Finished images were stored in matrices where both the front and the back of the body were represented by 50,364 pixels (maximum drawing height, 163 pixels; width, 502 pixels).

In experiment 3, participants used the emBODY tool to report, on separate trials, areas they considered as sensitive to (*i*) tactile and (*ii*) nociceptive stimulation, and (*iii*) capable of eliciting pleasurable (i.e., hedonic) sensations when touched.

Data Analysis. Data were preprocessed and visualized with MATLAB (MATLAB and Statistics Toolbox Release 2013b), and statistical analyses were conducted in R (42). In experiment 1, we computed the proportions for touching each member of the social network for different reasons. We then used χ^2 goodness-of-fit tests against uniform distribution for testing whether the likelihood for each type of touching would differ across different network members. For each reason, we also calculated Spearman correlation for the proportion of affirmative answers and network layer, as well the proportion of affirmative answers over all targeted members of the social network.

*All target children (subjects' own, acquaintances, strangers) were ultimately excluded from the analyses because of the small number of children reported in the national samples.

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In experiment 2, the data were first manually screened for anomalous painting patterns (e.g., doodling, coloring outside the body outline). Next, subjectwise TAMs for each network member (e.g., partner, mother, cousin) were subjected to mass univariate *t* tests to compare pixel intensities against zero to reveal regions where different social network members are consistently allowed to touch. To control for false positives caused by multiple comparisons, a false discovery rate (FDR) correction with α-level of 0.05 with no correlation assumptions was applied to the t-maps. An additional TAM variance map was calculated to reveal the areas where touch allowances were most strongly modulated by social relations.

To evaluate the similarity of the TAMs across different cultures, we applied *k*-means clustering ($k = 6$; based on the a priori number of network layers described earlier) on the FDR-corrected t-maps, which were standardized to *z*-scores before clustering. To identify the consistency of our data within the framework of the a priori social network structure, we calculated an adjacency matrix (i.e., a network) by computing the Spearman coefficient for each pair of TAMs for each country. We then considered the average network across countries and tested the similarity between the average touch network and the ideal social network using the Mantel test, a permutation-based method (1 million permutations) for assessment of the similarity between distance matrices.

To quantify the association between the touchable body area and the social relationship between the participants and each of their network members, we first calculated the TI as the proportion of colored pixels (i.e., with above-zero intensities) for each subject and for each target person. Subsequently, TIs were correlated with subjectwise emotional bond and network layer of each individual separately for each culture. To assess the effects of mere exposure to network members, TI scores were also correlated with lapse, i.e., the time since last meeting each network member. The correlation between TI and emotional bond in each country was further explored by testing for the impact of the structure of the network by calculating the emotional bond and TI values for each member of the social network (e.g., mother) and, for the impact of the bond itself, by calculating the TI associated with each value of emotional bond (e.g., emotional bond score 9). The impact of culture on the baseline touch allowances was investigated by performing a Bonferroni-corrected pairwise *t* test on subjectwise averaged TI values associated with strangers. To test for the effect of subject age on social-bond–dependent touching, we first calculated subjectwise Pearson correlation coefficients between different target individuals' emotional bond and TI. In a subsequent second-level linear regression model, these correlation coefficients were modeled with subject age.

The impact of the toucher's sex was inspected by running two-tailed *t* test on the subjectwise calculated difference of TIs of the male and female of the same formal relationship (e.g., aunt vs. uncle). The same procedure was repeated for average emotional bonds.

Finally, to reveal bodily regions whose touching was most dependent on the relationship status, we first ran subjectwise linear regression models in which paint intensities for each pixel and targeted individual were predicted with social bond, network layer, or lapse since last meeting a network member. Subjectwise regression coefficients were stored into separate β-maps, and a second-level analysis of two-tailed *t* test with FDR correction was used to determine bodily regions where the β values differed significantly from zero for each predictor variable. As the lapse since last meeting a stranger was by default set to 0, we also analyzed this correlation without strangers. The results were similar to those including strangers, and thus only the correlations of the full data set are shown.

In experiment 3, the data were analyzed similarly as in experiment 2. Pearson correlation coefficients were calculated between relationship-dependent TAM variance map, and tactile, nociceptive, and hedonic sensitivity maps obtained in experiment 3.

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1. Schino G (2001) Grooming, competition and social rank among female primates: A meta-analysis. *Anim Behav* 62(2):265–271.
2. Dunbar RIM (2010) The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. *Neurosci Biobehav Rev* 34(2):260–268.
3. Terry RL (1970) Primate grooming as a tension reduction mechanism. *J Psychol* 76(1): 129–136.
4. Schino G, Scucchi S, Maestripieri D, Turillazzi PG (1988) Allogrooming as a tension-reduction mechanism: A behavioral approach. *Am J Primatol* 16(1):43–50.
5. Ainsworth MDS (1989) Attachments beyond infancy. *Am Psychol* 44(4):709–716.
6. Hazan C, Shaver P (1987) Romantic love conceptualized as an attachment process. *J Pers Soc Psychol* 52(3):511–524.
7. Hertenstein MJ, Verkamp JM, Kerestes AM, Holmes RM (2006) The communicative functions of touch in humans, nonhuman primates, and rats: A review and synthesis of the empirical research. *Genet Soc Gen Psychol Monogr* 132(1):5–94.
8. Heslin R, Alper T (1983) Touch: A bonding gesture. *Nonverbal Communication*, eds Wiemann JM, Harrison RP (Sage, Philadelphia), pp 47–76.
9. Fisher JD, Rytting M, Heslin R (1976) Hands touching hands: Affective and evaluative effects of an interpersonal touch. *Sociometry* 39(4):416–421.
10. Erceau D, Guéguen N (2007) Tactile contact and evaluation of the toucher. *J Soc Psychol* 147(4):441–444.
11. Kleinke CL (1977) Compliance to requests made by gazing and touching experimenters in field settings. *J Exp Soc Psychol* 13(3):218–223.
12. Crusco AH, Wetzel CG (1984) The Midas touch: The effects of interpersonal touch on restaurant tipping. *Pers Soc Psychol Bull* 10(4):512–517.
13. Willis FNJ, Briggs LF (1992) Relationship and touch in public settings. *J Nonverbal Behav* 16(1):55–64.
14. Jones SE, Yarbrough E (1985) A naturalistic study of the meanings of touch. *Commun Monogr* 52(1):19–56.
15. DiBiase R, Gunnoe J (2004) Gender and culture differences in touching behavior. *J Soc Psychol* 144(1):49–62.
16. Remland MS, Jones TS, Brinkman H (1995) Interpersonal distance, body orientation, and touch: Effects of culture, gender, and age. *J Soc Psychol* 135(3):281–297.
17. Hill RA, Dunbar RIM (2003) Social network size in humans. *Hum Nat* 14(1):53–72.
18. Nummenmaa L, Glerean E, Hari R, Hietanen JK (2014) Bodily maps of emotions. *Proc Natl Acad Sci USA* 111(2):646–651.
19. Myowa-Yamakoshi M, Takeshita H (2006) Do human fetuses anticipate self-oriented actions? A study by four-dimensional (4D) ultrasonography. *Infancy* 10(3):289–301.
20. Löken LS, Wessberg J, Morrison I, McGlone F, Olausson H (2009) Coding of pleasant touch by unmyelinated afferents in humans. *Nat Neurosci* 12(5):547–548.
21. Olausson H, et al. (2002) Unmyelinated tactile afferents signal touch and project to insular cortex. *Nat Neurosci* 5(9):900–904.
22. Gazzola V, et al. (2012) Primary somatosensory cortex discriminates affective significance in social touch. *Proc Natl Acad Sci USA* 109(25):E1657–E1666.
23. Malinen S, Renvall V, Hari R (2014) Functional parcellation of the human primary somatosensory cortex to natural touch. *Eur J Neurosci* 39(5):738–743.
24. Guéguen N (2007) Courtship compliance: The effect of touch on women's behavior. *Soc Influence* 2(2):81–97.
25. Joule R-V, Guéguen N (2007) Touch, compliance, and awareness of tactile contact. *Percept Mot Skills* 104(2):581–588.
26. Goldman M, Fordyce J (1983) Prosocial behavior as affected by eye contact, touch, and voice expression. *J Soc Psychol* 121(1st half):125–129.
27. Graves FC, Wallen K, Maestripieri D (2002) Opioids and attachment in rhesus macaque (Macaca mulatta) abusive mothers. *Behav Neurosci* 116(3):489–493.
28. Stefano GB, et al. (2000) Endogenous morphine. *Trends Neurosci* 23(9):436–442.
29. Van Ree JM, et al. (2000) Endogenous opioids and reward. *Eur J Pharmacol* 405(1-3): 89–101.
30. Fabre-Nys C, Meller RE, Keverne EB (1982) Opiate antagonists stimulate affiliative behaviour in monkeys. *Pharmacol Biochem Behav* 16(4):653–659.
31. Keverne EB, Martensz ND, Tuite B (1989) Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. *Psychoneuroendocrinology* 14(1-2):155–161.
32. Schino G, Troisi A (1992) Opiate receptor blockade in juvenile macaques: Effect on affiliative interactions with their mothers and group companions. *Brain Res* 576(1): 125–130.
33. Nelson EE, Panksepp J (1998) Brain substrates of infant-mother attachment: Contributions of opioids, oxytocin, and norepinephrine. *Neurosci Biobehav Rev* 22(3): 437–452.
34. Crockford C, et al. (2013) Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proc Biol Sci* 280(1755):20122765.
35. Jourard SM (1966) An exploratory study of body-accessibility. *Br J Soc Clin Psychol* 5(3):221–231.
36. Stier DS, Hall JA (1984) Gender differences in touch: An empirical and theoretical review. *J Pers Soc Psychol* 47(2):440–459.
37. Silk JB, et al. (2010) Strong and consistent social bonds enhance the longevity of female baboons. *Curr Biol* 20(15):1359–1361.
38. Jones SE (1986) Sex differences in touch communication. *West J Speech Commun* 50(3):227–241.
39. Hall JA, Veccia EM (1990) More "touching" observations: New insights on men, women, and interpersonal touch. *J Pers Soc Psychol* 59(6):1155–1162.
40. Dunbar RIM (2008) Cognitive constraints on the structure and dynamics of social networks. *Gr Dyn Theory Res Pract* 12(1):7–16.
41. Roberts SGB, Dunbar RIM, Pollet TV, Kuppens T (2009) Exploring variation in active network size: Constraints and ego characteristics. *Soc Networks* 31(2):138–146.
42. R Core Team (2012) *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna).