

Research Article

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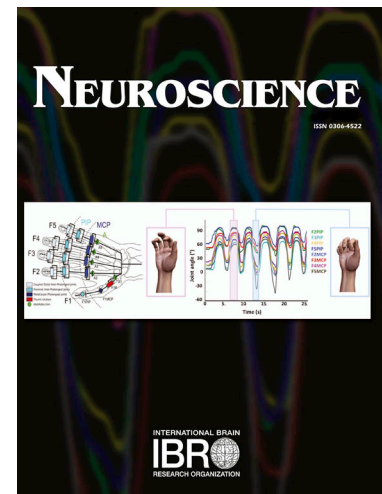
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Relationship-specific encoding of social touch in somatosensory and insular cortices

Abbreviated title: relationship-specific touch in the brain

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Abstract

Humans use touch to maintain their social relationships, and the emotional qualities of touch depend on who touches whom. However, it is not known how affective and social dimensions of touch are processed in the brain. We measured haemodynamic brain activity with fMRI from 19 subjects (10 males), while they were touched on their upper thigh by either their romantic partner, or an unfamiliar female or male confederate or saw the hand of one of these individuals near their upper thigh but were not touched. We used multi-voxel pattern analysis on pre-defined regions of interest to reveal areas that encode social touch in a relationship-specific manner. The accuracy of a machine learning classifier to identify actor for both feeling touch and seeing hand exceeded the chance level in the primary somatosensory cortex, while in the insular cortex accuracy was above chance level only for the touch condition. Restricting the task to classify the relationship (partner or stranger), while keeping the toucher sex fixed, amygdala, orbitofrontal cortex, and primary and secondary somatosensory cortices were able to discriminate toucher significantly above chance level.

These results suggest that information on the social relationship to the toucher is processed in a consistent manner in several regions. More complex information about toucher identity is processed in the primary somatosensory and insular cortices, both of which can be considered early sensory areas. More research is needed to understand the temporal order of these effects and the impact of contextual factors.

Keywords: affective touch; social network; fMRI; naturalistic touch

Introduction

Touch is the most intimate form of interpersonal communication. Both humans (Suvilehto et al., 2015) and nonhuman primates manage their social relations by means of mutual grooming or touching (Dunbar, 1991). Such touching is usually very relationship-specific (Dunbar, 2010). Behavioral studies have indicated that the social relationship between two individuals strongly influences how social touch is experienced (Heslin et al., 1983). A gentle squeeze can be interpreted as loving or playful when given by one's partner, or invasion of privacy when coming from a stranger. Human studies have shown that the closer affective relationship two individuals have, the more social touching they are willing to accept from each other and the more pleasant they experience each other's touch (Suvilehto et al., 2015). Because this effect is independent of the actual kinematics of the touch (Gazzola et al., 2012; Nummenmaa et al., 2016b), such as motion or pressure, it likely reflects top-down influences of the social relational information on the sensory qualities of touch.

While social touch is frequently considered affective, all affective touches need not be social. For example, being stroked by a rotary tactile stimulator can feel pleasant without being social. The perception and processing of touch does not simply reflect whether a touch is understood as social or not. Some studies have found that attributing somatosensory stimulation to a human or a computer does not impact the subjective ratings of the touch (Triscoli et al., 2013) or the modulation of event related potentials associated with the touch (Schirmer et al., 2011). Moreover, the affective properties and cortical processing of touch can be manipulated by different contextual cues (McCabe et al., 2008). Here, we specifically manipulate the social relationship component of experiencing and anticipating touch while acknowledging that this will also impact the affective properties of the stimuli.

Even though the relationship-specific nature of social touching is well established at the behavioral level, neuronal processing of the social dimensions of touch remain poorly understood. According to the classical view of somatosensory processing, passive touch is first processed in the primary somatosensory cortex (S1, specifically Brodmann's areas BA3b and BA1). The signal is then transmitted to the secondary somatosensory cortex (S2), where it can be integrated with audiovisual input (Keysers et al., 2010). It seems that this view of somatosensory processing is highly simplified and more recent studies have found that these areas are involved in the processing of the stimulus at multiple timepoints during the stimulus presentation (Eriksson Hagberg et al., 2019). While S1 is not conventionally considered to process the affective properties of touch, recent brain imaging studies have found modulation of S1 responses to subject's belief regarding who is touching (Gazzola et al., 2012; Scheele et al., 2014; Kreuder et al., 2017).

Several additional candidate areas have been proposed to be involved in the processing of affective aspects of touch. Several groups have suggested that the pleasantness of touch modulates the neural activity in the orbitofrontal cortex (Francis et al., 1999; McCabe et al., 2008), insular cortex (Kress et al., 2011; Lucas et al., 2015; Perini et al., 2015), anterior cingulate cortex (Rolls et al., 2003; Case et al., 2016), and superior temporal sulcus (Davidovic et al., 2016).

Because most research on touch has been conducted using artificial somatosensory stimuli, studying naturalistic touch can provide novel insight into how social touch is represented in the brain (Malinen et al., 2014). Prior studies on neural processing of naturalistic social touch have manipulated the belief of the subjects regarding who is touching them, while in reality the toucher was always the same person. They found that both experiencing and anticipating touch from a female experimenter modulated activity in the primary somatosensory cortex distinctly from when the subjects believed they were being touched or anticipated being touched by a male experimenter (Gazzola et al., 2012; Scheele et al., 2014). Additionally, intranasal oxytocin selectively enhances the

neural response in the insular cortex, orbitofrontal cortex and anterior cingulate cortex for female touch (Scheele et al., 2014). When subjects believed they were touched by their romantic partner or a stranger of the opposite sex (i.e. the same sex as their partner), relationship-specific responses to touch were observed in the orbitofrontal, posterior cingulate, and somatosensory cortices (Kreuder et al., 2017).

Although prior studies have investigated somatosensory (Gazzola et al., 2012) and affective (Kreuder et al., 2017) neural processing of affective touch, it remains unresolved how and where the relationship-specific information regarding social touch is represented in the brain. To that end, we used a realistic manipulation of social relationships between the touchers and subjects (partner versus male and female stranger) and used multivariate pattern recognition techniques for teasing apart the neural processing of social dimensions of touch. Previous research shows that there are clear sex differences in the social acceptability of touching, with touching by females being considered more appropriate by both sexes (Suvilehto et al., 2015). Accordingly, we also tested whether there are subjective and neural differences in processing of touches by male and female strangers. We expected to replicate the earlier findings of differential cortical activation in the primary somatosensory cortex and orbitofrontal cortices for touch from male and female stranger, in line with Gazzola et al. (2012), and for touch from partner and stranger, in line with Kreuder et al. (2017) and extend these findings by differentiating between the effect of gender and the social relationship.

Methods

Participants

Twenty healthy adult volunteers (10 male, average age = 29 years, SD = 8) participated in the experiment. One subject dropped out at the beginning of the scanning due to discomfort, leaving

19 subjects with complete data sets. They all had normal or corrected-to-normal vision, and gave written informed consent prior to participation. The study was conducted in accordance with the guidelines of the Declaration of Helsinki, and the Institutional Review Board of Aalto University had approved the study protocol. Subjects were heterosexual couples who had been dating for at least six months at the time of the experiment. Both members of the couples were scanned, and the order of scanning (male or female first) was counterbalanced across couples. Subjects were acquainted with the experimental setup and task prior to scanning.

Experimental design

The experimental design is summarized in **Figure 1**. During the functional magnetic resonance imaging (fMRI) the partner of the subject and a male and a female research assistant (unfamiliar to the participants) served as confederates. We used a total of 6 different male and 6 different female research assistants in different pairings in the scanning sessions. This was done to control for the impact of potential differences in the touch kinematics of the selected assistants. All confederates wore differently colored overalls, and the selection of clothing was counterbalanced across subjects. Prior to imaging, the partner of the subject and the two confederates were trained to touch the subjects in a uniform manner: they were instructed to stroke the subject's thigh at the same speed (approx. 4 cm s^{-1}) and similar pressure. Because in practice sessions the hands of the confederates tended to get cold in the scanner room, the confederates were provided with simple re-heatable gel heat pads to help maintain stable hand temperature throughout the experiment. More specifically, the confederates were instructed to touch their own neck or chest under the overall, every once in a while, to check that their fingers were not cold. If their hands required warming, they were to hold the heat pads until their fingers were warm once more.

The confederates received instructions for stimulus delivery via headphones. During the experiment, they took turns in (i) stroking the subject's upper thigh, (ii) bringing their hand to a near

(5–10 cm), or (iii) an intermediate (20–25cm) distance from the subject's upper thigh. All stimulation was targeted at the same location on the right leg of the subject. The target distances were indicated on a stick placed between the subject's thighs (see **Figure 1**). The target zone for touching was marked by cutting a 20 cm × 10 cm hole (from middle top of the thigh down towards the knee) into subjects' overalls to enable skin-to-skin contact and to make sure all assistants were touching the same area. Subjects were able to see the hand of the confederate performing the action. Stimulation begun with a confederate's hand descending to subject's visual field from the top of the scanner bore, and the hand stopping at the specified stimulus level. After the confederate received the signal to stop stimulation, they withdrew their hand horizontally from the visual field of the subject and stepped back to give space to the next confederate to deliver the next stimulus. The field of vision of the subject was marked on the scanner room floor with tape to help the confederates stay safely out of sight unless they were actively delivering a stimulus.

One researcher monitored the compliance with instructions during imaging for all the subject and the confederates, and the participants' actions were additionally recorded with an MRI compatible camera (12M-i, MRC-systems) to enable post factum verification of confederate compliance and timing with respect to the instructions.

Blood-oxygenation level dependent (BOLD) fMRI using echo planar imaging was used to measure the neural correlates of the stimulation in the subjects' brains. The stimulation was distributed over 5 imaging runs per participant. Due to technical issues, four subjects only completed four runs. In each imaging run, every possible combination of confederate and action type was presented six times. Over the course of the full five runs, each stimulus was repeated a total of 30 times (5 runs x 6 repeats per run). The stimuli were delivered in 6 s blocks of continuous stimulation (stroking or keeping the hand at the specified distance), with inter-stimulus interval (ISI) of 7.6 s. The order of the stimuli was pseudo-randomized.

The subjects were instructed to pay attention to the hand in their visual field (“When the experiment starts, your romantic partner and our research assistants will take turns in bringing their hand into your visual field. The hand will stop at different distances from your leg or touch your leg. Your task is to pay attention to the hand while it is in your visual field and observe who it belongs to. You will be able to tell the different people apart from the color of their overalls. Do you have any questions?”). Prior to scanning, the subjects were told that they could identify the confederates by the colors of their overalls. To further imprint the different colors of clothing to the different confederates, they were presented to the subject in those particular overalls. A total of 9 stimuli per run were “catch” trials, where the same assistant proceeded from one level to a more proximate level (high to middle, high to touch, or mid to touch) without the ISI. This reduced the predictability of the stimulation sequence for the subjects as the subjects could not be certain whether a seeing-hand-condition would be followed by a touch. This helped the subjects to pay attention to the stimulus during the whole stimulus duration, as per the task instructions.

Imaging data collection

MRI data were collected using a 3.0 T whole-body scanner (MAGNETOM Skyra 3.0, Siemens Healthcare, Erlangen) and a 32-channel receive head coil (Siemens) at the Advanced Magnetic Imaging Centre, Aalto NeuroImaging, Aalto University. The fMRI data were acquired with whole-brain T_2^* -weighted echo planar imaging (EPI) using the following imaging parameters: TR 1.52 s, TE 30 ms, flip angle 70° , 72×72 matrix, $2.7 \times 2.7 \text{ mm}^2$ in-plane resolution, 35 slices (3.7 mm thickness, no gap), using water excitation and in-plane acceleration using GRAPPA at $R = 2$. A total of 2150 volumes of functional data were acquired in the 5 runs. High-resolution anatomical reference images with isotropic 1 mm voxel size were collected using a T1-weighted MP-RAGE sequence. Subjects’ respiration and cardiac rates were measured during EPI sequences using BIOPAC system MP150CE.

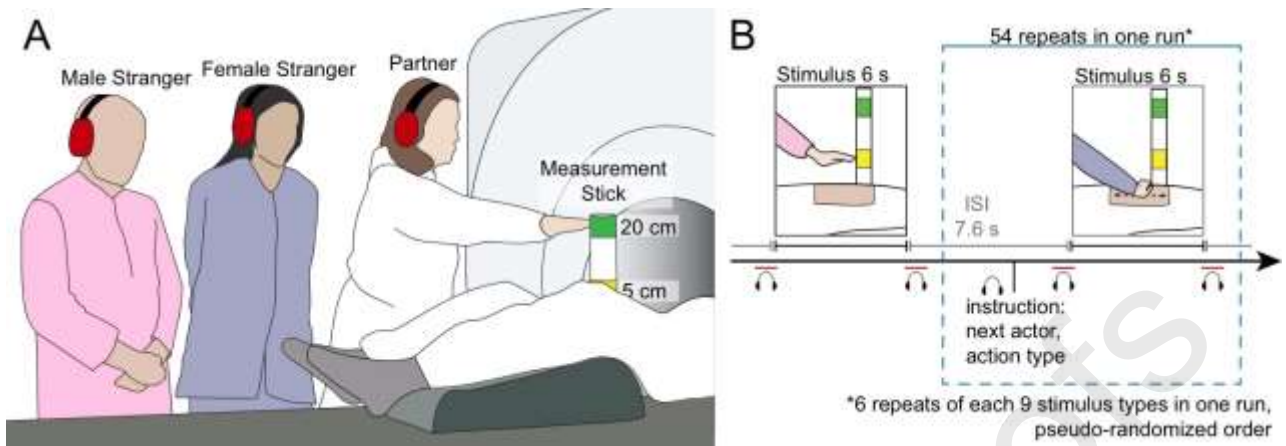


Figure 1 A) Experimental setup. Three confederates (partner, male stranger, and female stranger) stood next to the subject in the scanner room, confounded from the subject's view by the scanner bore, and received instructions for stimulation timing via headphones (thus not audible to the subject). A hole was cut to the subject's protective overalls to specify the area to be touched, and a measurement stick indicating distances for hand placement was fixed between the subject's thighs. B) Stimulation paradigm. At the beginning of each stimulus sequence the confederates heard which type of stimulus should be delivered by which confederate. Next, onset and offset of stimulation was indicated by a beep played through the headphones. Both types of instructions were played through the headphones and thus heard by all confederates, but not the subject. The subject was able to see the hand and sleeve of the active confederate during stimulation but not during inter-stimulus interval (ISI).

Self-reports

After the imaging session, all subjects completed an online behavioral rating of perceived pleasantness for each stimulus type administered by each confederate on a scale ranging from 1 (very unpleasant) to 10 (very pleasant). Subjects also rated their emotional bond with their partner as well as male and female strangers, and reported the touch allowance zones in their body for their partner and the female and male stranger (see details in Suvilehto et al., 2015) using the emBODY

tool (Nummenmaa et al., 2014). The touch area maps were preprocessed as described by Suvilehto et al. (2015, 2019) and subjected to mass univariate t-tests to compare pixel intensities against zero. The pleasantness ratings were analyzed using paired samples t-test for each pair of actors in each stimulus type. False detection rate (FDR) correction with α -level of 0.05 was used for both analysis types to correct for multiple comparisons.

fMRI data preprocessing and data analysis

The fMRI data were preprocessed using the FSL software (www.fmrib.ox.ac.uk, version 5.0.9) and custom MATLAB code (BRAMILA pipeline v2.0, available at <https://git.becs.aalto.fi/bml/bramila/>). Briefly, the EPI images were corrected for slice timing differences and then for head motion using MCFLIRT. Physiological noise (cardiac and respiration related signals) were modeled out using DRIFTER toolbox (Särkkä et al., 2012). Images were next co-registered to the Montreal Neurological Institute (MNI) standard brain (MNI152 2mm template) using FLIRT in a two-step registration procedure: from EPI to participant's anatomical image after brain extraction (9 degrees of freedom) and from anatomical to standard template (12 degrees of freedom). For univariate GLM analysis (but not MVPA), spatial smoothing was also applied using a Gaussian kernel of 8 mm full width at half maximum. 240-s-long Savitzky-Golay filter was applied to remove scanner drift (similar to Çukur, Nishimoto, Huth, & Gallant, 2013), and high pass temporal filter at 0.01 Hz cut-off frequency was applied. To control for motion and physiological artefacts, BOLD time series were cleaned using 24 motion-related regressors, signal from deep white matter, ventricles and cerebrospinal fluid as described in Power et al. (2012). Pre-processed data were inspected for extensive motion.

General Linear Model (GLM) on the whole brain was run as a two-way repeated measures analysis of variance with three levels of action (see hand at 20 cm, see hand at 5 cm, touch) and three levels of actor (partner, female stranger, male stranger). Pre-defined contrasts were

computed for each action and actor against baseline, as well as for see (see hand at 20 cm or 5 cm) and see versus touch, again using the whole brain. The subjective ratings were not used as a covariate in the GLM. The GLM analysis was run using Matlab (r2016a) and Statistical Parametric Mapping (SPM12) Matlab package. False Detection Rate (FDR) correction with alpha level 0.05 was used to determine significance of GLM results.

It is possible that the differences between different actors are patterns of activity within similar regions, as opposed to net activation change within a specific region. This kind of pattern-specific processing would not be distinguishable with GLM but can be detected using multi-voxel pattern analysis (MVPA). For MVPA, the pre-processing was done as outlined above, but no temporal or spatial filtering was applied. MVPA classification was run on the preprocessed data using scikit-learn version 0.18.1 on Python 3.6.0 with NumPy 1.11.3. For training and testing the classifier, we used the activity during the stimulus blocks, averaged over each EPI sequence by stimulus type. Regressor was shifted by 4.52 sec (3 TRs) to account for lag in hemodynamic response. Classification was run between-subjects in MNI space using leave-one-subject-out cross-validation. Scikit-learn implementation of C-Support Vector Classifier (SVC) with linear kernel was used in all of the classification analyses. For class-wise performance, we report class-wise recall, i.e. sensitivity, defined as $TP / (TP + FN)$, where TP is true positives and FN is false negatives per class. In the supplementary materials we also provide class-wise precision, also called positive predictive value, defined as $TP / (TP + FP)$ where FP = false positives; and f1, which is calculated as the harmonic mean of precision and recall. When the emphasis is not on class-wise performance, classifier performance is reported using accuracy (number of correct predictions per the total number of predictions).

Significance levels were defined using permutation testing by running the classifications on the same data with permuted (randomly assigned) labels with 10000 permutations and comparing

the classification score with the permutation scores. Results were corrected for multiple comparisons using FDR. We considered all regions of interest (ROI) used in one classification task (such as partner vs female stranger) to be a family of tests for the multiple comparison correction.

Bilateral ROIs were defined in MNI space (**Figure S1**). Areas related to processing somatosensation were defined as follows: primary (S1) and secondary (S2) somatosensory cortex from Juelich histological atlas (S1 was compiled from Juelich histological atlas areas BA1, BA2, BA3a and BA3b, bilateral; S2 was compiled from Juelich histological atlas areas Parietal operculum OP1-OP4, bilateral), insular cortex (INS) and anterior cingulate gyrus (ACG) from the Harvard-Oxford atlas. Additionally, key emotion and reward processing areas were defined as follows: amygdala (AMYG) and orbitofrontal cortex (OFC) from the Harvard-Oxford atlas, putamen (PUT) and thalamus (THA) from the AAL template, and dorsal caudate nucleus (DC) and ventral striatum (VS) from the Wake Forest University PickAtlas toolbox. Additionally, to assess how much visual input contributes to the classification, masks for visual cortex (VC, a combination of visual cortices V1, V2, V3, V4 and V5 from the Juelich histological atlas) and whole brain excluding visual cortex (whole brain minus VC) were included.

Results

Self-reports

Touch Allowance Maps (TAMs) (**Figure 2A**) were similar to those reported previously (Suvilehto et al., 2015, 2019). Most of the body was allowed to be touched by the partners. Male and female strangers were not allowed to touch the anterior torso, the upper thighs, the buttocks or the head. Female strangers were allowed to touch larger areas in the upper back and lower legs and feet than male strangers. On average, partners were allowed to touch 68% (SD 21%) of the body, which was significantly more than was allowed for female (mean 27%, SD 23%) or male (mean

21%, SD 18%) strangers; $t(18) = 8.6$ and $t(18) = 10.9$, $ps < 0.001$ respectively. The difference between touch allowances of female strangers and male strangers was also statistically significant ($t(18) = 3.0$, $p = 0.008$, paired).

Pleasantness ratings for each experimental condition (**Figure 2**) were higher for partners versus male and female strangers, and female versus male strangers in all conditions ($t(18) > 2.19$, $ps < 0.05$, paired) except for seeing hand at 20 cm ratings for male and female strangers, which did not differ from each other ($t(18) = 2.04$, $p = 0.56$, paired). As we had both male and female subjects, the strangers could be classified either by their sex (male and female stranger) or by their sex with respect to the subject (same sex as subject and opposite sex to subject). When inspecting pleasantness ratings for partner, same sex stranger, and opposite sex stranger, the difference between pleasantness ratings for same and opposite sex strangers were not significant in any of the three actions (**Figure S2**). Pleasantness ratings given by the male and female subjects were not statistically different, regardless of whether the strangers were considered as male/female stranger or same/opposite sex stranger.

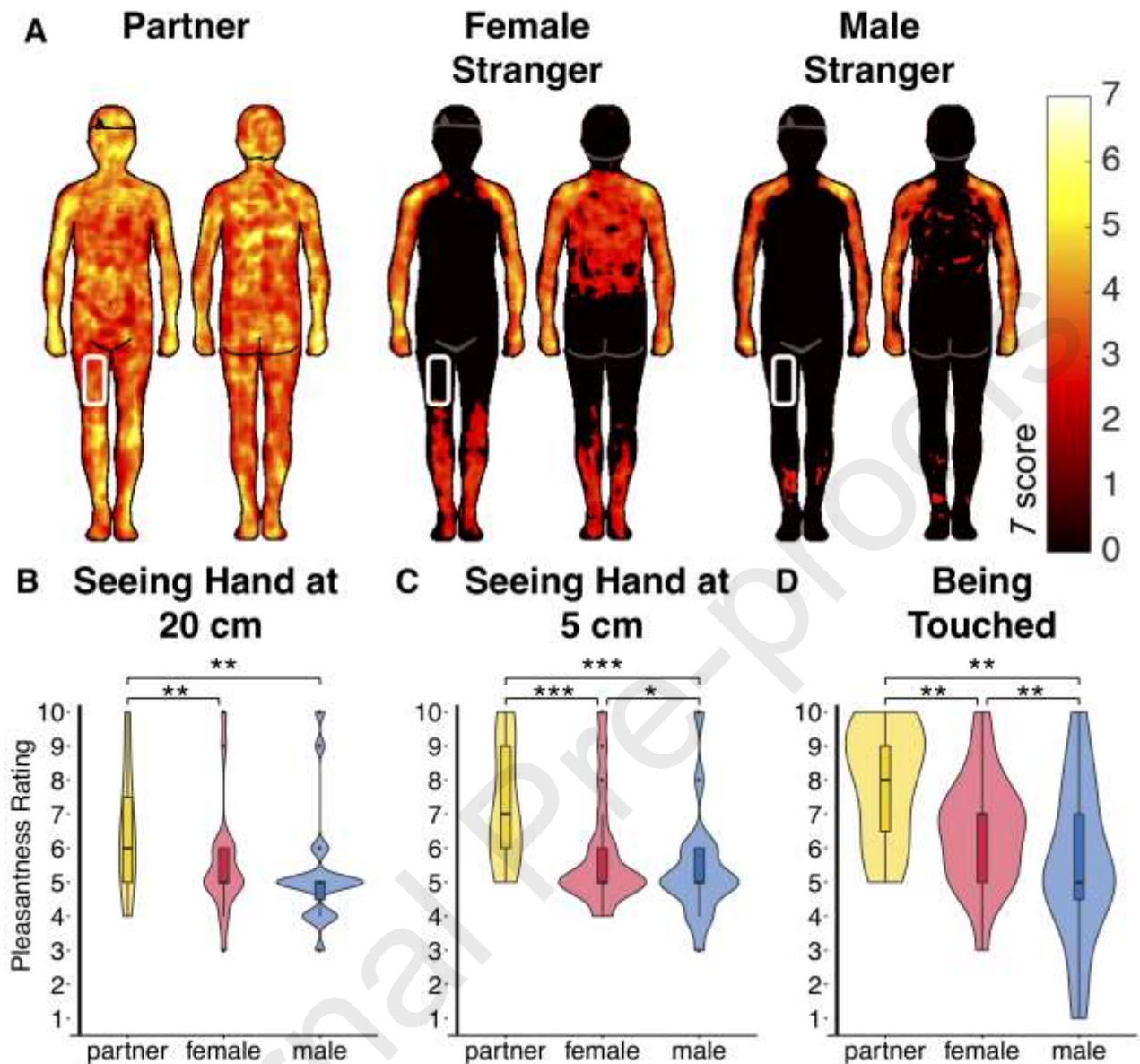


Figure 2 Self-reports from subjects. A) Touch allowance zones for partner, and female and male strangers. Colormap shows thresholded ($p < 0.05$, FDR corrected) T scores for touch allowances. White rectangle depicts the approximate location of touch in the imaging experiment. Bottom row displays subjective pleasantness ratings of B) seeing hand at 20 cm from the leg, C) seeing hand at 5 cm from the leg, and D) being touched by the partner or the two confederates. The violin plots in B–D shows the estimated density distribution of the ratings, while the box plot inside each violin depicts median (black bar) and first and third quartiles (limits of the box) of the observed values. Significant differences in pleasantness ratings are marked with asterisks (* $p < 0.05$, ** $p <$

0.01, *** $p < 0.001$, FDR-adjusted for multiple comparisons). See also **Figure S2** for subjective pleasantness ratings shown for same sex strangers and opposite sex strangers.

Regional effects in the General Linear Model

Whole-brain general linear model (GLM) analysis showed increased activation in insular cortices, secondary somatosensory cortices and contralateral primary somatosensory cortex (**Figure 3**) when feeling touch compared to baseline. Compared to baseline, there was increased activity in the visual cortices, with additional clusters at the temporal poles and ipsilateral amygdala for seeing hand at 5 cm and at 20 cm. When feeling touch and seeing hand (at both distances) were contrasted directly against each other, significant differences were seen in S1, S2 and anterior cingulate cortex. In visual areas, there was significantly less activation for the being touched than the for the exclusively visual conditions, although the subjects were able to see the hand in all three conditions. There were no significant differences between the two visual conditions (seeing hand at 5 cm and 20 cm). The GLM analysis revealed no statistically significant differences across the confederate categories (partner, male stranger, female stranger) in a pairwise comparison, but see **Table S1** for the main effect pertaining to the actor.

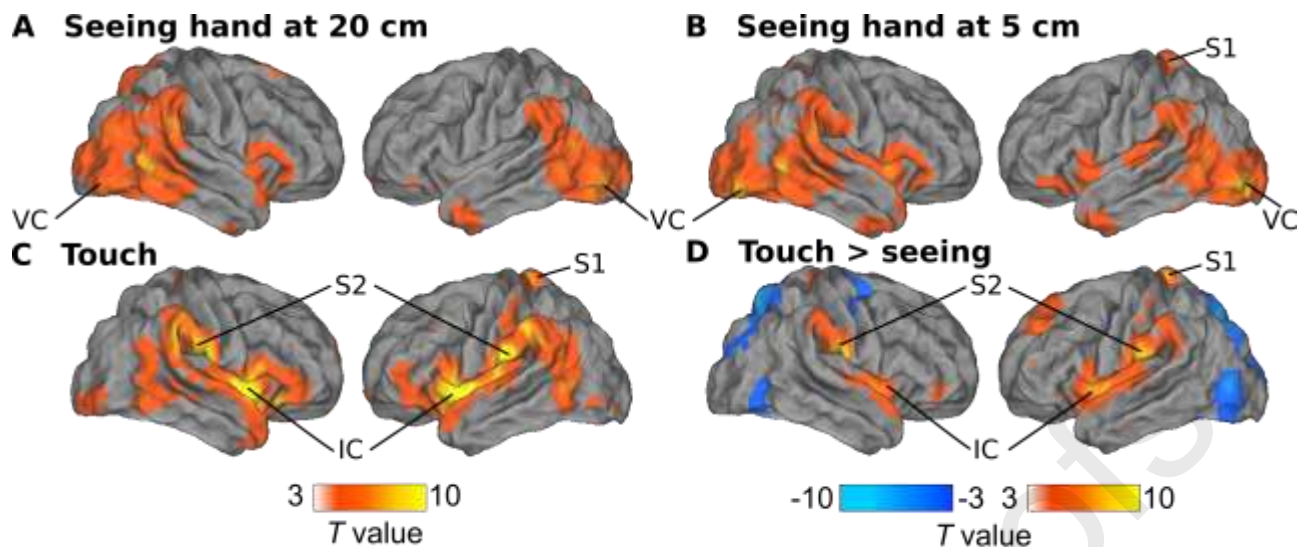


Figure 3 Main effect of different actions (A–C) and the contrast touch – see (D) ($p < 0.05$, False Detection Rate corrected). Callout lines show the activations at primary (S1) and secondary (S2) somatosensory cortices, visual cortices (VC), and insular cortex (IC). The associated NIfTI files can be accessed at <https://neurovault.org/collections/3263/>.

Multivariate analyses with Multivoxel Pattern Analysis

First, we used MVPA on the largest ROI (whole brain minus visual cortices) to confirm whether it was possible to decode relationship-specific information using MVPA. We used MVPA to test whether brain responses to feeling social touch and seeing a hand in the peripersonal space were relationship-specific. In the whole brain minus VC ROI, the actor delivering the touch could be classified consistently above permutation-derived chance level (0.33) for all actors (mean recall = 0.49). This was not the case for either of the visual-only events. In visual-only events mean recall rate was lower and only some actors could be classified at significantly above chance level (**Figure 4**), when using the whole brain minus VC mask. Different estimates of class-wise classifier accuracy (precision and F_1) gave similar results (see **Figure S3**).

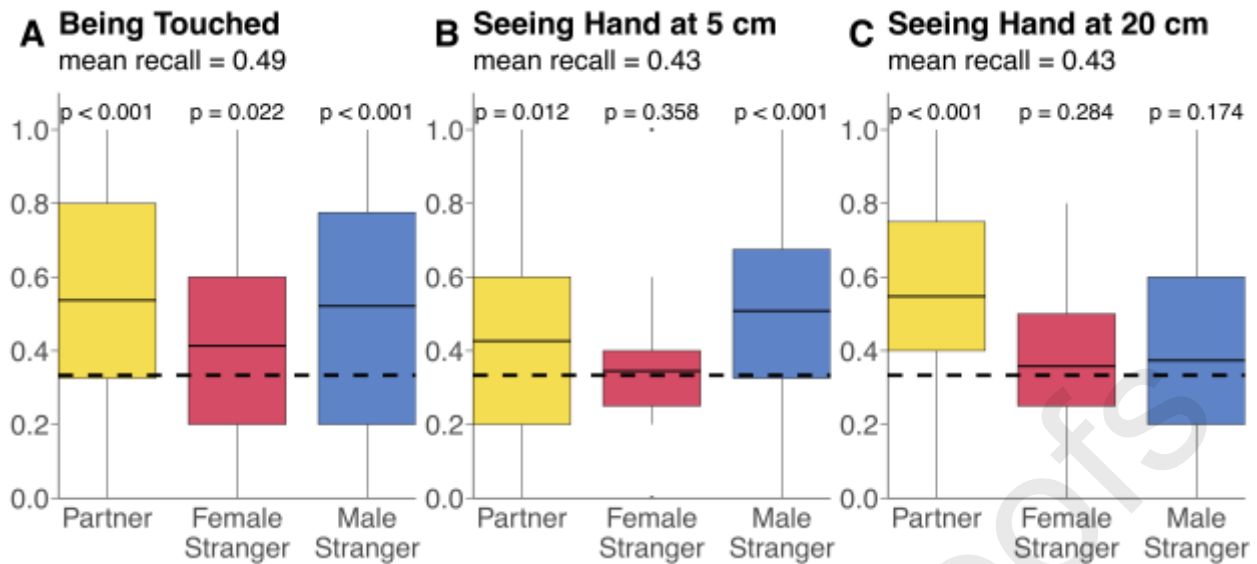


Figure 4 Class-wise recall when classifying the confederate category in A) being touched, B) seeing hand at 5 cm, and C) seeing hand at 20 cm conditions separately, using the whole brain minus VC ROI. Central line shows mean, edges of box show 25th and 75th quantile. Significance levels were obtained by permutation testing the classifier with 10 000 permutations, reported p -values are FDR-corrected for multiple comparisons.

To demonstrate the classifier performance in a general case and to inspect how detailed classification is possible, we ran the classifier on all 9 types of stimuli in the whole brain minus VC ROI. The classifier performed better at predicting the action (touch, seeing hand at 5 cm, seeing hand at 20 cm) than predicting confederate (partner, male stranger, female stranger) (**Figure S4**). Many more misclassifications occurred between actors in same action type (e.g. confusing partner's hand at 20 cm with female stranger's hand at 20 cm) than between different action types. Misclassifications were more common between male and female stranger than between partner and either stranger.

Second, we looked at the different pre-defined ROIs to reveal which brain regions contain relationship-related neural codes for seeing hand in the peripersonal space and experiencing touch.

This was done in two steps, first by classifying between all three confederates (Table S2 and Figure 5) and later, by classifying between pairs of confederates (Table S3 and Figures 6 and S5). Above-chance level actor classification accuracy for both touch and seeing hand was found in the whole brain minus VC ROI and in S1 ($p_s < 0.024$). In insular cortex, accuracy was above chance level for touch ($p = 0.014$) but not for seeing hand events. In visual cortices, classifier accuracy exceeded chance level for seeing hand at 20 cm ($p = 0.011$), all p -values FDR-corrected. Classifier accuracy did not exceed chance level in any other tested ROIs (**Figure 5**).

Next, we tested whether social touch is encoded in terms of the de facto sex of the toucher (c.f. Gazzola et al., 2012; Scheele et al., 2014 who tested only male subjects) or in terms of the toucher being same or opposite sex with the subject. To that end, we attempted to classify the toucher identity from categories partner (always opposite sex), same sex stranger, and opposite sex stranger, rather than the actual sexes of the confederates (**Figure 5**). This classification was successful at above chance level at whole brain minus VC for touch ($p = 0.001$) and seeing hand at 20 cm ($p = 0.001$). Classification of touch was successful also for insular cortex ($p = 0.023$). Unlike when classifying actor based on their de facto sex (male or female), we were not able to classify actor with respect to the sex of the subject (same or opposite sex) from primary somatosensory cortex for any of the action types ($p_s > 0.1$).

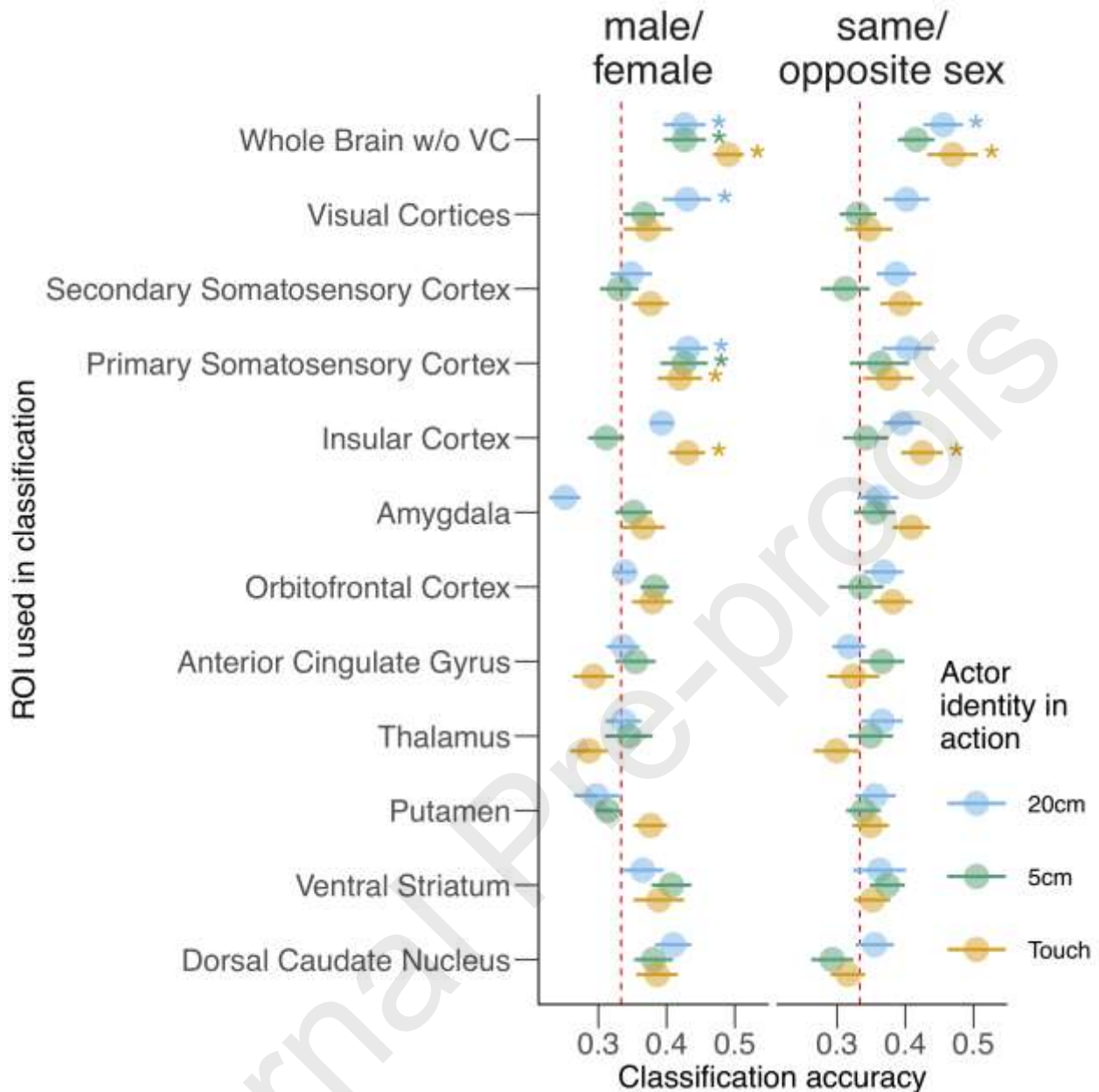


Figure 5 Mean classification accuracy of actor identity separately for each condition and ROI. The left column depicts actor identity based on de facto gender of actor (partner, male stranger, female stranger) and the right column depicts actor identity with respect to subject sex (partner, opposite sex stranger, same sex stranger). Dashed line indicates the a priori chance level (0.33), permutation-based chance levels used for statistical testing were in the range of [0.325,0.332]. Error bars show SEM, * denotes $p < 0.05$ (FDR-corrected).

We next looked at the specific binary classification of the touch by partners and strangers. We first tested how well we can classify the partner's touch from the touch of an opposite-sex stranger. This classification was successful in several ROIs (**Figure 6**). In addition to whole brain minus VC ROI (accuracy 0.61, $p = 0.018$), the classifier performed at significantly above chance level in S1 (mean accuracy 0.62, $p = 0.018$), S2 (mean accuracy 0.64, $p = 0.018$), amygdala (mean accuracy 0.62, $p = 0.018$) and orbitofrontal cortex (mean accuracy 0.62, $p = 0.018$, all p -values FDR corrected).

Then, we attempted classifying between the strangers from each other depending on their actual sex or whether they were of the same or opposite sex with the participant. Classifying between the strangers was not possible in any of the selected ROIs (**Figure S5**). This was the case regardless of whether we looked at the sex of the stranger (male, female) or the sex of the stranger with respect to the sex of the subject (same sex, opposite sex).

Finally, we classified the relationship but without fixing the sex of the toucher. The sexes of the touchers were either consistently different (partner vs same sex stranger) or varied in congruence of the sexes between the subjects (partner vs male stranger and partner vs female stranger) (**Figure 6**). All three cases could be classified from the whole brain minus VC ROI (accuracies > 0.68 , $ps = 0.001$, FDR corrected). Exact classification accuracies for classifying actor in touch conditions are also presented in **Tables S2 and S3**.

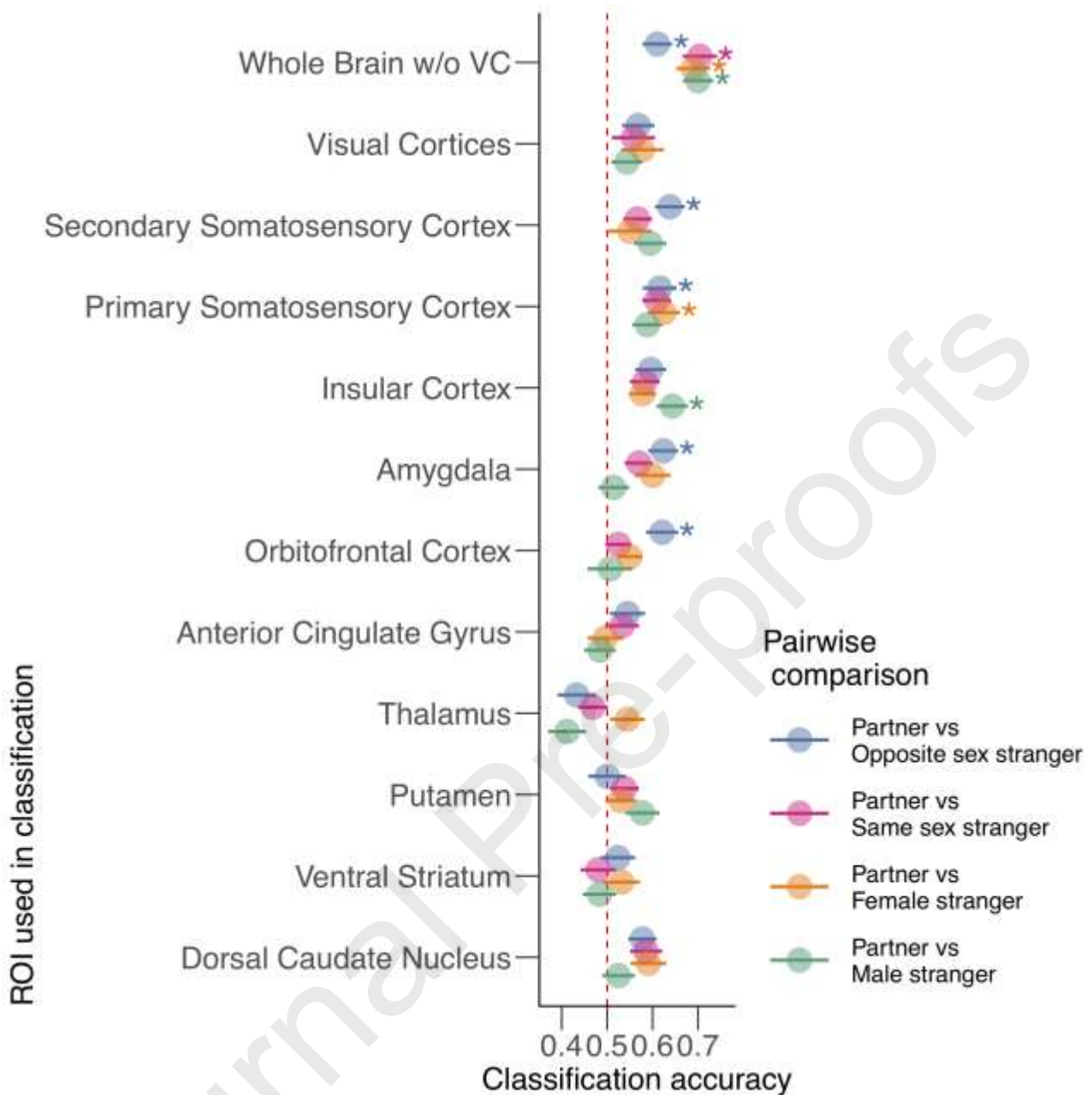


Figure 6 Mean accuracy of classifying actor identity when subject was being touched in various ROIs. Dashed line depicts a priori chance level (0.5), error bars show SEM, * denotes $p < 0.05$ (FDR-corrected). All of the pairwise classifications were possible in the whole brain minus VC ROI. Moreover, classifying partner vs. opposite sex stranger was possible in S1, S2, amygdala, and orbitofrontal cortex, and classifying partner vs male stranger was possible in the insular cortex. See also **Table S3** for the classification accuracies and exact p-values.

Discussion

Our main finding was that naturalistic social touch is coded in a relationship-specific manner in the primary somatosensory cortices as well as in the insular cortex. Above-chance level accuracy was also found in the amygdala, orbitofrontal cortices, and secondary somatosensory cortices, but only when classifying partner vs. opposite sex stranger. These effects were observed even though the actual kinematics of the social touching were carefully matched, and in the absence of any significant between-condition differences in univariate GLM analyses. This suggests that specific activity patterns, rather than global activity changes, in the somatosensory and insular cortex contain relationship-specific neural codes of social touch.

Self-report data support the notion that social touching is perceived in relationship-specific manner, with respect to both touching allowances and felt pleasure (**Figure 2**). Touch by partners was rated statistically significantly more pleasant than touch by strangers. While modulating the pleasantness of the touch in isolation is not possible in a highly naturalistic set-up such as the one used here, prior studies have shown that pleasure derived from felt (Nummenmaa et al., 2016b; Kreuder et al., 2017) and seen (Gazzola et al., 2012) touch is dependent on who the subject believes is touching them, independent of the kinematic properties of the touch. Moreover, touch allowance zones were significantly larger for partners versus strangers, in accordance with previous studies (Suvilehto et al., 2015, 2019). Interestingly, effects of social relationship on touching were much more profound at the subjective rather than neural level.

As expected, GLM revealed activation in the contralateral S1 and bilateral S2 during social touch (**Figure 3**). This accords with previous work using naturalistic touch (Gazzola et al., 2012; Malinen et al., 2014). Activation was also found in bilateral insular cortex, in agreement with other studies using soft, stroking touch (Olausson et al., 2002; Björnsdóttir et al., 2009). However, GLM responses were indistinguishable between different actors.

In contrast, MVPA revealed relationship-specific responses to both touch and seeing hand in the peripersonal space. Toucher identity could be classified significantly above chance level from the whole brain minus VC ROI (**Figure 4**). The classification was conducted using leave-one-participant out cross-validation, resulting in activity patterns that were consistent across subjects. More misclassifications occurred between different actors in the same action (e.g. touch by male and female stranger) and very few misclassifications occurred between action types (e.g. see female stranger's hand at 20 cm or 5cm). This suggests that action-specific signals were more consistent across subjects than the relationship-specific signals (**Figure S4**).

One of our findings was that the amplitudes of the net BOLD responses e.g. in somatosensory cortices did not distinguish between the touches by a partner and a stranger, whereas the multivariate analysis resulted in significant differences. This could result from two mutually non-exclusive reasons. First, the information regarding social aspects of touch is likely represented in cell populations interleaved at sub-voxel resolution in these areas. Second, the net gain effect of social dimensions of touching in the studied areas could be insufficient or absent, and social information is represented in a multivariate, distributed pattern. Both alternatives however suggest the interpretation that within a single region (such as somatosensory cortices or insular cortices) there is no simple amplitude modulation by social touching, but rather a more fine-grained representation of social information.

Regions of interest

The MVPA revealed two distinct sets of regions with different characteristic response profiles. First, in a number of ROIs (amygdala, OFC, S2), we were able to classify between two touchers, but only for specific toucher pairs. This suggests that these areas process a single feature or a limited set of features of the socio-affective stimulus. Second, in S1 and IC the classifier was able to distinguish between all three touchers. These areas have close structural and functional connections

to the regions able to classify some pairs of touchers, thus it is possible that S1 and IC combine the feature-specific information from the single-tasking areas to a more complete representation of the social stimulus.

Thus, S1 and IC appear to contain the most detailed representation of touchers' identity, as evidenced by classification results (**Figure 5**). These regions are typically considered to be parts of the bottom-up somatosensory pathway, yet in our study they were modulated by social aspects of touch in the absence of differential tactile kinematics. Similar results of top-down modulation of sensory processing in S1 have been found by modifying subjects' belief of tactile stimulus by labeling skin cream as 'basic' or 'rich' (McCabe et al., 2008) or by giving subjects placebo nasal spray the subjects believed to impact pleasantness of touch stimuli (Ellingsen et al., 2013). In line with this, also the assumed identity of the person touching the subject modulates S1 activation (Gazzola et al., 2012; Scheele et al., 2014). The present study using multivariate approach demonstrates that such high-level social information about the touchers' identity is represented in the somatosensory cortices even in a naturalistic case, where the subject is touched by different individuals to whom they have different social relationships.

In addition to classifying experienced touch, the classifier was also able to distinguish actor identity in S1 when subject was seeing hand but not experiencing touch (**Figure 5**). This might be related to anticipatory coding of tactile sensations in S1. For example, tickling and anticipation of tickling lead to similar S1 responses (Carlsson et al., 2000). This accords with the result showing S1 activation when we see touch-like movement in the peripersonal space (Schaefer et al., 2012). Therefore, processing seen and felt touch on S1 might not exclusively reflect the tactile stimulation but could also be modulated by relationship-specific expectations related to the social touch.

Insular cortical activation distinguished all three actor categories above chance level. In particular, IC was the only ROI where we were able to classify all of the three actors both when the

strangers were defined as-is (partner, male stranger, female stranger) and when they were defined with respect to the sex of the subject (partner, same sex stranger, opposite sex stranger). This suggests a very detailed representation of toucher identity and could be related to a specialized group of neurons called C-Tactile (CT) afferents (Vallbo et al., 1993; Olausson et al., 2002).

The touch stimulus in this study was administered at 4 cm/s and since it was administered by hand, it was neutral in temperature. These touch features are optimal for CT afferents (Ackerley et al., 2014), which synapse to IC (Olausson et al., 2002). CT-optimal touch has been shown to convey sensual/erotic as well as affiliative intentions (Kirsch et al., 2017). The erotic intentions associated with CT-optimal touch, and the difference in how welcome such touches are from different people (Nummenmaa et al., 2016a), might explain why these classifications were successful.

In contrast with S1 and IC, a number of other ROIs only contained very specific social information regarding touch. Amygdala, OFC, and S2 could be used to classify between touch from the partner vs. touch from an opposite sex stranger, i.e. when the sex of the toucher was kept constant (**Figure 6**). However, any of the other classifications failed in these areas. It is not clear whether OFC, amygdala, and S2 process the same feature of the stimulus.

The role of OFC in processing the pleasantness and unpleasantness of touch is well established (Rolls et al., 2003, 2008; McCabe et al., 2008; McGlone et al., 2012). Changes in OFC activation do not necessarily need to relate to tactile properties of the touch, but it can also reflect whether subject believes they are touched by their partner or an opposite sex stranger (Kreuder et al., 2017).

On the other hand, amygdala processes both positively and negatively valenced stimuli as long as they are salient (Adolphs, 2010). Limited evidence exists for the role of amygdala in affective tactile processing (Rolls et al., 2003; Ellingsen et al., 2013). It has been suggested that amygdala codes for the biological relevance of affective touch and thus provides input to other regions on the

importance of the touch stimulus (Voos et al., 2013). Possibly, both amygdala and OFC could be responding to the differential pleasantness (or unpleasantness) in touch by partner versus stranger.

S2 integrates somatosensory input with audiovisual input (Keysers et al., 2010). It has been reliably activated by both affective and discriminative processing of touch (Morrison, 2016). Ellingsen et al. (2013) found that placebo, which subjects believed to be oxytocin, enhanced the S2 BOLD response to pleasant touch and diminished S2 BOLD response to painful touch. This suggests that S2 might also relate to the experienced pleasantness of the touch. However, a recent rTMS study indicates that S2 might be related to the perception of touch intensity, not touch pleasantness (Case et al., 2017). Thus, the specific socio-affective feature of touch that S2 encodes is debatable.

There are strong structural and functional connections between the areas with a detailed representation of actor identity and the areas with a more limited representation of actor identity. IC is functionally connected to OFC (Cauda et al., 2011) and amygdala (Shi and Cassell, 1998). S1 has dense reciprocal connections to S2 (Disbrow et al., 2003) and is also connected to the OFC (Carmichael and Price, 1995). Therefore, it is possible that amygdala, OFC, and S2 process more simplistic features of the stimuli and provide feedback to the early sensory processing areas, which then combine the input from multiple regions. However, the temporal cascade of affective processing of social touch cannot be directly tested with the present fMRI design.

Our results suggest that the observed effects may be related to the subjective pleasantness. For example, the results of MVPA were more robust for touch than for the visual conditions and the differences in pleasantness were stronger for touch than for visual conditions (**Figures 2 and 4**). However, if the results reflected only the change in pleasantness, we would expect to see similar classification accuracies for partner vs same sex stranger and partner vs opposite sex stranger, as the pleasantness ratings of same and opposite sex strangers are similar. Instead, we see several areas (S1, S2, amygdala, OFC) differentiate between partner and opposite sex stranger but not

partner and same sex stranger (see **Table S3** for easy comparison). This suggests that the signal is not entirely pleasantness-driven. It is still possible, and even likely, that pleasantness explains some of the results we are seeing but more studies are needed to disentangle these factors.

Limitations and future directions

Our results show social relationship specific changes in the neural correlates of social touch. Earlier research has shown that merely the belief of the toucher identity can modulate the affective meaning of the touch (Gazzola et al., 2012; Nummenmaa et al., 2016b). Due to the naturalistic experimental design, it was not feasible to modulate the different affective factors of the touch, such as pleasantness, independent of the toucher identity. Therefore, it is not possible to determine and evaluate the specific features of the qualia which drive these results. It is entirely possible that factors which were not even measured, such as stimulus salience and familiarity, could be driving these results. For example, it is possible that the BOLD-fMRI classifier is mainly picking up signal related to the saliency of the touch, which could however be pleasantly valenced for partner and unpleasantly valenced for the stranger. However, the present data does not allow disentangling these two options.

Pleasantness is a likely candidate for the source of at least some of the effects presented here. However, subjective pleasantness ratings for the stimuli were collected only once, after the imaging session. This was done to ensure that the results stem from the experience of being touched rather than the act of evaluating the stimulus, since evaluating (as opposed to purely observing) affective stimuli is known to impact cortical activity in several of our areas of interest (Hutcherson et al., 2005). Due to this experimental design choice, the self-report measures cannot be directly contrasted with the neural correlates for the stimuli. However, this is an interesting and relevant research question. Future studies should consider passive measures of affect, such as collecting

physiological measures during the scanning, which might enable acquiring stimulus-by-stimulus reactions without interfering with experiencing the stimulus.

In this study we imaged both parties of heterosexual romantic couples. The data from the male and female participant of each couple were collected on the same day and same confederates were used as strangers for both parties. It is possible that the two parties of one romantic couple are not fully statistically independent due to these factors. Earlier studies (Coan et al., 2006) suggest that couple-specific information, such as relationship satisfaction, might modulate the neural correlates of touch such that people more satisfied in their relationships would show a larger difference between being touched by their spouse versus a stranger. However, we did not collect this information from our participants and would not have sufficient power to do reliable correlational analyses. Moreover, it is possible that there is some systematic kinematic or temporal variation in the touches of the partners and strangers that could contribute to the classification accuracy. Unfortunately, touch kinematics could not be directly measured in this study. However, if such variation would exist, it should be considered as an inherent feature of the way humans touch close ones versus strangers, rather than a mere sensory confound. It is also possible that the dyads have established mutual touching routines or patterns over their relationship that make them immediately recognizable thus increasing the statistical dependency between the subject pairs. However, we safeguarded against such possibilities with the standardization of the touching task.

In contrast with previous studies (Gazzola et al., 2012; Scheele et al., 2014), we were not able to classify between the two strangers. This might be explained by different instructions to subjects. In the earlier studies, the subjects were instructed to imagine that they were looking for a date and that the toucher was “coming on to them”, whereas in our experiment the subject was instructed to simply observe the stimulus. Imagining the romantic interest led to more extreme differences in

pleasantness ratings in, for example, Gazzola et al.'s (2012) study compared to this study, potentially contributing to different outcomes.

More generally, the contextual factors related to social touch and their impact on the interpretation and processing of social touch are not very well understood. For example, when conducting a physical examination, it is acceptable for a doctor to touch their patient in ways which would not be acceptable if the same two individuals would meet at a social situation. Even within a given environment and within a given social or professional relationship, like doctor and patient at a hospital, situational cues can impact the message conveyed by touch (Davin et al., 2019). More research is needed to establish the role of different contextual factors in how social touch messages are conveyed and understood and how they impact the cortical processing of touch.

In conclusion, our findings reveal several brain regions involved in the relationship-specific processing of social touch. This was the first study to investigate the neural correlates of social touch by one's real-life romantic partner and contrast it to touch by male and female strangers. The most detailed representation of relationship-specific social touch was found in early sensory areas, namely primary somatosensory cortex and insular cortex.

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References:

- Ackerley R, Backlund Wasling H, Liljencrantz J, Olausson H, Johnson RD, Wessberg J (2014) Human C-tactile afferents are tuned to the temperature of a skin-stroking caress. *J Neurosci* 34:2879–2883.
- Adolphs R (2010) What does the amygdala contribute to social cognition? *Ann N Y Acad Sci* 1191:42–61.
- Björnsdóttir M, Löken L, Olausson H, Vallbo A, Wessberg J (2009) Somatotopic organization of gentle touch processing in the posterior insular cortex. *J Neurosci Off J Soc Neurosci* 29:9314–9320.
- Carlsson K, Petrovic P, Skare S, Petersson KM, Ingvar M (2000) Tickling expectations: neural processing in anticipation of a sensory stimulus. *J Cogn Neurosci* 12:691–703.
- Carmichael ST, Price JL (1995) Sensory and premotor connections of the orbital and medial prefrontal cortex of macaque monkeys. *J Comp Neurol* 363:642–664.
- Case L, Laubacher CM, Olausson H, Wang B, Spagnolo PA, Bushnell MC (2016) Encoding of Touch Intensity But Not Pleasantness in Human Primary Somatosensory Cortex. *J Neurosci* 36:5850–5860.
- Case L, Laubacher CM, Richards EA, Spagnolo PA, Olausson H, Bushnell MC (2017) Inhibitory rTMS of secondary somatosensory cortex reduces intensity but not pleasantness of gentle touch. *Neurosci Lett* 653:84–91.
- Cauda F, D’Agata F, Sacco K, Duca S, Geminiani G, Vercelli A (2011) Functional connectivity of the insula in the resting brain. *Neuroimage* 55:8–23.
- Coan JA, Schaefer HS, Davidson RJ (2006) Lending a Hand: Social Regulation of the Neural Response to Threat. *Psychol Sci* 17:1032–1039.

- Çukur T, Nishimoto S, Huth AG, Gallant JL (2013) Attention during natural vision warps semantic representation across the human brain. *Nat Neurosci* 16:763–770.
- Davidovic M, Bjornsdotter M, Olausson H, Bjornsdotter M (2016) Posterior superior temporal sulcus responses predict perceived pleasantness of skin stroking. *Front Hum Neurosci* 10.
- Davin L, Thistlethwaite J, Bartle E, Russell K (2019) Touch in health professional practice: a review. *Clin Teach* 16:559–564.
- Disbrow E, Litinas E, Recanzone GH, Padberg J, Krubitzer L (2003) Cortical connections of the second somatosensory area and the parietal ventral area in macaque monkeys. *J Comp Neurol* 462:382–399.
- Dunbar RIM (1991) Functional significance of social grooming in primates. *Folia Primatol (Basel)* 57:121–131.
- Dunbar RIM (2010) The social role of touch in humans and primates: behavioural function and neurobiological mechanisms. *Neurosci Biobehav Rev* 34:260–268.
- Ellingsen D-M, Wessberg J, Eikemo M, Liljencrantz J, Endestad T, Olausson H, Leknes S (2013) Placebo improves pleasure and pain through opposite modulation of sensory processing. *Proc Natl Acad Sci U S A* 110:17993–17998.
- Eriksson Hagberg E, Ackerley R, Lundqvist D, Schneiderman J, Jousmäki V, Wessberg J (2019) Spatio-temporal profile of brain activity during gentle touch investigated with magnetoencephalography. *Neuroimage* 201.
- Francis S, Rolls ET, Bowtell R, McGlone F, O'Doherty J, Browning a, Clare S, Smith E (1999) The representation of pleasant touch in the brain and its relationship with taste and olfactory areas. *Neuroreport* 10:453–459.
- Gazzola V, Spezio ML, Etzel JA, Castelli F, Adolphs R, Keysers C (2012) Primary somatosensory cortex discriminates affective significance in social touch. *Proc Natl Acad Sci* 109:E1657-66.

- Heslin R, Nguyen TD, Nguyen ML (1983) Meaning of touch: The case of touch from a stranger or same sex person. *J Nonverbal Behav* 7:147–157.
- Hutcherson CA, Goldin PR, Ochsner KN, Gabrieli JD, Feldman Barrett L, Gross JJ (2005) Attention and emotion: Does rating emotion alter neural responses to amusing and sad films? *Neuroimage* 27:656–668.
- Keysers C, Kaas JH, Gazzola V (2010) Somatosensation in social perception. *Nat Rev Neurosci* 11:417–428.
- Kirsch LP, Krahé C, Blom N, Crucianelli L, Moro V, Jenkinson PM, Fotopoulou A (2017) Reading the mind in the touch: neurophysiological specificity in the communication of emotions by touch. *Neuropsychologia*.
- Kress IU, Minati L, Ferraro S, Critchley HD (2011) Direct skin-to-skin vs. indirect touch modulates neural responses to stroking vs. tapping. *Neuroreport* 22:646–651.
- Kreuder A-K, Scheele D, Wassermann L, Wollseifer M, Stoffel-Wagner B, Lee MR, Hennig J, Maier W, Hurlmann R (2017) How the brain codes intimacy: The neurobiological substrates of romantic touch. *Hum Brain Mapp* 00.
- Lucas M V., Anderson LC, Bolling DZ, Pelphrey KA, Kaiser MD (2015) Dissociating the Neural Correlates of Experiencing and Imagining Affective Touch. *Cereb Cortex* 25:2623–2630.
- Malinen S, Renvall V, Hari R (2014) Functional parcellation of the human primary somatosensory cortex to natural touch. *Eur J Neurosci* 39:738–743.
- McCabe C, Rolls ET, Bilderbeck A, McGlone F (2008) Cognitive influences on the affective representation of touch and the sight of touch in the human brain. *Soc Cogn Affect Neurosci* 3:97–108.
- McGlone F, Olausson H, Boyle JA, Jones-Gotman M, Dancer C, Guest S, Essick G (2012) Touching and feeling: Differences in pleasant touch processing between glabrous and hairy skin in

humans. *Eur J Neurosci* 35:1782–1788.

Morrison I (2016) ALE meta-analysis reveals dissociable networks for affective and discriminative aspects of touch. *Hum Brain Mapp* 00:n/a-n/a.

Nummenmaa L, Glerean E, Hari R, Hietanen JK (2014) Bodily maps of emotions. *Proc Natl Acad Sci* 111:646–651.

Nummenmaa L, Suvilehto JT, Glerean E, Santtila P, Hietanen JK (2016a) Topography of human erogenous zones. *Arch Sex Behav* 45:1–10.

Nummenmaa L, Tuominen L, Dunbar R, Hirvonen J, Manninen S, Arponen E, Machin A, Hari R, Jääskeläinen IP, Sams M (2016b) Social touch modulates endogenous μ -opioid system activity in humans. *Neuroimage* 138:242–247.

Olausson H, Lamarre Y, Backlund H, Morin C, Wallin BG, Starck G, Ekholm S, Strigo I, Worsley K, Vallbo a B, Bushnell MC (2002) Unmyelinated tactile afferents signal touch and project to insular cortex. *Nat Neurosci* 5:900–904.

Perini I, Morrison I, Olausson H (2015) Seeking pleasant touch: neural correlates of behavioral preferences for skin stroking. *Front Behav Neurosci* 9.

Power JD, Barnes KA, Snyder AZ, Schlaggar BL, Petersen SE (2012) Spurious but systematic correlations in functional connectivity MRI networks arise from subject motion. *Neuroimage* 59:2142–2154.

Rolls ET, Grabenhorst F, Parris BA (2008) Warm pleasant feelings in the brain. *Neuroimage* 41:1504–1513.

Rolls ET, O'Doherty J, Kringelbach ML, Francis S, Bowtell R, McGlone F (2003) Representations of pleasant and painful touch in the human orbitofrontal and cingulate cortices. *Cereb cortex* (New York, NY 1991) 13:308–317.

Särkkä S, Solin A, Nummenmaa A, Vehtari A, Auranen T, Vanni S, Lin FH (2012) Dynamic

retrospective filtering of physiological noise in BOLD fMRI: DRIFTER. *Neuroimage* 60:1517–1527.

Schaefer M, Heinze H-JJ, Rotte M (2012) Embodied empathy for tactile events: Interindividual differences and vicarious somatosensory responses during touch observation. *Neuroimage* 60:952–957.

Scheele D, Kendrick KM, Khouri C, Kretzer E, Schläpfer TE, Stoffel-Wagner B, Güntürkün O, Maier W, Hurlemann R (2014) An oxytocin-induced facilitation of neural and emotional responses to social touch correlates inversely with autism traits. *Neuropsychopharmacology* 39:2078–2085.

Schirmer A, Teh KS, Wang S, Vijayakumar R, Ching A, Nithianantham D, Escoffier N, Cheok AD (2011) Squeeze me, but don't tease me: Human and mechanical touch enhance visual attention and emotion discrimination. *Soc Neurosci* 6:219–230.

Shi C-J, Cassell MD (1998) Cortical, thalamic, and amygdaloid connections of the anterior and posterior insular cortices. *J Comp Neurol* 399:440–468.

Suvilehto JT, Glerean E, Dunbar RIM, Hari R, Nummenmaa L (2015) Topography of social touching depends on emotional bonds between humans. *Proc Natl Acad Sci* 112:13811–13816.

Suvilehto JT, Nummenmaa L, Harada T, Dunbar RIM, Hari R, Turner R, Sadato N, Kitada R (2019) Cross-cultural similarity in relationship-specific social touching. *Proc R Soc B Biol Sci* 286:20190467.

Tricoli C, Olausson H, Sailer U, Ignell H, Croy I (2013) CT-optimized skin stroking delivered by hand or robot is comparable. *Front Behav Neurosci* 7:208.

Vallbo Å, Olausson H, Wessberg J, Norrsell U (1993) A system of unmyelinated afferents for innocuous mechanoreception in the human skin. *Brain Res* 628:301–304.

Voos AC, Pelphrey KA, Kaiser MD (2013) Autistic traits are associated with diminished neural

response to affective touch. Soc Cogn Affect Neurosci 8:378–386.

Journal Pre-proofs

Supplementary materials

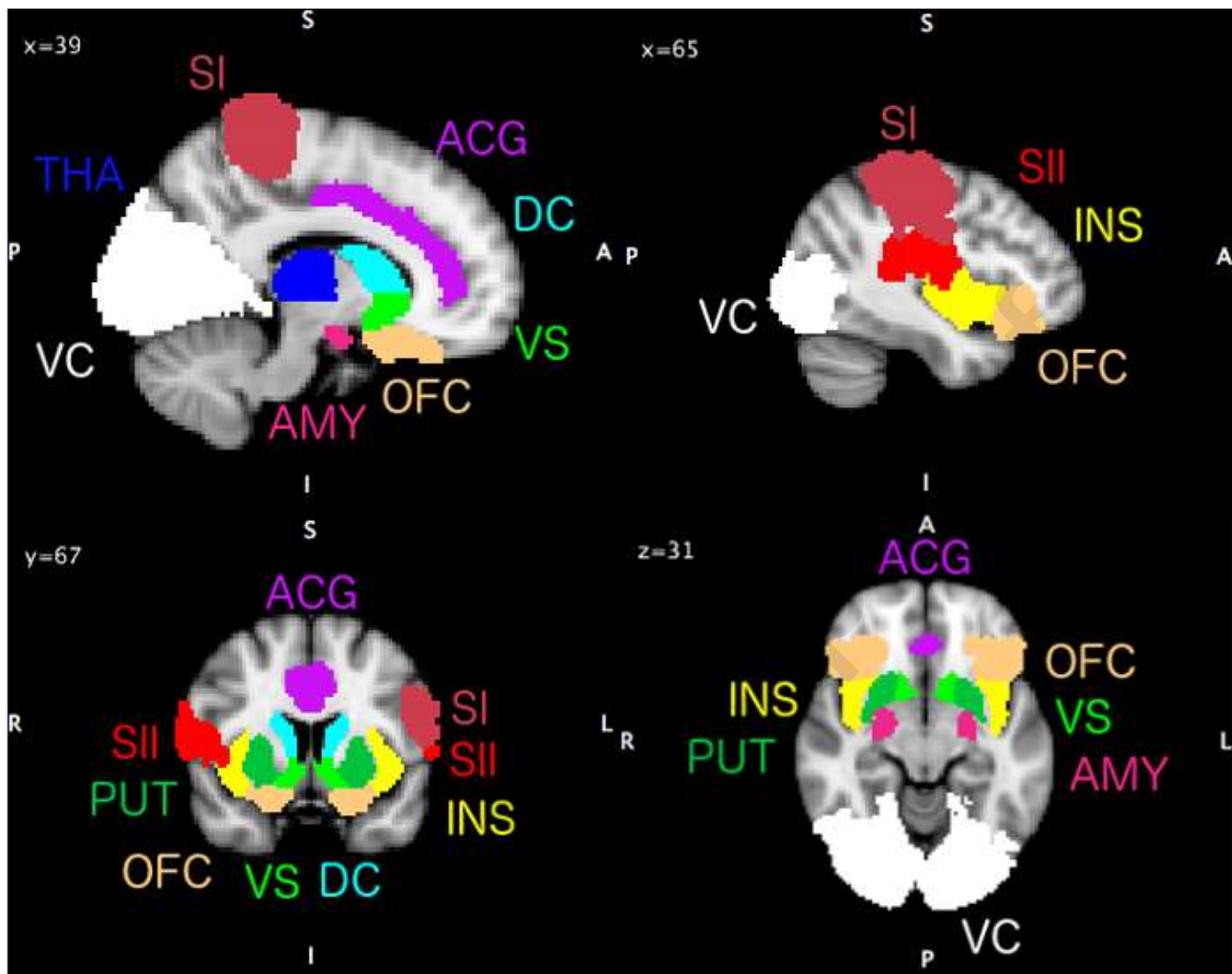


Figure S1 Visualisations of the bilateral ROI used in classification analyses. The abbreviations are (ACG) anterior cingulate gyrus, (AMY) amygdala, (DC) dorsal caudate nucleus, (INS) insular cortex, (OFC) orbitofrontal cortex, (PUT) putamen, (SI) primary somatosensory cortex, (SII) secondary somatosensory cortex, (THA) thalamus, (VS) ventral striatum. Whole brain minus VC mask is the inverse of the VC mask, and is not separately visualised.

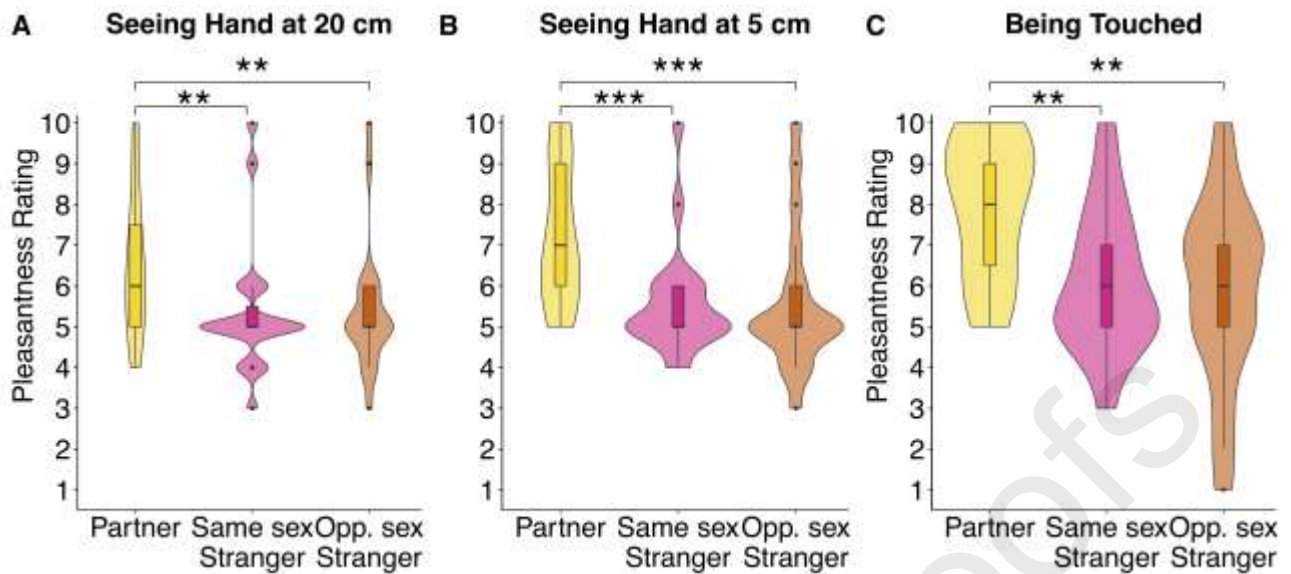


Figure S2 Pleasantness ratings for each experimental condition presented for partner, same sex stranger, and opposite sex stranger. In contrast to comparisons of male and female stranger, the pleasantness ratings for same sex stranger and opposite sex stranger are not statistically different in any condition. Pleasantness ratings in every condition are significantly different for partner vs both strangers.

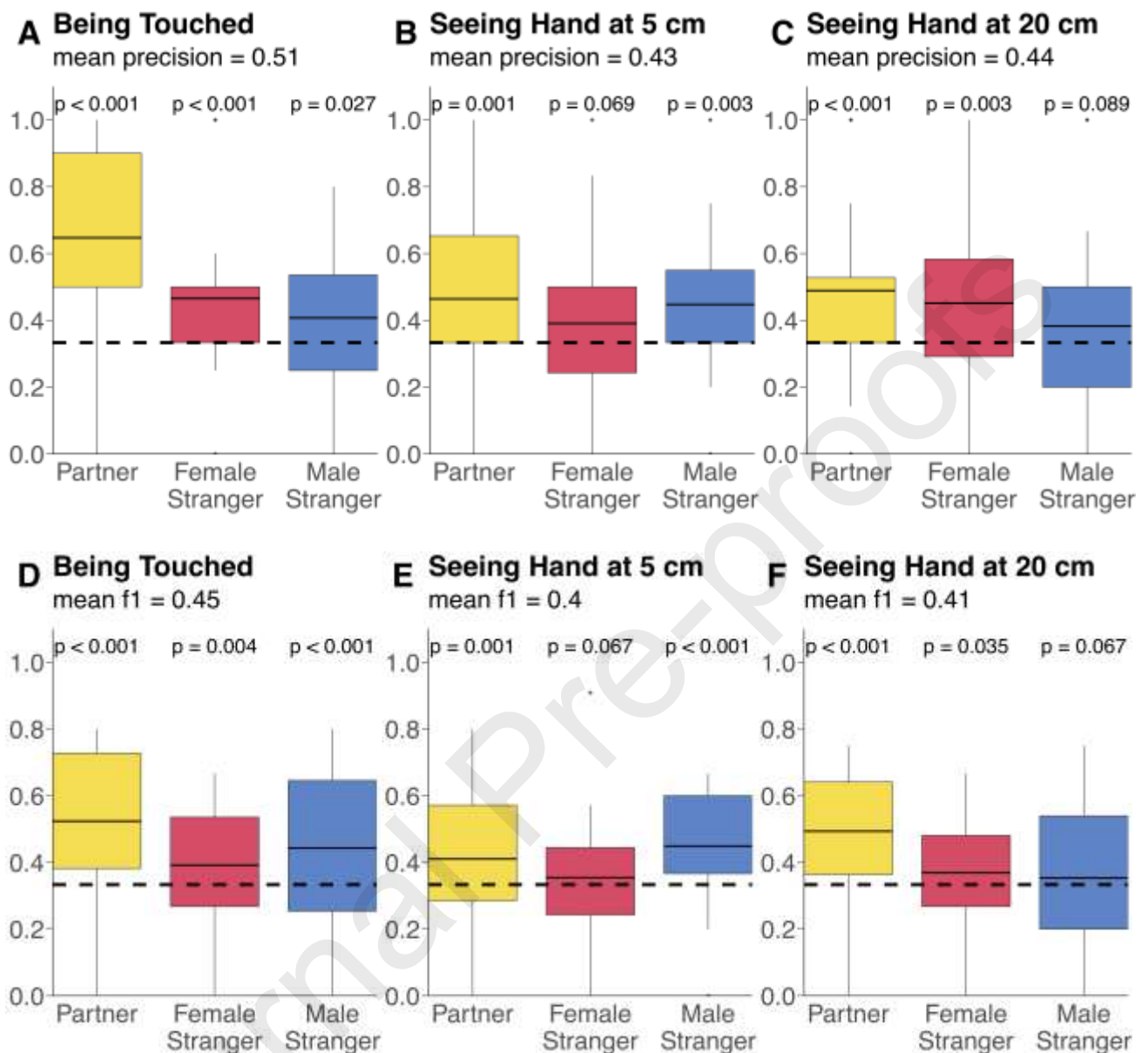
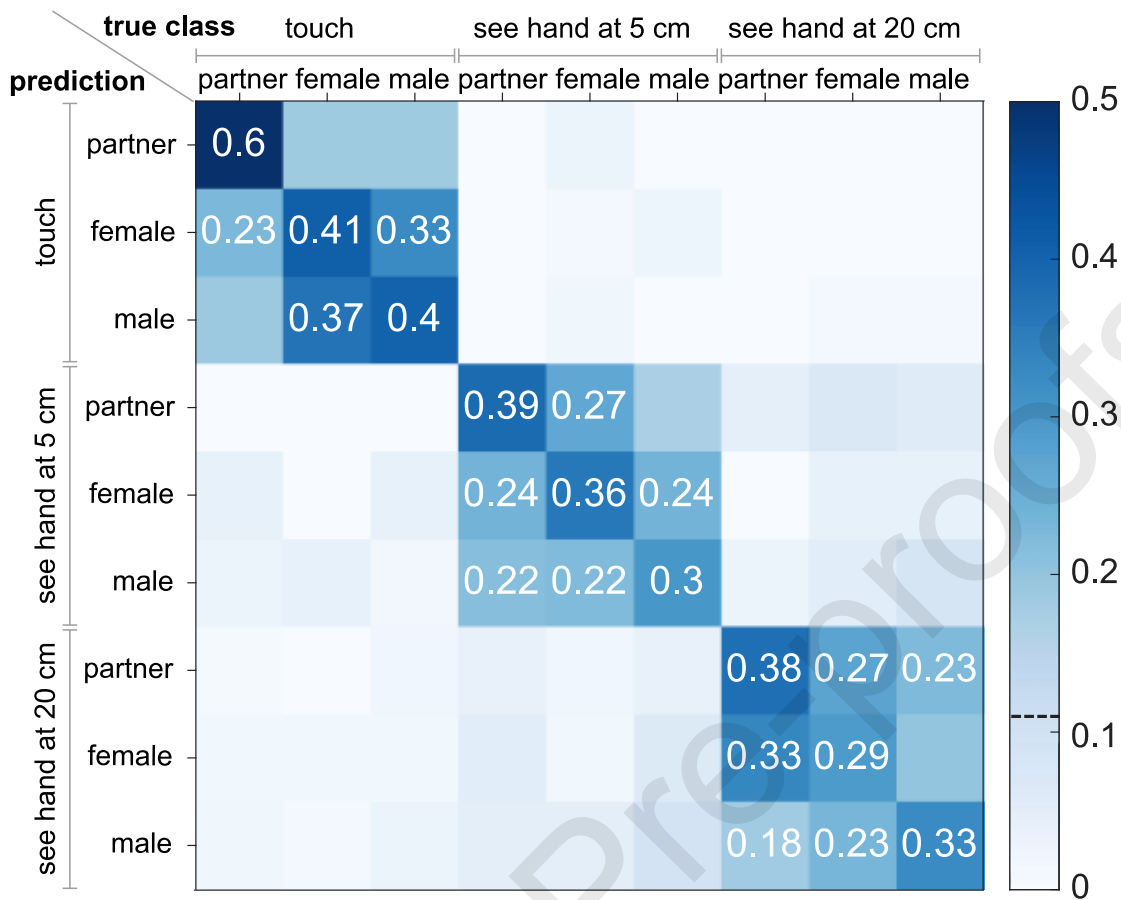


Figure S3 Different classifier performance measures. Top row (A-C) shows precision, and bottom row (D-F) shows F₁, a measure combining recall (Figure 5) and precision (this figure, A-C), when classifying actors within an action type (for example, “whose hand is the subject seeing”). Central line shows mean, edges of box show 25th and 75th quantile. Significance levels were obtained by permutation testing the classifier with 10 000 permutations, reported *p*-values are FDR-corrected for multiple comparisons.

A. Normalized to show precision



B. Normalized to show recall

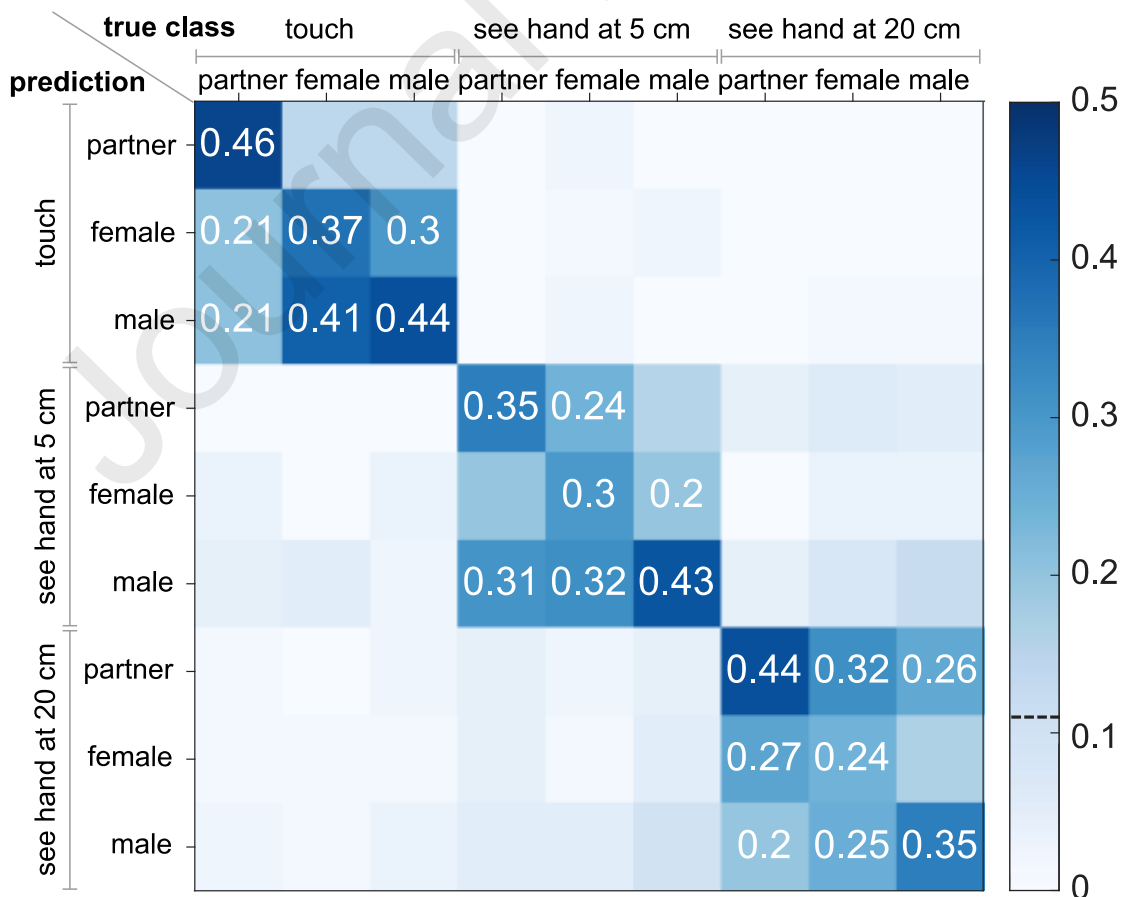


Figure S4 Un-thresholded confusion matrix of between-subjects classification of all actions using whole brain minus VC mask. More confusions occur between different confederate categories in same action (e.g. touch by male and female strangers) and very few misclassifications occur between action types. Entries in A) are normalized to show precision on the diagonal and entries in B) are normalized to show recall on the diagonal. Average precision (A) or recall (B) from leave one subject out cross validation is shown in white for cells above chance level. This was determined by bootstrapping confidence interval from classification folds (computational chance level 1/9 is outside 95% confidence interval bounds).

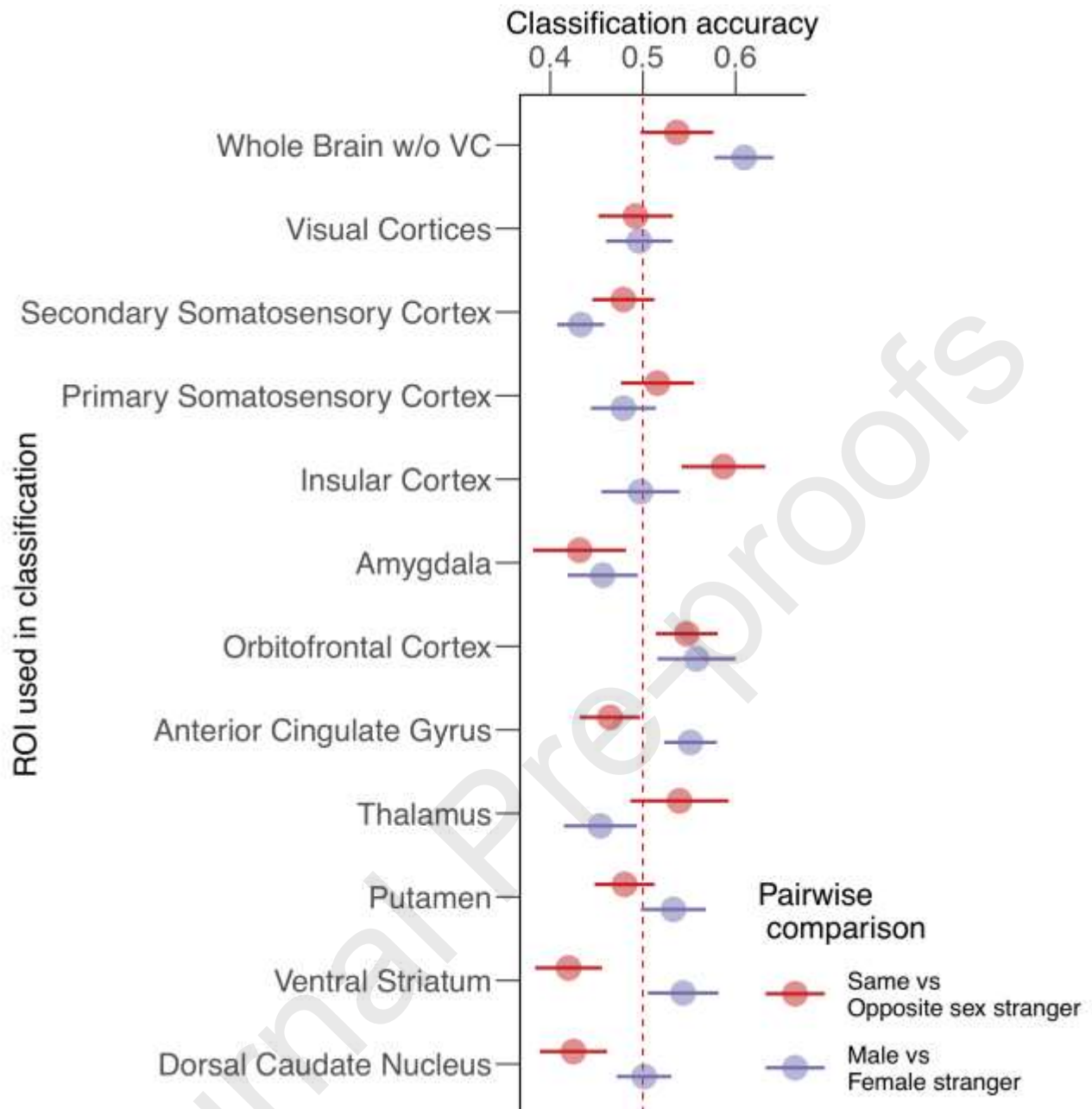


Figure S5 Complementing Figure 6 – binary classification accuracies for the two strangers.

Classifying between the two strangers was not possible in any of the inspected ROI, regardless of whether they were labeled as male and female stranger or same and opposite sex stranger.

Table S1: SPM ANOVA results for main effect of actor identity (3 levels: partner, female stranger, male stranger) and main effect of action (3 levels: see hand at 20cm, see hand at 5cm, touch) and their interaction. The coordinates are in MNI space, minimum cluster size 10 voxels. The associated NIfTI files can be accessed at <https://neurovault.org/collections/3263/>.

	position			cluster size (voxels)	z score	p value (FDR corr)
	x	y	z			
main effect of actor						
	20	-26	26	33	5.07	0.022
	-30	-32	42	63	4.85	0.022
	30	-30	-16	24	4.62	0.022
main effect of action						
	6	-90	-12	61622	7.19	0.00
	-28	36	-8	25	3.49	0.003
	-36	-16	-40	60	3.42	0.004
	-34	-22	-24	28	3.16	0.007
	-34	-48	20	87	3.13	0.007
	18	4	28	27	3.08	0.008
	8	-36	-50	23	3.08	0.008
	46	-10	-26	32	3.03	0.009
	-8	-4	74	24	2.83	0.014
	-10	34	-22	58	2.83	0.014
	6	-36	16	75	2.8	0.015
	16	-30	-26	14	2.75	0.017
	-54	-34	-24	134	2.72	0.018
	16	-38	6	20	2.71	0.019
	36	8	24	67	2.70	0.019
	-30	24	-34	16	2.66	0.021
	-38	8	40	17	2.60	0.023
	-4	46	52	10	2.58	0.024
	-18	-32	-22	14	2.54	0.027
	-2	-32	-22	13	2.50	0.028
	-14	8	60	15	2.49	0.029
	-62	-14	-20	16	2.39	0.036
	-24	6	64	27	2.38	0.036
	10	36	-24	13	2.36	0.037
interaction actor x action						
	40	-34	42	39	5.23	0.007

Table S2: Classification accuracies in touch. Accuracies shown are estimates derived from 19 folds of cross validations (leave one subject out), p-values have been determined by running 10 000 permutations with shuffled class labels. Right-adjusted cells signal cases that are significantly above chance level. P-values have been FDR corrected due to multiple comparisons.

ROI	partner, male stranger, female stranger		partner, opposite sex stranger, same sex stranger	
	accuracy	p value	accuracy	p value
Whole brain w/o VC	0.49	0.001	0.47	0.001
VC	0.37	0.149	0.35	0.411
S2	0.38	0.142	0.39	0.103
S1	0.42	0.024	0.38	0.194
Insular cortex	0.43	0.014	0.42	0.023
Amygdala	0.37	0.194	0.41	0.068
OFC	0.38	0.142	0.38	0.187
ACG	0.29	0.901	0.32	0.696
Thalamus	0.29	0.901	0.30	0.823
Putamen	0.38	0.142	0.35	0.411
Ventral striatum	0.39	0.142	0.35	0.411
Dorsal caudate	0.39	0.142	0.32	0.710
chance level 0.33				

Table S3: Accuracies shown are estimates derived from 19 folds of cross validations (leave one subject out), p-values have been determined by running 10 000 permutations with shuffled class labels. Bold text signals cases that are significantly above chance level at $\alpha=0.05$. P-values have been FDR corrected due to multiple comparisons.

ROI	partner v opposite sex stranger		partner v same sex stranger		partner v male stranger		partner v female stranger	
	acc.	p	acc.	p	acc.	p	acc.	p
Whole brain w/o VC	0.61	0.018	0.70	0.001	0.70	0.001	0.69	0.001
VC	0.57	0.108	0.56	0.187	0.54	0.334	0.58	0.114
S2	0.64	0.018	0.57	0.168	0.59	0.087	0.55	0.219
S1	0.62	0.018	0.61	0.070	0.59	0.087	0.62	0.029
Insular cortex	0.60	0.052	0.58	0.128	0.64	0.013	0.58	0.114
Amygdala	0.62	0.018	0.57	0.168	0.51	0.563	0.60	0.090
OFC	0.62	0.018	0.52	0.345	0.51	0.563	0.55	0.219
ACG	0.54	0.238	0.53	0.329	0.48	0.661	0.50	0.508
Thalamus	0.43	0.901	0.47	0.729	0.41	0.956	0.54	0.244
Putamen	0.50	0.520	0.54	0.327	0.58	0.139	0.53	0.287
Ventral striatum	0.52	0.356	0.48	0.674	0.48	0.661	0.53	0.287
Dorsal caudate	0.58	0.103	0.59	0.128	0.52	0.493	0.59	0.098
chance level 0.5								