Distinction of self-produced touch and social touch at cortical and spinal cord levels

Rebecca Boehme[a,b,1], Steven Hauser[c], Gregory J. Gerling[c], Markus Heilig[a], and Håkan Olausson[a,b,d]

[a]Center for Social and Affective Neuroscience, Linköping University, 58185 Linköping, Sweden; [b]Center for Medical Image Science and Visualization, Linköping University, 58185 Linköping, Sweden; [c]Systems Engineering, University of Virginia, Charlottesville, VA 22904; and [d]Department of Clinical Neurophysiology, Linköping University Hospital, 58185 Linköping, Sweden

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Differentiation between self-produced tactile stimuli and touch by others is necessary for social interactions and for a coherent concept of "self." The mechanisms underlying this distinction are unknown. Here, we investigated the distinction between self- and other-produced light touch in healthy volunteers using three different approaches: fMRI, behavioral testing, and somatosensory-evoked potentials (SEPs) at spinal and cortical levels. Using fMRI, we found self–other differentiation in somatosensory and sociocognitive areas. Other-touch was related to activation in several areas, including somatosensory cortex, insula, superior temporal gyrus, supramarginal gyrus, striatum, amygdala, cerebellum, and prefrontal cortex. During self-touch, we instead found deactivation in insula, anterior cingulate cortex, superior temporal gyrus, amygdala, parahippocampal gyrus, and prefrontal areas. Deactivation extended into brain areas encoding low-level sensory representations, including thalamus and brainstem. These findings were replicated in a second cohort. During self-touch, the sensorimotor cortex was functionally connected to the insula, and the threshold for detection of an additional tactile stimulus was elevated. Differential encoding of self- vs. other-touch during fMRI correlated with the individual self-concept strength. In SEP, cortical amplitudes were reduced during self-touch, while latencies at cortical and spinal levels were faster for other-touch. We thus demonstrated a robust self–other distinction in brain areas related to somatosensory, social cognitive, and interoceptive processing. Signs of this distinction were evident at the spinal cord. Our results provide a framework for future studies in autism, schizophrenia, and emotionally unstable personality disorder, conditions where symptoms include social touch avoidance and poor self-vs.-other discrimination.

sensorimotor integration | self-touch | affective touch | sensory attenuation | self-concept

Differentiating between self and nonself is crucial for interactions with one's physical and social environment. On a basic level, people need to know the boundary between self and nonself. This embodied self is likely established through afferent information from all senses (1). Within this framework, tactile sensation, together with proprioception and interoception, plays an important role for embodiment (2–7) and thereby for the broader sense of self (8–10).

To differentiate between self and other, the brain needs to predict the sensory consequences of self-produced actions (11–13). According to the efference copy theory, the brain suppresses perception of self-produced sensory stimuli (14, 15). A consequence of this cancellation is the observation that people cannot tickle themselves (15). The suggested mechanism for this phenomenon is an attenuation of cortical sensory processing (16–18). Such attenuation has been found for auditory and visual processing (19–21). As sensory modalities differ based on their specific physical constraints, these findings cannot be generalized to the tactile domain (22). It is presently unknown whether attenuation of cortical sensory processing is also the mechanism through which the distinction between self- vs. other-touch is determined.

Previous brain-imaging studies on self–other distinction in the tactile domain are inconsistent, reporting weaker activation (16), deactivation (18), and even stronger activation during self-produced tactile stimulation (23). However, these early studies are constrained by small sample sizes (n = 8–12). They also used tools for stimulation, which are less ecologically valid stimuli for the study of social touch or self-touch. Skin-to-skin touch and touch by tools are processed differently in the brain: skin-to-skin touch strongly activates the insula and the anterior cingulate cortex (ACC) (24–26). Touch by other plays a key role in social bonding in humans, nonhuman primates, and other species alike (27). Understanding the neural processes that allow the organism to discriminate between other- vs. self-touch is important for understanding social cognition and conditions in which it is impaired.

Being touched by others to signal affective content is related to interoception (28) and is processed differently from discriminative touch, which most often serves the purpose of exploration. Being touched by others is specifically associated with the activation of areas involved in social cognition, including the insular cortex and the posterior superior temporal sulcus (29–31). It remains unclear how the brain differentiates self- and other-produced slow, light skin-to-skin touch—the kind of touch people use to stroke their loved ones (32).

Behavioral studies suggest that self-touch and/or being touched by others [especially slow stroking (33)] contribute to

Significance

The earliest way humans can learn what their body is and where the outside world begins is through the tactile sense, especially through touch between parent and baby. In this study, we demonstrated differential processing of touch from self and others at cortical and spinal levels. Our results support top-down modulation of dorsal horn somatosensory processing, as recently shown in animal studies. We provide evidence that the individual self-concept relates to differential self- vs. other-processing in the tactile domain. Self- vs. other-distinction is necessary for successful social interaction with others and for establishing a coherent self. Our results suggest an association between impaired somatosensory processing and a dysfunctional self-concept, as seen in many psychiatric disorders.

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[1]To whom correspondence should be addressed. Email: rebecca.bohme@liu.se.

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establishing the bodily self (5, 34), and perceptual differences between self-touch and touching someone else might drive social interactions (35). Considering the important role touch plays in social interactions and development (36), it is important to establish how ecologically valid conditions of self-touch and being touched by others are differentiated.

Here, we asked whether the brain processes skin-to-skin touch of a type often used to signal affective content differently when delivered by oneself ("self-touch") or someone else ("other-touch"). In study 1, we compared blood oxygen level-dependent (BOLD) response during self-touch and other-touch during fMRI. We hypothesized that a greater difference between activations during other-touch and self-touch in the insula and the ACC would be associated with the individual self-concept (37). Insula and ACC are brain areas related to interoception (38), body ownership (39, 40), salience (41), and self–other distinction (42).

During self-touch in study 1, we found widespread deactivation, while activations were only related to the movement of the hand. Other-touch was related to activation in somatosensory and social cognition areas. We investigated the consequences of this finding further in study 2 using three tests in a second cohort: (*i*) we tested tactile detection thresholds to assess perceptual consequences of the observed deactivation. (*ii*) We asked participants where they perceived the touch sensation, because during self-touch we only found activation in primary somatosensory cortex (S1) contralateral to touching hand, not contralateral to the touched arm. (*iii*) During fMRI, we tried to manipulate the deactivation during self-touch by applying an additional tactile stimulus on the touched area, which participants were supposed to detect. We hypothesized to overcome the attenuation of BOLD signals related to self-touch by this modulation of the salience of tactile input in the touched area.

In studies 1 and 2, we found a widespread robust deactivation during self-touch including in areas involved in early stages of somatosensory processing such as the thalamus and the brainstem. Therefore, and consistent with recent findings of a prominent cortical control of mechanosensory dorsal horn processing (43), we asked if signs of this self–other difference can be found already at spinal cord levels. This was tested in study 3 using somatosensory-evoked potentials (SEPs), which were measured at cortical and cervical levels.

Results

Study 1. An overview of activations and deactivations during the three different conditions can be found in Table 1. For more details, see *SI Appendix*.

Functional imaging of social touch. A network of areas known to be involved in social touch and social cognition showed a significantly increased BOLD signal in response to receiving touch by the experimenter (one-sample *t* test: other-touch > 0; Fig. 1, *Top*, Table 1, and *SI Appendix*, Table S1). This included the somatosensory cortex insula, superior temporal gyrus, supramarginal gyrus, striatum, amygdala, cerebellum, inferior parietal lobule, and prefrontal areas.

The difference between self-touch and other-touch. As expected, both self-touch and object-touch were associated with an activation of the left primary motor cortex (M1) (contralateral to the moving hand), left somatosensory cortex, premotor, and striatal areas (one-sample *t* test: self-touch > 0, object-touch > 0). We did not find any activation of somatosensory areas in the right hemisphere (contralateral to the stationary arm). For the self-touch condition, we found a widespread deactivation, including the insula, ACC, superior temporal gyrus, amygdala, parahippocampal gyrus, and prefrontal areas (one-sample *t* test: self-touch < 0; Fig. 1, *Bottom*, Table 1, and *SI Appendix*, Table S2).

The main contrast of interest in this experiment was the difference between other-touch and self-touch (other-touch > self-touch) (Fig. 2, *Top* and Table 2). We found a clear distinction in multiple regions: ACC, superior temporal gyrus, striatum, prefrontal areas, and amygdala. Notably, the right S1 (contralateral to the stationary arm) was significantly more activated when receiving touch than during self-touch ([20 −38 68], $t = 8.09$, $P < 0.001$). In addition, we found conjunctions for the two conditions [i.e., significant activation during other-touch Λ deactivation during self-touch (44)] bilaterally in the amygdala, in the right striatum, superior temporal gyrus, posterior cingulate, and prefrontal areas (Fig. 2, *Bottom* and *SI Appendix*, Table S3).

To explore this difference between self-touch and other-touch, we compared parameter estimates for the three conditions in a posteriori regions of interest (ROIs) implicated in somatosensory processing (brainstem, thalamus, S1, posterior and anterior insula, ACC; Fig. 3). There was a statistically significant difference in activation between the conditions [$F(18, 140) = 18.4$, $P < 0.0005$, Wilks' $\Lambda = 0.075$] for all regions except for the right S1 (contralateral to the stationary arm) [all regions: $F(2) > 14$, $P < 0.0005$; right S1: $F(2) = 2.5$, $P = 0.086$]. A post hoc test in the right somatosensory cortex revealed a difference in parameter estimates between the conditions other-touch and self-touch ($P = 0.034$, with Fisher's least-significant difference) but not when comparing these conditions to object-touch (other vs. object: $P = 0.61$; self vs. object: $P = 0.11$).

To explore the effect of the self-touch–related deactivation, we contrasted self-touch with object-touch (object-touch > self-touch). This contrast revealed that the deactivation was specific for the self-touch condition, therefore not related to the movement, which was also occurring during object-touch (*SI Appendix*, Table S4). There was no area in which we found a higher BOLD signal for self-touch than for object-touch (self-touch > object-touch).

During self-touch, M1 and S1 showed functional connectivity with areas involved in motor control (descending motor pathways, *SI Appendix*, Figs. S3 and S4 and Tables S5 and S6) and with left posterior insula [with left M1: [−42 −6 −2], $t = 5.67$, $P = 0$ 001; and left S1: [−42 −6 −2], $t = 5.04$, $P = 0.005$; both family-wise error (FWE) small volume correction for posterior insula ROI].

Study 2.

Behavior.

Perception rating. Considering the finding during self-touch of widespread deactivation and the lack of activation in the right S1 (contralateral to the touched forearm), we asked participants in study 2, where they felt the touch during self-touch and other-touch. We used a scale that offered a nuanced response possibility (0 = left arm, 10 = right hand). Subjects reported to perceive touch by the experimenter on their left arm (mean = 1.75 ± 3.2), while the perception during self-touch was rated as in between left arm and right hand [mean = 5.9 ± 3.7; not significantly different from midpoint 5: $t(15) = 0.663$, $P = 0.52$].

Detection thresholds. We tested tactile perception thresholds during the different touch conditions. Fifteen out of 17 subjects were able to detect the weakest filament (0.08 mN), when no additional stimulation occurred. The two subjects who failed to detect this filament were able to detect the next weakest one (0.39 mN) (mean = 0.12 ± 0.1).

During being-touched by the experimenter, the mean force of the weakest perceived filament was 4.85 mN (±5.73; range: 0.08–19.61). During self-touch, the mean detection force was 13.41 mN (±9.45; range: 0.08–39.23), i.e., >100 times higher than for the "no additional stimulation" condition. During object-touch, the mean force of the above-threshold von Frey hair was 0.15 mN (±0.1; range: 0.08–0.39). A Kruskal–Wallis test detected a statistically significant difference in detection thresholds between conditions [$\chi^2(3) = 49.92$, $P < 0.001$; Fig. 4]. A post hoc Wilcoxon signed-rank test showed that detection thresholds during self-touch were significantly higher than in the three other conditions (nothing: $Z = -3.5$, $P < 0.001$; object: $Z = -3.5$, $P < 0.001$; other: $Z = -3.3$, $P = 0.001$). The relatively larger variance during the self-touch condition prompted a comparison of variances using

Table 1. Overview over activations (↑) and deactivations (↓) during the three different touch conditions

Region	Hemisphere	Other-touch	Self-touch	Object-touch
Superior frontal gyrus	R	↑	↓	
	L		↑↓	
Medial frontal gyrus	R	↑	↓	
	L		↑↓	↑
Middle frontal gyrus	R		↓	
	L	↑	↑↓	
Inferior frontal gyrus	R	↑	↓	↑
	L	↑		↑
Postcentral gyrus	R	↑↓		↑
	L	↑	↑	↑
Precentral gyrus	R	↑↓	↓	↑
	L	↑↓	↑↓	↑
Paracentral lobule	L		↑	
Paracentral gyrus	L			↑
Insula	R	↑	↓	
	L	↑		↑
Superior temporal gyrus	R	↑	↓	
	L		↓	
Middle temporal gyrus	R	↑	↓	↓
	L	↑	↓	↑
Inferior temporal gyrus	R			↓
Supramarginal gyrus	R	↑	↓	
	L		↓	
Inferior parietal lobule	R	↑		
	L	↑		
Precuneus	R		↓	↓
Cuneus	R	↑		↑
	L	↑		
Superior occipital gyrus	R			↓
	L		↓	
Middle occipital gyrus	R			↓
	L		↑	↑
Inferior occipital gyrus	L	↑		↑
Lingual gyrus	R	↑		↑
	L	↑	↑	↑
Fusiform gyrus	L	↑		
Anterior cingulate	R		↓	
	L		↓	
Cingulate gyrus	R	↑	↓	
	L		↓	
Posterior cingulate	R		↓	
	L		↓	
Subcallosal gyrus	L		↓	
Hippocampus	R		↓	
Parahippocampal gyrus	R	↑	↓	↓
Amygdala	R	↑	↓	
	L	↑		
Putamen	R	↑	↓	
	L	↑		↑
Caudate	R	↑		
	L	↑		
Thalamus	L		↓	↑
Claustrum	R		↓	
	L		↓	
Cerebellum	R	↑↓	↑↓	↑
	L	↑	↓	

The table includes all regions that are significantly activated or deactivated in at least one of the conditions compared with baseline during study 1 ($P < 0.05$; FWE-corrected for the whole brain at the voxel level). Both activation and deactivation (↑↓) might be present in the same area, if they belong to separate clusters within the same anatomical region. For detailed (de-)activation tables, see *SI Appendix*. L, left; R, right.

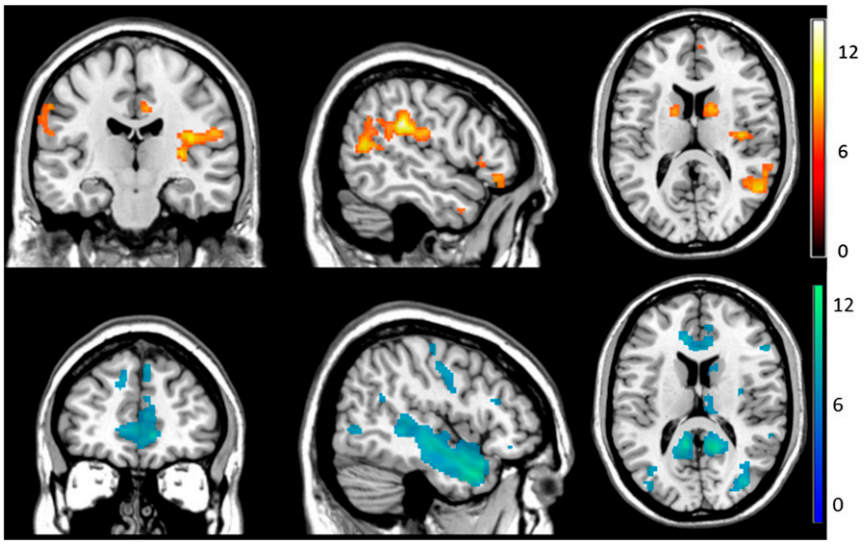

Fig. 1. Distinct BOLD signal during social touch and self-touch. (*Top*) Other-touch activated areas involved in social cognition, display of slices [53 −18 14]. (*Bottom*) Self-touch deactivated a widespread network of areas, display of slices [47 46 15]. Both thresholded at $P < 0.05$; FWE-corrected at the whole brain level; cluster size > 20.

Levene's test of homogeneity of variances. Variances were indeed different when including all three touch conditions [$F(2,48) = 12.9$, $P < 0.001$] but not when comparing variances between self-touch and other-touch [$F(1,32) = 2.6$, $P = 0.116$]. Detection thresholds during self-touch were unrelated to the self-concept clarity scale ($R = -0.24$, $P = 0.42$) and did not explain BOLD signal during self-touch in somatosensory ROIs (all R values < 0.17, all P values > 0.6).

fmri.

Replication of study 1. Regarding the self-other-touch paradigm, we replicated our findings, in this independent sample, using a shortened version of the study 1 paradigm (*SI Appendix*).

Modulation of self-touch–related deactivation via salience manipulation. We hypothesized that directing the subjects' attention to their left forearm would reduce the deactivation during self-touch. The above-threshold filament during self-touch was used during the detection task, and the subjects were able to detect stimulation reliably (mean = 84.67 ± 17.7% correct). However, we found no difference on the whole brain level between self-touch brain processing for the runs with and without salience manipulation (self-touch-detection-run > self-touch-first-run). We also compared β values for the anatomical ROIs along the somatosensory processing pathway between the two runs (*SI Appendix*, Figs. S1 and S2) and found no interaction between run and condition [$F(9, 77) = 0.71$, $P = 0.07$, Wilks' $\Lambda = 0.92$].

Touch Processing Relates to Self-Concept. Based on our a priori hypothesis that the self-concept would be related to touch processing, we performed a correlational analysis with the difference between other- and self-touch in the insula and the ACC—ROIs

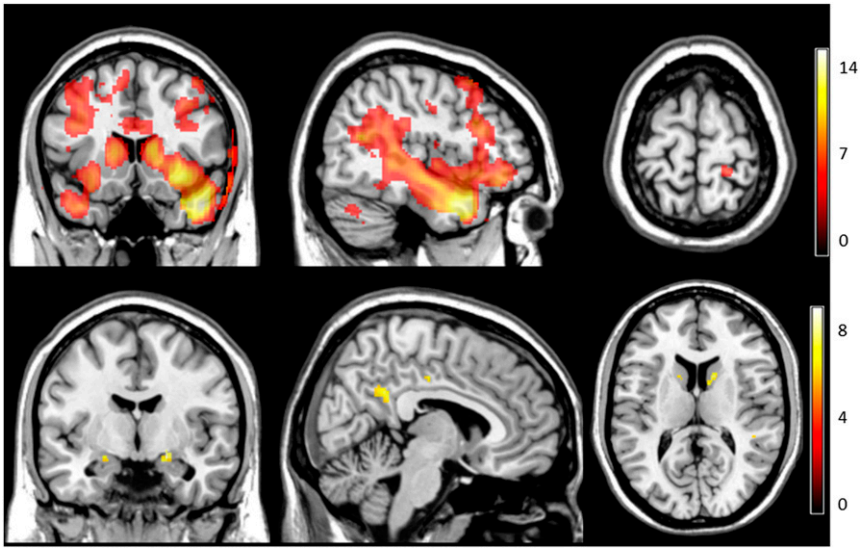

Fig. 2. Differential encoding of other-touch and self-touch. (*Top*) A widespread network showed higher activation for other-touch than for self-touch, display of slices [44 15 69], cluster size > 20. (*Bottom*) Conjunction of activation during other-touch and deactivation during self-touch. Display of slices [6 −6 12], cluster size > 5. Both thresholded at $P < 0.05$; FWE-corrected at the whole brain level.

Table 2. The difference between other-touch and self-touch, study 1

Cluster	Region	Hemisphere	x	y	z	t	P
55159	Amygdala	R	30	−4	−16	14.88	<0.001
			24	−6	−14	13.91	
			28	−4	−24	13.04	
			32	2	−24	12.90	
	Superior temporal gyrus		46	12	−30	14.57	
			36	0	−18	13.91	
			40	16	−30	13.57	
			54	−6	−14	12.88	
			40	12	−38	12.04	
	Insula		44	−15	10	11.32	
	Middle temporal gyrus		54	2	−20	12.99	
	Inferior frontal gyrus		28	12	−12	12.87	
	Cerebellum	L	−20	−78	−36	12.35	
			−16	−84	−34	11.24	
	Anterior cingulate		−2	30	4	11.41	
	Putamen	R	18	6	−4	11.40	
	Middle temporal gyrus		60	−10	−8	11.39	
772	Cerebellum	R	32	−76	−34	8.91	<0.001
			20	−74	−30	8.84	
			24	−76	−28	8.80	
			10	−82	−34	8.27	
			20	−84	−34	8.24	
			38	−70	−30	7.89	
			40	−60	−36	5.78	0.0148
			42	−58	−42	5.69	0.0194
66	Postcentral gyrus	R	20	−38	68	8.09	<0.001
80	Middle frontal gyrus	L	−30	50	2	7.09	<0.001
46	Precentral gyrus	R	42	−10	36	6.14	0.0047

FWE-corrected at the voxel level; $P < 0.05$; cluster size > 20. L, left; R, right.

that are related to interoception and self–other processing (28, 42). Following correction for multiple testing, the self-concept clarity correlated with the BOLD signal for the self–other difference in the left anterior insula ($R = 0.42$, $r^2 = 0.18$, $P = 0.007$) and in the left ACC ($R = 0.442$, $r^2 = 0.2$, $P = 0.004$), i.e., a clearer self-concept was related to more distinctly different BOLD signals during other-touch and self-touch. A relationship of the same directionality existed in the other ROIs, which did not survive correction for multiple comparisons (*SI Appendix*, Fig. S8).

Study 3. We tested if there were signs of differential somatosensory processing during self- and other-touch in SEPs. We found that SEP amplitudes for radial nerve stimulation were lower during self-touch than during other-touch at the cortical level [C3/4: self mean = 1.17 ± 0.56 μV, other mean = 1.5 ± 0.5 μV, $t(9) = 2.9$, $P = 0.018$; CZ: self mean = 0.66 ± 0.3 μV, other mean = 0.89 ± 0.4 μV, $t(9) = 2.6$, $P = 0.029$, Fig. 5*A* (where C3/4 and CZ indicate electrode positions according to the 10–20 system)]. This was specific for self-touch and not related to the movement, as we did not find such a difference between object-touch and other-touch [C3/4: obj. mean = 1.4 ± 0.7 μV, $t = 0.8$, $P = 0.4$; CZ: obj. mean = 0.85 ± 0.41 μV, $t(8) = 0.01$, $P = 0.99$]. Descriptively, amplitudes during object-touch were between the other two conditions. Amplitudes at the cervical level did not differ between other-touch and self-touch [other mean = 0.75 ± 0.38 μV, self mean = 0.83 ± 0.31 μV, $t(7) = 0.56$, $P = 0.58$].

Furthermore, we found shorter latencies for other-touch than for self-touch at the cortical level [C3/4: self mean = 20.94 ± 1.1 ms, other mean = 19.97 ± 0.63 ms, $t(9) = 2.3$, $P = 0.049$; Fig. 5*B*] and at the cervical level [self mean = 15.4 ± 0.9 ms, other mean = 14.34 ± 1.41 ms, $t(7) = 3.4$, $P = 0.012$]. Other-touch did not differ from object-touch [C3/4: obj. mean = 20.17 ± 0.5 ms, $t(8) = 1.5$, $P = 0.15$; CZ: obj. mean = 20.36 ± 0.5 ms, $t(8) = 1.3$, $P = 0.21$; cervical: obj. mean = 14.95 ± 0.6 ms, $t(8) = 1.6$, $P = 0.14$], while cortical latencies were significantly slower during self-touch than during object-touch [C3/4: $t(8) = 2.3$, $P = 0.04$; CZ: $t(8) = 3.1$, $P = 0.007$; cervical: $t(7) = 1.7$, $P = 0.14$].

Discussion

Differentiating between self and others is essential for social abilities and for ignoring self-produced stimuli. Here, we demonstrated how sensory attenuation helps to tell apart self-touch and social touch by others. We found a widespread deactivation during self-touch and an activation during touch by others in areas that are involved in somatosensory processing, social cognition, and salience. The finding was robust and replicated in an independent sample. The self-produced attenuation involved early somatosensory processing areas such as brainstem and thalamus. Contrary to our hypothesis, the attenuation was not overpowered by increased attention toward the touched body part. Behaviorally, the sensory attenuation was reflected in a 100-fold increase in tactile detection thresholds. Furthermore, a difference between the processing of self- and other-touch was evident already at the cervical spinal level: SEP latencies were shorter during being touched than during self-touch. We also found that the differential encoding of self- and other-touch in ACC and insula were associated with the individual self-concept clarity.

Our main goal was to understand how people differentiate between touch stimuli delivered by self or others. We found that a large variety of areas encoded self-touch and other-touch differently, many of which are involved in social and emotional processing. Specifically, superior temporal gyrus and prefrontal cortex have been suggested to be involved in multimodal integration of emotion-carrying stimuli (22). Self-touch was associated with widespread negative changes of the BOLD signal, which are generally assumed to reflect an inhibition of neuronal activity (45, 46). This deactivation is in line with other studies about sensory attenuation (19) and fits well with the efference

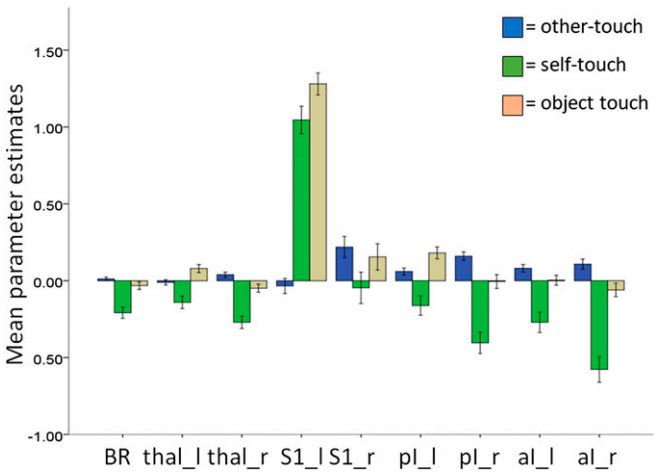

Fig. 3. Parameter estimates for regions involved in processing tactile sensory information differ for the three conditions. Other-touch by the experimenter (blue), self-touch (green), and object-touch (brown); main effect of condition [$F(22, 136) = 18.4$, $P < 0.0005$, Wilks' $\Lambda = 0.063$]. Error bars represent the SE. aI, anterior insula; BR, brainstem; l, left; pI, posterior insula; r, right; thal, thalamus.

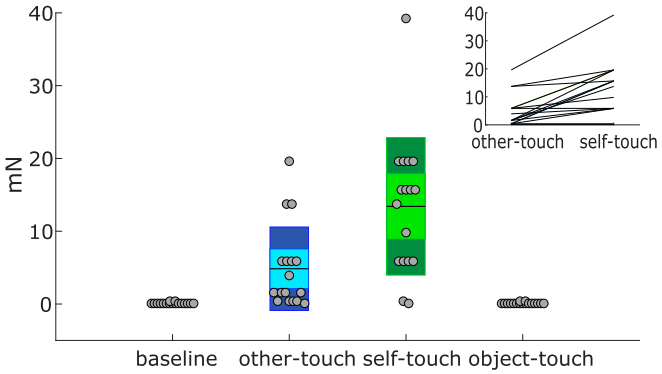

Fig. 4. Detection thresholds for von Frey filaments during four conditions: baseline (no additional touch stimulation), self-touch, other-touch, and object-touch. The plot indicates mean (midline), 95% confidence interval (dark box), one SD (light box), and individual data points. The small plot indicates individual values for each subject during other-touch and self-touch.

copy theory, i.e., that the brain predicts the sensory outcome of its own actions to suppress their perception (11).

Sensory attenuation for self-produced stimuli has been described for tactile stimulation of the glabrous skin (i.e., the palm of the hand) (15–18) but not for social skin-to-skin touch, which is considered part of the interoceptive system (28). One study included brushing of the hairy/skin and reported higher activation in S1 for self-produced than for externally produced stimulation (23). There are important differences between our fMRI study design and previous imaging studies: our results are based on a large sample including a replication in an independent sample, while previous studies had smaller sample sizes (n = 8–12). In addition, we used skin-to-skin stimulation instead of a tool to deliver the tactile stimulation (24–26).

Furthermore, we show that the deactivation was specific for the self-touch condition and not related to the movement per se, since it was significantly different from the object-touch condition. This result would also be predicted by the efference copy theory, because touching an object is an active exploration, while self-touch is usually a self-grooming behavior, during which the produced sensory information is of lower significance.

We found activation in the left S1 (contralateral to the moving hand) but not in the right S1 (contralateral to the stimulated forearm). Exploration mediated by the glabrous skin of the hand perhaps elicits a dominant percept during self-touch of the arm. This is supported by the observation that active tactile exploration enhances perception compared with passive tactile stimulation (47–49).

The insular cortex might be involved in modulation of sensory percepts, as left posterior insula was functionally connected to left S1 and M1 during self-touch. Notably, transcranial magnetic stimulation of the M1 is effective in reducing pain, but the mechanisms are unclear (50–52). Since the insula is a key area in pain processing (53), the pain-inhibiting effect of transcranial magnetic stimulation of the M1 might be mediated by similar interactions of sensorimotor and insular cortices as the sensory attenuation during self-touch.

In the second study, we replicated our findings from study 1 in an independent cohort. Furthermore, we explored the behavioral consequences of the deactivation. Participants reported that they perceived the touch during the self-touch condition in their right hand and in their left arm. This perception was not reflected in the imaging results since we found no activation in right S1 (contralateral to the forearm) during self-touch. One possible explanation for the discrepancy between perception and fMRI results might be that we were unable to detect subtle activations with our imaging paradigm. However, we did find significant activations during other-touch in right S1. Another explanation might be that participants reported a perception in the left arm even though their cortical processing was related to the right hand (54). Prediction of touch sensation in the left arm might affect their evaluation. Alternatively, higher cognitive function, i.e., knowing that their left arm is being touched, might impact the rating, creating an "illusion" of a sensation in the left arm.

Perceptual thresholds reflected the attenuation of brain processing during self-touch. We found that participants were distinctly worse at detecting additional tactile stimuli while they were stroking their own arm. This cannot simply be due to a shift in attention toward the hand movement since the threshold during self-touch was manifold higher than that during both other- and object-touch. Notably, this finding indicates that the efference copy is not perfect—because if it were, the additional stimulation would elicit a prediction error and would be detected easily. Furthermore, the tactile impairment during self-touch is consistent with earlier observations that focal decreases in BOLD signal in somatosensory areas are related to an increase in perceptual thresholds (55).

Self-touch increased the detection threshold even above the force that activates nociceptors [above 5 mN (56)]. This suggests that touching one's own arm might have analgesic effects. However, pain is signaled in distinct neural pathways, and our study was not designed to address pain and touch interactions. Previously "self-anesthesia" was experimentally demonstrated for heat pain (57). The insular cortex is a candidate region for pain inhibition by self-touch since it is an important hub in the processing of pain and interoception (28). Interindividual differences in pain tolerance are related to insular size (58) and to response to pain (59, 60). Therefore, pain perception might change when altering insular activity levels, e.g., via being touched by someone else (61, 62) or via self-touch. This might provide a mechanistic explanation for the widely observed behavior of rubbing a hurting spot of one's own body.

Furthermore, we asked if it was possible to manipulate the sensory attenuation by changing the salience of the tactile stimulus. Specifically, we hypothesized that pairing self-touch with monetary reward in a stimulus-detection paradigm might alter the salience of the sensory input and increase subjects' attention toward their arm. Redirecting attention toward trajectory perturbations during self-touch reduces self-reported ticklishness (63), and perception of tactile stimuli can be attenuated by manipulating body ownership (64). However, we found no difference in cortical processing after increasing subjects' attention toward the touched arm. This suggests that sensory attenuation of self-produced sensory input is a robust mechanism.

Components of cortical and even spinal SEPs were differentially modulated by self-touch and other-touch. The finding of lower amplitudes at the cortical level during self-touch is consistent with our imaging results of a widespread cortical deactivation. The finding that being touched by someone else shortens latencies already at the cervical spinal level suggests that descending modulation alters sensory processing as early as in the dorsal horn.

Motor systems, somatosensory systems, or both might drive the modulation of cortical and spinal cord processing and thereby modulate the sense of body ownership (65). Several studies demonstrate that movement has a gating effect on SEPs (66, 67). This was shown for voluntary movement by the ipsi- and contralateral hand (68), for active and passive movements (69), and by transcranial magnetic stimulation of M1 (70). Similarly, touch can affect SEP components at the cortical level (71, 72), and transcranial magnetic stimulation of S1 reduces SEP amplitudes at the cortical level (73). A combinatory modulation by motor and somatosensory systems is also suggested by our finding that amplitudes during object-touch were in-between other-touch and self-touch. In addition, functional connectivity of motor and somatosensory areas with the insula during self-touch further strengthens this hypothesis.

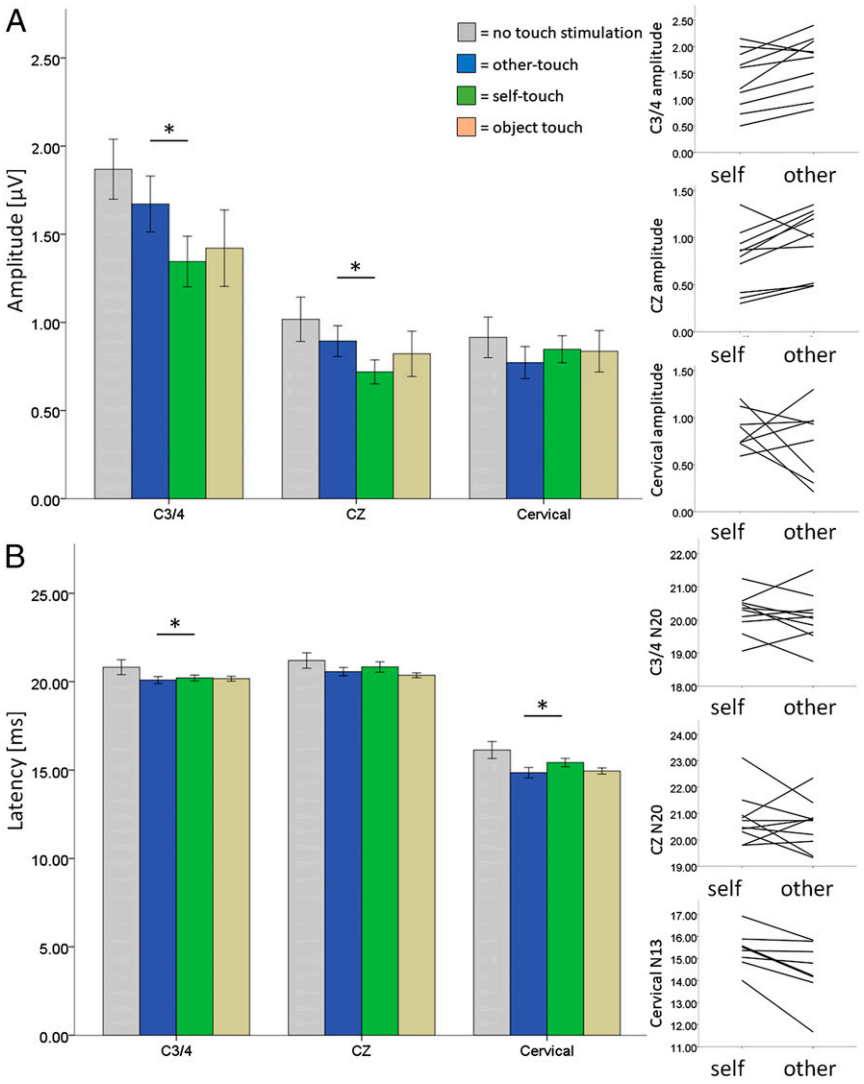

Fig. 5. Amplitude and latency of SEPs differs between other-touch and self-touch. (*Left*, *A*) Amplitudes at the cortical level (C3/4 and CZ) were higher for other-touch than for self-touch. (*Left*, *B*) Latencies at the cortical level (C3/4) and at the cervical level were shorter for other-touch than for self-touch. Gray indicates no touch stimulation; blue, other-touch; green, self-touch; brown, object-touch. Error bars indicate SE. (*Right*) Line plots depicting individual values for self-touch and other-touch. *$P < 0.05$.

A previous study, which found no modulation by touch attribution (human vs. machine) of early components of electrophysiological measures (74), emphasizes the importance of bottom-up signals during early processing of tactile stimuli. However, we obtained a shortened latency at the spinal cord level during other-touch, demonstrating that top-down signaling can also be important for early sensory processing. This suggests top-down modulation of tactile inputs, possibly allowing contextual information to influence somatosensory processing already in the dorsal horn. It is suggested that the N13 potential component of the cervical SEP is generated by gray matter in the dorsal horn (75, 76), possibly by interneurons (77, 78). As demonstrated in mice, neurons in the dorsal horn receive extensive inputs from cortical regions and from interneurons, and it is suggested that the low-threshold mechanoreceptor "recipient zone" of the dorsal horn performs complex processing similar to the retina (43, 79). Indeed, context-specific top-down modulation at the human spinal cord level has been recently reported for nocebo effects (80). Touch by others usually is a highly relevant stimulus—be it a warning sign or a romantic cue. Therefore, it seems pertinent that descending pathways render our tactile system more excitable for touch by others compared with self-generated signals.

Participants who were less sure about "what kind of person they are" (37) showed less of a difference between self-touch and other-touch in both the left ACC and left insula. The ACC is implicated in self–other distinctions (42), and the insula plays an important role in interoception and bodily awareness, thereby contributing to establishing a self-concept (38). Somatosensory and insular cortices, together with brainstem areas, may provide a base representation of the self (81, 82), while prefrontal and cingulate cortices form a higher-order representation. Participants with a clearer self-concept might be better at differentiating between stimuli arising from themselves and from others. Alternatively, participants who differentiate more clearly between signals coming from themselves and others might have developed a stronger self-concept clarity (8, 9).

Conclusion

Self-produced touch led to a widespread deactivation in the brain, which clearly differentiated it from affective touch by someone else. This differentiation was robust and emerged already at early

stages of sensory processing. Lower cortical SEP amplitudes during self-touch supported this finding. On the behavioral level, sensory attenuation elevated perceptual thresholds during self-touch. Spinal SEPs were faster during other-touch compared with self-touch, suggesting context-specific top-down modulation of somatosensory perception at the level of the spinal cord. Our experimental paradigms are well suited for further investigations in psychiatric patients with dysfunctional self–other differentiation and altered interoceptive abilities, e.g., in autism, schizophrenia, or borderline personality disorder. The paradigms should also be of interest for mechanistic studies of chronic pain conditions with impaired suppression of nociception and for understanding the analgesic effects of motor cortex stimulation.

Methods

Participants. A total of 54 healthy volunteers participated; 27 (13 male; age, 23.4 ± 3.2 y) were part of the first study, 17 (8 male; age, 27.3 ± 7.3 y) were part of the second study, and 10 (4 male; age, 27.7 ± 6 y) were part of the third study. Exclusion criteria were any psychiatric disorder, alcohol or substance abuse, or any other major health concern as assessed during a structured telephone interview. The Linköping Regional Ethics Review Board, the local ethics committee, approved the study (2016/360-31), and written informed consent was obtained after complete study description. All subjects filled out the self-concept clarity scale (37) and received monetary compensation. Relevant data are accessible at https://zenodo.org/record/1482906 (83).

Study 1: Self-Other-Touch Paradigm. Participants were first trained in an MRI simulator system (PST MR Simulator System; BlindSight GmbH). Here, they were acquainted with the scanner environment, received instructions about the task, and trained to keep their head still while performing the stroking movement. Head movements were tracked, and subjects viewed their performance on a screen in real time (MoTrak Head Motion Tracking System; Psychology Software Tools). Through this feedback, participants learned to minimize head movements while moving their arm.

Across all experiments, three different conditions were utilized: self-touch, other-touch, and object-touch. During "self-touch," participants stroked their own forearm. During "other-touch," they were stroked by the experimenter. During "object-touch," participants stroked a pillow. Our main interest was the difference between self-touch and other-touch. The third condition, the object-touch, was a control for movement during self-touch. Participants were instructed to gently stroke their left forearm, which was placed on their belly, like they would stroke someone they like, using index and middle fingers of their right hand (32). In the object-touch condition, they were instructed to perform the same movement on a rectangular pillow filled with sand with a soft, skin-like surface. Subjects viewed instructions on a screen through goggles (VisuaStim Digital; Resonance Technologies). In a separate session, we used motion-tracking equipment to record the hand-to-forearm contact characteristics of two of the participants to confirm that there was no consistent difference in stroking velocity or touched area between self-touch and other-touch (*SI Appendix*). The textual cues were presented in Swedish for 3 s: "Active, please stroke your arm"; "Active, please stroke the object"; "Passive, your arm will be stroked by the experimenter." When the text turned green, the participant was stimulated or had to perform the stimulation as long as the text was on the screen, i.e., during a period of 12 s. The experimenter was standing next to the scanner bore and received auditory cues on when to perform the stroking action via headphones. The experimenter watched the motion that the participant was doing and mimicked this as closely as possible. Each condition occurred 10 times with 12 s of rest between each stroking block, resulting in a total length of 13 min.

Study 2: Detection Paradigm. Study 2 had two aims: to replicate the findings from study 1 in an independent cohort of participants and to study the effect of salience manipulation during self-touch. In the first run, participants performed a shortened version of the self-other-touch task (five repetitions of each condition, resulting in a total length of 6 min). In the second run, the participants were instructed to signal the presence of an additional weak tactile stimulation during self-touch (see below). Correct answers led to monetary reward to further increase the salience of perception from the left arm. They were not informed about this second run until after the first run.

Before entering the scanner, participants of the second cohort completed a tactile detection threshold test using von Frey monofilaments (Bioseb). Subjects sat comfortably, resting their left, exposed arm on their belly. They were blindfolded and instructed to report if they felt the stimulation with the filament during four conditions (order counterbalanced across subjects): without any additional stimulation, while stroking their left arm with their right hand, while stroking the object, and while being stroked by the experimenter on the left arm. The filaments were presented in an ascending-descending order (0.08–78.5 mN). The perceptual threshold was defined as the smallest filament that was detected in at least 5 out of 10 trials. Stimulations during fMRI were made with filament forces at the individually determined perception threshold during self-touch.

Since we found only motion-related activation during self-touch in study 1 (see *Results*), we asked if the touch perception during self-touch was restricted to the moving hand. This question was addressed in a psychophysical rating run performed after the anatomical scan. Participants stroked their own arm and were stroked on the left arm by the experimenter (each condition occurred twice). After stroking, they were asked "Where did you feel the stimulation?", and presented with a visual analog scale ranging from the "left arm" to "right hand." A cursor could be moved between these two endpoints using two buttons. We then ran a shortened version of the self-other-touch paradigm (5 instead of 10 repetitions per condition; 6 min).

In the second run, participants were instructed to pay close attention to their left arm and to try to detect stimulation with the filament during the self-touch condition. This paradigm contained the same three conditions: self-touch (10 repetitions), other-touch (10 repetitions), and object-touch (5 repetitions). Object-touch was only included for consistency and was not of particular interest in this run. In four of the self-touch trials, the experimenter stimulated the left forearm (close to the wrist) that the participant was stroking, while the participant's stroking hand was moving in a proximal direction, by providing approximately 2 s of indentation with the filament as in the detection task. An actual stimulation only occurred in 4 out of the 10 self-touch trials, because we were interested in the effect of enhanced attention toward the left arm, not in the actual effect of the filament stimulation. After the 12-s stroking interval, a question appeared on the screen, asking if they felt any stimulation by the filament. Participants responded via one of two buttons ("yes" or "no") on a button box, using the left index and middle finger. Correct answer led to the feedback "correct, +10 Swedish crowns (SEK, ∼1 Euro)," and incorrect answer led to the feedback "incorrect, −10 SEK," and the subjects were paid according to their performance. MRI data from two subjects of the second cohort had to be excluded (one because of technical problems and the other because of abnormalities in brain morphology) resulting in fMRI data from 15 subjects.

fMRI. For both studies, a 3.0 Tesla Siemens scanner (Prisma; Siemens) with a 12-channel head coil was used to acquire T2-weighted echo-planar images (EPIs) containing 48 multiband slices (repetition time: 1,030 ms; echo time: 30 ms; slice thickness: 3 mm; matrix size: 64 × 64; field of view: 488 × 488 mm^2; in-plane voxel resolution: 3 mm^2; flip angle: 63°). In study 1, we collected 801 EPIs per subject. In study 2, we collected 418 EPIs during the replication (first) run and 868 during the detection (second) run. T1-weighted anatomical images were also acquired. fMRI data were analyzed using statistical parametric mapping (SPM12; Wellcome Department of Imaging Neuroscience; https://www.fil.ion.ucl.ac.uk/spm) in Matlab R2016a (MathWorks). The following steps were performed: motion correction, coregistration of the mean EPI and the anatomical image, spatial normalization to the Montreal Neurological Institute T1 template, and segmentation of the T1 image using the unified segmentation approach (84). Normalization parameters were applied to all EPIs. Finally, all images were spatially smoothed with an isotropic Gaussian kernel of 6-mm full width at half-maximum.

For statistical analysis of the BOLD response, the general linear model approach was used as implemented in SPM12. For the self-other-touch paradigm (study 1), blocks of stimulation (self, other, and object) were convolved with the hemodynamic response function. Additional regressors of no interest were the cue phase, which included the motor preparation and the period of 1 s after the active conditions, when subjects stopped their movement and put their arm back into a resting position. To account for movement associated variance, realignment parameters were included as regressors-of-no-interest. Because this paradigm might be prone to more movement artifacts, we also included the first temporal derivative of motion parameters in *x*,*y*,*z* directions plus additional regressor censoring scans with more than 1-mm scan-to-scan movement (85). In addition, we compared movement parameters between conditions and found no significant difference [$F(12, 146) = 0.756$, $P = 0.69$]. Individual contrast images were taken to a random effects group-level analysis, where one-sample and two-sample *t* tests were used. In the self-other-touch paradigm, contrasts of interest were self-touch and being-touched as well as the difference between these two conditions. Furthermore, we included the object-touch condition as a control for movements during self-touch and compared self-touch to object-touch.

For the detection paradigm (study 2), we performed the same analysis with the additional regressor-of-no-interest "detection," containing those self-touch trials, when actual stimulation with the monofilament occurred.

To correct for multiple comparisons, statistics were reported using FWE correction at the voxel level across the whole brain. For a posteriori exploration of β values in key regions for somatosensory processing (brainstem, thalamus, S1, insula), we used anatomical ROIs as provided in the aal-wfu-pickatlas (86). ROIs of the anterior and posterior insular were based on ref. 87. For the conjunction analysis, we used the conjunction-null-hypothesis approach, as provided in SPM12 (44, 88). In addition, we analyzed psychophysical interaction during self-touch with seeds at the individual peaks in M1 and S1 under the hypothesis to find functional connectivity with the insula (cf. *SI Appendix*).

In study 2, we aimed to replicate our findings from study one and also compared self-touch–related activation during the first run (basic self-other-touch task) and the second run (detection), resulting in the contrast [self-touch_run1 < self-touch(increased salience/no stimulation)_run2].

Correlation of BOLD Signals with Self-Concept Clarity. A correlational analysis of self-concept-clarity values and the differential activation between other-touch and self-touch was performed using fMRI data from study 1 and from the first run of study 2 (replication run) using SPSS19 (IBM Corp.). Complete data were available from 40 participants and entered into this analysis. Missing data points were due to one missing questionnaire and two excluded subjects (as mentioned above: one because of technical problems and the other because of abnormalities in brain morphology). Parameter estimates were extracted from six ROIs [bilateral anterior and posterior insula (87) and ACC (86)], and self-touch β values were subtracted from other-touch β values. The ROIs had been chosen a priori based on their relevance in affective touch processing [posterior insula (29)], interoception [anterior insula (38)], self–other processing [ACC (42, 89)], and their role in the interoceptive predictive coding model (11). We performed a Bonferroni correction for multiple testing, resulting in a new significance threshold of 0.00833 (for six tests and an α level of 0.05).

Study 3: SEPs During Touch. In study 3, 10 volunteers (age, 27.7 ± 6 y; 4 male) participated in a measurement of SEPs. A stimulation electrode was placed on the base of the thumb, targeting the radial nerve. According to a standard clinical neurophysiology protocol, 300 nonpainful pulses at a maximum of 100 mA (individually adjusted to the minimum current for each participant necessary to evoke a thumb twitch) at 1 Hz were administered, resulting in a length of 5 min for each condition (baseline, self-touch, other-touch, touching a pillow). Subjects were asked to close their eyes, recline and relax, during the four conditions. As in studies 1 and 2, subjects were instructed to perform slow, gentle stroking on their left forearm using their right hand. The stimulated skin area during self-touch and other-touch included the sensory radial nerve territory. The subjects completed two runs of each condition in a randomized order. Recording electrodes were placed on the Erb's point (targeting the brachial plexus), the C6 cervical level, and on C3, C4, CZ, and FZ scalp positions. Electrode skin impedance was always less than 10 kΩ. Data were acquired for 100 ms after each pulse using a Nicolet EDX system with an AT2+6 amplifier (Carefusion) and recorded and analyzed using Synergy 20.0 (Carefusion). Recordings were referenced to Fz and bandpass-filtered (2 Hz to 2 kHz), the amplifier range was 5 mV, and the display sensitivity was 20 μV per division. Waveforms were averaged over the 300 pulses for each recording electrode and over the two runs per condition and analyzed with regard to amplitude and latency (N13 cervically, N20 cortically) (90). Baseline to peak amplitude was calculated automatically, with the baseline defined as the value right before the averaged waveform and with automatically selected peaks, which were inspected individually and manually adjusted if detected incorrectly by the algorithm. Values from the Erb's point electrodes were excluded due to too many missing values because of noise. Values were compared using paired *t* tests. Based on our behavioral and imaging findings, we expected to find differences between self- and other-touch at the cortical and possibly cervical spinal levels.

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