

Shared Neural Mechanisms Underlying Social Warmth and Physical Warmth

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Abstract

Many of people's closest bonds grow out of socially warm exchanges and the warm feelings associated with being socially connected. Indeed, the neurobiological mechanisms underlying thermoregulation may be shared by those that regulate *social warmth*, the experience of feeling connected to other people. To test this possibility, we placed participants in a functional MRI scanner and asked them to (a) read socially warm and neutral messages from friends and family and (b) hold warm and neutral-temperature objects (a warm pack and a ball, respectively). Findings showed an overlap between physical and social warmth: Participants felt warmer after reading the positive (compared with neutral) messages and more connected after holding the warm pack (compared with the ball). In addition, neural activity during social warmth overlapped with neural activity during physical warmth in the ventral striatum and middle insula, but neural activity did not overlap during another pleasant task (soft touch). Together, these results suggest that a common neural mechanism underlies physical and social warmth.

Keywords

social connection, warmth, temperature, insula, ventral striatum, functional MRI, interpersonal relationships, emotions, brain

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The ability to connect and maintain deep emotional bonds with other people is fundamental to a happy and fulfilled life. However, even though close relationships are known to be critical for survival early in life and for health and well-being later on (Bowlby, 1988; House, Landis, & Umberson, 1988; Taylor, 2007), the experience of feeling socially connected has received little empirical attention thus far. In particular, little is known about the neural mechanisms that underlie feelings of social connection.

One proposal is that being socially integrated is so crucial to survival that it is necessary to have a neurobiological system in place that leads individuals to seek out social connection and reinforces these experiences to ensure that they continue. Indeed, it has been suggested that the basic homeostatic mechanisms involved in temperature perception and regulation may be involved in monitoring for and reinforcing social connection (Panksepp, 1998; Panksepp, Nelson, & Bekkedal, 1997). That is, the neural circuitry underlying thermoregulation, the processes associated with maintaining people's

relatively warm core body temperature (including the motivation to seek out warm stimuli and the perceived pleasantness of physical warmth; Rolls, Grabenhorst, & Parris, 2008), may have been coopted to maintain *social warmth*, the experience of feeling loved by and connected to other people. According to this view, the neural systems in place to detect signs of social connection may have borrowed from the neural systems that detect physical warmth, which sheds light on one reason why connecting with other people is often described as "heartwarming."

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Even before birth, warmth and connection develop concurrently, initially in the warm, protected environment of the mother's womb. Following birth, infantcaregiver interactions, such as being held or rocked to sleep, are characterized by increases in external physical warmth from the close proximity of a caregiver. From these early interactions, warmth may have come to signal that one is socially connected and cared for (Panksepp, 1998). This overlap between physical and social warmth may have been either selected for over the course of our evolutionary history or learned associatively across an individual's life span. As evidence of the critical role of warmth in early life, pups placed in a warm environment after being deprived of maternal care, food, and water continue to develop normally and even survive longer relative to those in cold environments (Stone, Bonnet, & Hofer, 1976). Furthermore, pups removed from their mothers and placed in warm cages show fewer signs of distress than those placed in relatively cold or hot cages (Blumberg, Efimova, & Alberts, 1992). Thus, in some cases, physical warmth may serve as a proxy for closeness to the caregiver. Finally, in Harlow's (1958) famous study of infant macaques and their surrogate cloth or wire mothers, the cloth mothers were also heated by a 100 W light bulb, which made them not only a source of contact comfort but also of physical warmth. Hence, the observed preference for a soft cloth mother cannot be disentangled from the preference for a warm mother.

Similar to nonhuman mammals, human infants require both physical warmth (Costeloe, Hennessy, Gibson, Marlow, & Wilkinson, 2000; Day, Caliguiri, Kamenski, & Ehrlich, 1964; Silverman, Fertig, & Berger, 1958) and nurturing care for normal development (Bowlby, 1988). For instance, premature infants placed in relatively warmer incubators for the first 5 days of life were more likely to survive than those placed in cooler incubators (Silverman et al., 1958), and many children raised in institutional settings without the presence of a nurturing figure show stunted physical, cognitive, and socioemotional development (Gunnar, Bruce, & Grotevant, 2000). These early experiences may provide the building blocks for detecting social warmth later in life.

More recent research from the embodied-cognition literature supports this association between social and physical warmth in humans. Holding warm compared with cold stimuli led participants to rate a fictional target as interpersonally warmer (Williams & Bargh, 2008) and to rate themselves as psychologically closer to an experimenter and a friend (IJzerman & Semin, 2009). Furthermore, as evidence that feeling cold is associated with a lack of social connection, holding a cold (vs. a warm or neutral) pack led to increases in self-reported loneliness (Bargh & Shalev, 2012). Moreover, participants who were socially excluded reported a room to be colder

than did included participants (Zhong & Leonardelli, 2008). Collectively, these results suggest that there is an overlap between the experience of social connection and physical warmth.

Although such evidence points to the possibility that feelings of social connection and feelings of physical warmth are interrelated, no studies have focused on whether experiences of physical and social warmth activate overlapping neural regions (although see Kang, Williams, Clark, Gray, & Bargh, 2011, for a study on the neural mechanisms linking temperature perception with subsequent trust behavior). The few studies to assess neural activity to innocuous, warm (vs. neutral) thermal stimuli have found increased activity in the insula, a region associated with processing interoceptive cues (Becerra et al., 1999; Craig, 2003; Davis, Kwan, Crawley, & Mikulis, 1998; Olausson et al., 2005; Rolls et al., 2008; Verhagen, Kadohisa, & Rolls, 2004). Indeed, lesions to the insula can result in selective loss of nonpainful thermal sensation (Cattaneo, Chierici, Cucurachi, Cobelli, & Pavesi, 2007). Additionally, the ventral striatum (VS), pregenual anterior cingulate cortex (pACC), and orbitofrontal cortex show more activity the more pleasant a warm stimulus is rated, which suggests that these regions may code for the rewarding component of warmth (Rolls et al., 2008).

Although to our knowledge, no imaging studies have explored the general experience of connecting with other people in the absence of stress or pain, some have assessed neural responses to viewing pictures of loved ones. Viewing a romantic partner (vs. a friend) or one's own child (vs. a familiar but unrelated child) leads to increased activity across a broad array of neural regions, including the caudate, middle insula, VS, ventral tegmental area, pACC, and anterior cingulate cortex more broadly (Acevedo, Aron, Fisher, & Brown, 2012; Aron et al., 2005; Bartels & Zeki, 2000, 2004). Relevant to social connection, subjects who show the most middle-insula activity also rate themselves as closer to their romantic partner, and greater activity in the VS is associated with longer relationship length (Acevedo et al., 2012). Together, these findings suggest that the insula, particularly the middle insula, and the VS play important roles in processing both physical and social warmth; however, these studies did not focus on more interactive forms of social connection beyond passively viewing pictures of loved ones.

Following the premise that mechanisms involved in temperature perception have been coopted to detect signs of social connection, we tested two consequences of this potential social-physical warmth overlap. First, we investigated whether experiencing social warmth increases feelings of warmth and whether experiencing physical warmth increases feelings of social connection. Second, we examined whether physical and social

warmth share overlapping neural activity in the insula and VS. To test these questions, we asked participants to hold a warm pack and a ball for the physical-warmth manipulation and to read loving and neutral messages from their closest friends and family members for the social-warmth manipulation. Following each manipulation, participants were asked to rate their feelings of warmth and connection in response to each task. In addition, because similarities between neural responses to social and physical warmth could be attributed to the perceived pleasantness of each experience, we included an additional task involving a soft, pleasant touch to investigate the unique contribution of warmth to the experience of connection.

Method

Participants

Twenty young adults (mean age = 20.2 years, 13 females) who were either University of California, Los Angeles, (UCLA) undergraduates or friends of UCLA undergraduates were determined eligible to participate after identifying at least six close friends and family members (i.e., close others) who would be willing to be contacted in regards to the study. All participants were deemed scanner ready (right-handed, not claustrophobic, free of metal, not pregnant if female) during an initial e-mail screening. Of these participants, 55% identified as Asian or Asian American, 40% as Caucasian, and 5% as Latina. Procedures were run in accordance with the guidelines of the UCLA Institutional Review Board.

Procedure

Prescan message collection. Prior to the scanning session, participants' close others were contacted via e-mail to help create the social-warmth task. Participants prerated how close they were to their close others on a scale from 1, not at all close, to 10, extremely close (average rating = 8.17, range = 6–10). We sent e-mails to close others explaining that we were conducting a study exploring the brain's response to messages from friends and family members, and we asked that they provide us with 12 brief messages to the participant. Half of the messages were to be about why they loved and appreciated the participant, and the other half were facts. Contacts were asked not to discuss the messages with the participants so that all participants remained unaware of potential study goals.

Imaging procedures. In the scanner, participants completed three tasks: a social-warmth task, a pleasant-touch task, and a physical-warmth task. The social-warmth and

pleasant-touch tasks were counterbalanced, and the scan always ended with the physical-warmth task. This was done to ensure that the pleasant-touch runs remained temperature neutral and to avoid carryover effects from the physical-warmth runs.

During the social-warmth task, participants read the messages from their close friends and family members on scanner-compatible goggles. A 2-s cue explaining whom the messages were from was followed by two messages (either both positive or both neutral) for 6 s each in a block design. Each block was separated by 7 s of rest. Examples of positive messages from actual close others included "Whenever I am completely lost, you are the person I turn to," and "I love you more than anything in the world." Examples of neutral messages included "You have curly hair," and "I have known you for 10 years." During the pleasant-touch task, a research assistant slowly brushed (approximately one brushstroke per second) the participant's left inner forearm with a soft brush and provided neutral touch with a stationary wooden dowel for 10 s each. Finally, in the physical-warmth task, the participant held a warm pack and a neutral, roomtemperature ball for 10 s each. Stimuli were repeated 5 times in each condition. Conditions were counterbalanced, and no condition was presented twice in a row.

Postscan self-report ratings. After the scan, participants rated the extent to which they felt connected after reading the positive and neutral messages and how warm the warm pack and ball felt; these ratings served as manipulation checks for the social- and physical-warmth tasks, respectively. Additionally, responses to "how warm [participants felt] after reading these messages" and the extent to which they felt connected during each condition were collected. Finally, participants reported how pleasant each condition was (e.g., "how good did it feel to read the messages," as an example from the social-warmth task). Ratings were made on a 7-point Likert scale ranging from 1, not at all, to 7, very.

Image acquisition. Data were acquired on a Siemens Trio 3-T MRI scanner with foam padding surrounding the participants' head to restrict movement. For each participant, we acquired a high-resolution structural T2-weighted echo-planar imaging volume—spin-echo, repetition time (TR) = 5,000 ms, echo time (TE) = 34 ms, matrix size = 128×128 , resolution = $1.6 \times 1.6 \times 3$ mm, field of view (FOV) = 200 mm, 36 slices, 3-mm thick, flip angle = 90° , bandwidth = 1302 Hz/Px—that was coplanar with the functional scans. For the social-warmth task, two functional scans each lasting 7.5 min were acquired—gradient-echo, TR = 2,000 ms, TE = 30 ms, flip angle = 90° , matrix size = 64×64 , resolution = $3.1 \times 3.1 \times 4.0$ mm, FOV = 200 mm, 33 axial slices, 4-mm thick, flip

angle = 90°, bandwidth = 2604 Hz/Px. Additionally, two pleasant-touch scans lasting 3 min and 45 s each, and one physical-warmth scan lasting 5.5 min, were acquired. Signal loss resulting from dropout in ventral frontal and subcortical regions was relatively low, with 62% and 100% signal acquired in these regions, respectively.

fMRI data analysis. Imaging data were analyzed using Statistical Parametric Mapping (SPM) software (SPM8; Wellcome Department of Cognitive Neurology, Institute of Neurology, London, England). For preprocessing, images for each subject were realigned to correct for head motion, normalized into a standard stereotactic space, and smoothed with an 8-mm Gaussian kernel, full width at half maximum (FWHM), to increase signal-tonoise ratio. The 12 s during which messages were on the screen for the social-warmth task and the 10-s stimulation period for the pleasant-touch and physical-warmth tasks were modeled as blocks. Rest periods during which participants viewed a fixation cross between blocks served as the implicit baseline. Linear contrasts for each experimental condition relative to its control condition (positive messages compared with neutral messages, brush compared with dowel, and warm pack compared with ball) were computed for each participant. These individual contrast images were then used in group-level analyses. One participant was removed because of signal dropout, which left a final imaging sample of 19. In addition, 2 subjects were removed from analyses for the physicalwarmth task because the warm packs for these individuals malfunctioned. One subject was removed from analyses for the pleasant-touch task because a different brush, rated by this subject as unpleasant, was used.

Group-level results were examined in two ways. First, activity to each of the three tasks was examined across the whole brain. Then, to examine shared neural activity to social and physical warmth, we tested both tasks (each condition relative to its control condition) against the conjunction null, which identifies neural regions that were active during both tasks. For regions showing overlapping neural activity, we then used the MarsBar Toolbox (Brett, Anton, Valabregue, & Poline, 2002) to extract parameter estimates from that functional region of interest (ROI) for each task separately (for display purposes). We also ran the conjunction between social warmth and pleasant touch and between physical warmth and pleasant touch.

Analyses were corrected for multiple comparisons using the 3DClustSim function in AFNI software (Medical College of Wisconsin, Milwaukee, WI), which uses a Monte Carlo simulation to determine the minimum cluster size necessary to maintain a false-discovery rate (FDR) of .05. Based on the parameters of this study $(79 \times 95 \times 68 \text{ dimensions}, 3.5 \times 3.5 \times 5 \text{ voxels}, smoothing kernel of 8 mm FWHM; 10,000 iterations), results of 3DClustSim$

indicated a voxel-wise threshold of p < .001 combined with a minimum cluster size of 21, which corresponded with a corrected p < .05. This threshold (p < .001, 21 voxels) was used for all analyses. All coordinates are reported in Montreal Neurological Institute (MNI) format.

Results

Postscan self-report

Consistent with the task manipulations, results revealed that participants felt more connected after reading the loving messages from close others (M = 5.93, SD = 0.96) than after reading the neutral messages (M = 3.92, SD = 1.29), t(19) = 7.27, p < .01. In addition, participants rated the warm pack as warmer (M = 5.00, SD = 0.94) than the ball (M = 3.22, SD = 1.48), t(9) = 5.51, p < .01.²

With regard to the more general measure of perceived pleasantness, the positive messages were experienced as more pleasant (M = 6.15, SD = 0.92) than the neutral messages (M = 4.10, SD = 1.77), t(9) = 3.96, p < .01, the warm pack as more pleasant (M = 5.74, SD = 1.10) than the ball (M = 3.79, SD = 0.86), t(18) = 5.77, p < .01, and the brushing as more pleasant (M = 5.6, SD = 1.10) than the dowel (M = 2.89, SD = 1.15), t(18) = 7.65, p < .01. However, when comparing across tasks (each condition relative to its control), we found that the pleasant-touch task (brushing vs. dowel) was rated the most pleasant (M = 2.68 SD = 1.53), followed by the social-warmth task (positive vs. neutral messages; M = 2.05, SD = 1.64) and the physical-warmth task (warm pack vs. the ball; M = 1.95, SD = 1.47). Indeed, the pleasant-touch task was rated as marginally more pleasant than the physical-warmth task, t(17) = -1.86, p =.08. There were no other differences in pleasantness across the conditions—social vs. physical warmth: t(9) = 1.04, p =.33; pleasant touch vs. social warmth: t(9) = -1.80, p = .11.

In line with the hypothesis that there is an interplay between social and physical warmth, results showed that reading the positive messages from close friends and family members led to increased feelings of warmth (M = 6.14, SD = 0.71) compared with reading the neutral messages (M = 3.80, SD = 1.52), t(9) = 5.44, p < .01, d = 1.98. Furthermore, simply holding the warm pack led to increased ratings of connection (M = 2.42, SD = 1.39) compared with holding the ball (M = 1.63, SD = 1.17), t(18) = 3.34, p < .01, d = 0.78. Brushing also led to marginal increases in feelings of connection (M = 2.35, SD = 1.31) compared with the dowel (M = 1.95, SD = 1.31), t(18) = 1.93, p = .07.

When comparing across tasks (each condition relative to its control), we found that participants reported feeling significantly more "connected" during the social-warmth task (positive vs. neutral messages: M = 2.00, SD = 1.22) compared with the physical-warmth task (warm pack vs. ball: M = 0.79, SD = 1.03), t(18) = 3.67, p < .01, or the

pleasant-touch task (brush vs. dowel: M = 0.47, SD = 1.07, t(18) = 4.12, p < .01. There were no differences in self-reported feelings of connection during the physical-warmth task compared with the pleasant-touch task, t(17) = 0.95, p = .36.

Imaging results

Neural activity to physical warmth. First, neural activity during exposure to warm compared with neutral stimuli was examined across the whole brain. Replicating previous work on the brain's response to warm stimuli, we found greater activity in the bilateral VS, left middle insula, and left anterior insula when participants were holding the warm pack compared with when they were holding the ball. There was also increased activity in the right posterior insula as well as in the primary and secondary somatosensory cortices, which is consistent with results of studies that involve warm, cutaneous sensory stimuli (Becerra et al., 1999; Craig, 2003; Davis et al., 1998; Olausson et al., 2005; Rolls et al., 2008; Verhagen et al., 2004; see Table 1 for a full list of activations).

Neural activity to social warmth. Next, we assessed activity to reading positive, loving messages from friends and family members compared with neutral messages. As expected, participants displayed extensive activity in the VS, the anterior and middle insula, the pACC, and the ventral tegmental area to reading the positive messages (vs. neutral messages). There was also increased activity in several neural regions previously associated with mentalizing (dorsomedial prefrontal cortex, temporal pole, precuneus) as well as increased activity in septohypothalamic regions previously implicated in affiliative responding (Moll et al., 2012; see Table 2 for a full list of activations).

Neural activity to pleasant touch. Neural activity to pleasant as opposed to neutral touch did not lead to increased activity in the VS. Instead, brushing (vs. the dowel) led to increased activity in the right posterior insula (x = 38, y = -18, z = 22), t(17) = 5.51, and primary and secondary somatosensory cortices, a finding that replicated prior work on pleasant touch (Olausson et al., 2002; see Table 3 for a full list of activations).

Shared neural activity across tasks. To assess shared neural regions associated with processing social and physical warmth, we ran a conjunction analysis between neural activity during exposure to positive messages (vs. neutral messages) and neural activity during exposure to warm stimuli (vs. the ball). The conjunction analysis revealed shared neural activity in the left VS (x = -16, y = 0, z = -8), t(16) = 4.78, k = 84, and left middle insula (x = -38, y = 4, z = -16), t(16) = 4.58, k = 21, during thesocial and physical-warmth tasks, in which participants read positive (vs. neutral) messages and held the warm pack (vs. the ball), respectively (Fig. 1). It is important to note that there was no overlapping neural activity during the social-warmth and pleasant-touch tasks, which suggests that the shared neural responses to physical and social warmth may not be solely due to increases in perceived pleasantness. Finally, the conjunction between activity during physical warmth and pleasant touch (brush vs. dowel) revealed activity in the left posterior insula (x = 42, y = -16, z = 18), t(16) = 4.75, k = 216,extending into the secondary somatosensory cortex (x =58, y = -18, z = 24), t(16) = 4.51.

Discussion

The relationship between social and physical warmth has received increasing empirical attention; however, the neural mechanisms underlying both forms of warmth

Table 1. Brain Regions More Active When Participants Held a Warm Pack Compared With a Neutral Object

			MNI coordinates				
Anatomical region	Hemisphere	Brodmann's area	x	У	\overline{z}	t(16)	k
Ventral striatum	Left	_	-16	4	-4	5.81	321
Ventral striatum	Right	_	16	4	-6	4.97	30
Anterior insula	Left	_	-26	24	-8	4.83	53
Middle insula	Left	_	-40	2	-12	4.85	37
Posterior insula	Right	_	40	-16	16	5.83	377
Secondary somatosensory cortex	Right	40	46	-22	22	4.59	_
Primary somatosensory cortex	Right	2	58	-18	24	5.13	_
Primary somatosensory cortex	Right	2	48	-24	56	4.87	186
Inferior parietal lobule	Left	40	-58	-26	28	4.78	33
Dorsomedial prefrontal cortex	Left	8	-8	44	50	4.26	34

Note: All activations were significant at p < .001, 21 voxels. Statistics in the t column show values at peak coordinates. Cluster voxel extent is represented by k; an activation that does not include a k value extends from the larger cluster listed above that activation. MNI = Montreal Neurological Institute.

Table 2. Brain Regions More Active When Participants Read Positive Messages From Loved Ones Compared With Neutral Messages From Loved Ones

			MN	II coordir			
Anatomical region	Hemisphere	Brodmann's area	\bar{x}	У	\overline{z}	t(18)	k
Brainstem/periaqueductal gray	Left	_	-4	-26	-20	7.24	1,097
Ventral tegmental area	Right	_	8	-12	-20	4.78	_
Ventral tegmental area	Left	_	-8	-16	-18	4.64	_
Substantia nigra	Left	_	-10	-22	-8	3.77	_
Septal area		_	0	4	-2	6.09	_
Hypothalamus	Left	_	-4	-10	0	4.53	_
Ventral striatum	Left	_	-12	2	-4	4.56	_
Ventral striatum	Right	_	4	6	-2	6.04	_
Anterior/middle insula	Left	_	-38	8	-12	5.35	178
Middle temporal gyrus	Right	21	54	0	-10	6.39	346
Anterior/middle insula	Right	_	44	16	-8	4.44	_
Pregenual cingulate cortex	Left	_	-2	40	10	7.41	770
Pregenual cingulate cortex	Right	32	10	30	-4	5.20	59
Dorsomedial prefrontal cortex	Right	10	6	58	20	7.06	_
Corpus callosum	Right	_	14	10	24	6.70	52
Dorsal anterior cingulate cortex	Right	32	8	26	28	5.92	100
Midcingulate cortex	Left	31	-6	-16	46	5.09	21
Temporal pole	Left	38	-52	12	-22	5.58	190
Temporal pole	Right	28	28	6	-20	6.61	145
Superior temporal gyrus	Left	22	-56	-38	8	5.44	103
Precuneus	Left	7	-18	-60	54	4.46	24
Caudate	Left	_	-12	18	14	5.72	63
Cerebellum	Left	_	-2	-50	-36	4.83	119
Cerebellum	Left	_	0	-76	-26	4.29	21
Premotor cortex	Left	6	-48	-2	56	5.48	89
Premotor cortex	Left	6	-18	-4	76	4.36	21
Inferior frontal gyrus	Left	45	-42	28	2	5.46	74
Hippocampus	Right	_	22	-26	-6	4.67	84
Occipital cortex	Left/Right	17/18/19	-24	-96	24	8.28	4,546

Note: All activations were significant at p < .001, 21 voxels. Statistics in the t column show values at peak coordinates. Cluster voxel extent is represented by k; an activation that does not include a k value extends from the larger cluster listed above that activation. MNI = Montreal Neurological Institute.

Table 3. Brain Regions More Active When Participants Were Brushed Compared With Touched With a Dowel

Anatomical region	Hemisphere	Brodmann's area	MNI coordinates				
			x	у	\overline{z}	t(17)	k
Primary somatosensory cortex	Right	2	30	-38	64	8.37	501
Primary somatosensory cortex	Left	1/2/3	-56	-24	36	7.86	808
Inferior parietal lobule	Right	40	58	-34	24	5.86	662
Secondary somatosensory cortex	Right	40	44	-24	24	5.61	_
Posterior insula	Right	_	38	-18	22	5.51	_
Premotor cortex	Left	6	-62	4	30	5.61	79
Motor cortex	Left	4	-32	-12	56	5.86	662
Motor cortex	Right	4	38	-6	60	4.44	35

Note: All activations were significant at p < .001, 21 voxels. Statistics in the t column show values at peak coordinates. Cluster voxel extent is represented by k. An activation that does not include a k value extends from the larger cluster listed above that activation. MNI = Montreal Neurological Institute.

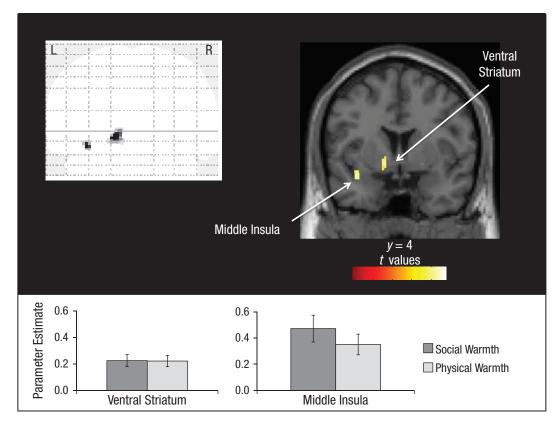


Fig. 1. Results for the conjunction between social warmth (positive messages as opposed to neutral messages) and physical warmth (warm pack as opposed to ball). The glass brain and coronal slice show activations in the left ventral striatum and left middle insula for this conjunction. The graphs show parameter estimates from these functional regions of interest (ROIs) during the social-warmth and physical-warmth tasks. Error bars represent ± 1 SE. L = left, R = right.

have not been examined together. The present study adds to previous work from the embodied-cognition literature by showing that self-reported feelings of warmth increased following a social-warmth induction and feelings of connection increased after participants simply held a warm object. Furthermore, in support of the theory that social warmth is built on basic mechanisms involved in temperature perception and regulation, physical and social warmth displayed overlapping neural mechanisms in the middle insula and VS, regions associated with processing warmth and with highly rewarding outcomes. Indeed, these findings are consistent with research showing that physical warmth is processed interoceptively (as opposed to cutaneous touch, which is processed exteroceptively; Craig, 2002), and thus, whereas warmth may seem like a more external, sensory stimulus, it is actually more closely linked with internal motivational and affective states. Together, these results suggest a potential mechanism by which social warmth, the contented subjective experience of feeling loved and connected to other people, has become such a pleasant experience and lend credence to the description of connection experiences as "heartwarming."

An interesting finding was that social warmth did not show any overlapping activity with a task involving pleasant physical touch. This suggests that the shared activity to social and physical warmth in this study was not solely due to increases in positive affect. In other words, even though the pleasant-touch task (relative to its control task) was rated the most pleasant, only neural activity during physical warmth showed a similar pattern as social warmth. This is not to say that physical touch does not play a role in feelings of social connection. In fact, physical affection in the form of sensual or affiliative touch between close others is likely a major part of feeling close and connected. Future work exploring neural activity to touch from a close other as opposed to an inanimate object held by an experimenter (as in this study) may further elucidate the role of physical touch in the experience of social connection and add to existing work using interpersonal touch (Coan, Schaefer, & Davidson, 2006; Inagaki & Eisenberger, 2011).

These results may have implications for the beneficial effects of physical warmth on social relationships. Indeed, even small manipulations that increase physical warmth have been shown to bolster social bonds. After holding

warm objects, participants reported feeling closer to other people (IJzerman & Semin, 2009), increased their trusting behavior (Kang et al., 2011), and in the current study, felt more socially connected. Furthermore, participants both inside and outside of the lab appear to seek out physical warmth following social rejection (Bargh & Shalev, 2012; Zhong & Leonardelli, 2008). Given the importance of social connections for general well-being and happiness, the present results may inform larger interventions designed to combat feelings of isolation or loneliness through temperature manipulations.

In the present study, the insula and VS, regions known to have a high density of μ-opioid receptors (Cross, Hille, & Slater, 1987; Jones et al., 1999; Zubieta et al., 2001) were the only regions to show activity to both social and physical warmth. Although not explicitly tested here, μ-opioids may contribute to the shared neural circuitry underlying physical and social warmth (Handler, Geller, & Adler, 1992; Panksepp, 1998). With regard to physical warmth, µ-opioids have been shown to play a role in temperature regulation, such that µ-opioid agonists (e.g., morphine, heroin) can increase body temperature (Clark, Murphy, Lipton, & Clark, 1983) and μ-opioid antagonists can decrease body temperature (Handler et al., 1992; Spencer, Hruby, & Burks, 1988). In addition, animal research has highlighted a role for µ-opioids in the socialbonding processes that may underlie feelings of social warmth. Thus, morphine, a µ-opioid agonist, can reduce crying to social separation and speed the comfort response, characterized by a relaxing of the body when being held by an experimenter. Conversely, naloxone, an opioid antagonist, increases crying behavior when chicks are in a group and delays the comfort response to being held by an experimenter when separated from the group, which suggests that the chicks are no longer feeling a sense of comfort from their social experiences (Panksepp, Bean, Bishop, Vilberg, & Sahley, 1980). An interesting direction for future studies will be to incorporate pharmacological interventions of the μ-opioid system with self-reports on subjective experiences of social connection to present a clearer picture of how exactly opioids contribute to feelings of social warmth from positive social experiences.

In sum, the current study elucidates a shared neural mechanism by which the brain processes pleasant, warm stimuli and the feelings associated with connecting with close others, or social warmth. Furthermore, these results highlight one way by which social integration is critical to survival and further the study of the feelings associated with social connection.

Author Contributions

T. K. Inagaki and N. I. Eisenberger developed the study concept, and both authors contributed to the study design. Testing, data collection, and data analysis were performed by T. K.

Inagaki. Both T. K. Inagaki and N. I. Eisenberger interpreted the data and drafted the manuscript. Both authors approved the final version of the manuscript for submission.

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Declaration of Conflicting Interests

The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Notes

- 1. This task also included a condition in which participants held cold packs. However, in an effort to keep the control conditions similar across tasks, we focused on the neutral condition for the comparison, and thus results from the cold-pack condition are not included here.
- 2. For some items, data were obtained only from a small subset of the sample (n = 10) because a scale was missing in the first several participants' questionnaire packets. Thus, these behavioral results should be interpreted with caution.

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