Emotion

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Social connection may stem from afferent pathways that bring bodily information to the brain and mind. In support of this perspective, research from animals and humans shows that physical warmth causally affects experiences of social connection. However, whether physical warmth affects feelings of social connection and the brain's response to close others remains unknown. In the current study, 42 participants completed an fMRI scan as they viewed images of a close other and strangers while holding warm, cold, and room-temperature objects. Following the scan, participants reported on their feelings of social connection and pleasure in response to the three temperature conditions. Results revealed a specific effect of physical warmth on brain activity to close others as compared with cooler temperatures (both cold and room temperature) and strangers (e.g., in the ventral striatum, middle-insula, ventromedial prefrontal cortex, pregenual cingulate cortex). Cooler temperatures had no effect on brain activity to close others (vs. strangers). Further, physical warmth increased feelings of social connection, even when adjusting for feelings of pleasure, but not vice versa, suggesting physical warmth may have specific effects on feelings of social connection. Results add to an emerging literature on the contribution of physical warmth to social connection and furthers understanding of why and how connecting with others is a basic need for humans.

Keywords: embodiment, interoception, James-Lange theory of emotion, social warmth, somatosensory afference

Supplemental materials: http://dx.doi.org/10.1037/emo0000749.supp

Social connection—the affectively pleasant experience of being close to and bonded with others—is commonly described as a warm experience. *Warm feelings*, *warmhearted*, *warmly received*, and other similar descriptions abound in writings depicting feelings of social connection dating back to the 1500's (Merriam-Webster.com, n.d.) to popular contemporary fiction (e.g., Murakami, 2013). Further, nearly every language has a term for warmth that also describes socioemotional experience, suggesting a universal experience across cultures (Alberts & Decsy, 1990). Beyond language, emotional experience has long been theorized to arise from physical experience (Darwin, 1872; James, 1884; Panksepp, 2004; Schachter & Singer, 1962) and, in the social cognition literature, has been identified as a central social trait (Asch, 1946; Fiske, Cuddy, & Glick, 2007; Williams, Huang, & Bargh, 2009). Inspired by these intellectual traditions, recent researchers have proposed that socially warm feelings of connection arise from afferent signals that bring physiological sensations to the brain and mind (Inagaki & Eisenberger, 2013). From this perspective, the foundation of social connection with others may be, in part, a physically warm experience. However, scant research has explored the direct effect of physical warmth on social warmth in humans. The current investigation, therefore, assessed the causal contribution of physical warmth (body) to the subjective, psychological experience of social connection (mind) and, as a step toward understanding the mechanism by which such effects occur, brain activity in response to targets of social connection.

The hypothesis that physical warmth would affect social connection has strong theoretical and empirical roots in the behavioral neuroscience literature on the infant–caregiver bond; the first and primary experience of social connection. Early interactions with a caregiver provide the stimulation an infant needs to survive to independence; often concurrently satisfying both social connection and physical needs. Separation from the caregiver early in life may be so detrimental to the infant *because* separation represents a loss of these multiple, intertwined, sensory and social stimulations (Hofer, 1994). Harlow's seminal study on infant macaques was the first to inadvertently highlight physical warmth's contribution to social connection (Harlow, 1958). Separated infants housed with both a food-providing wire caregiver and a cloth-covered caregiver strongly preferred the cloth surrogate. However, as originally described by Harlow, the cloth-covered caregiver had "a lightbulb beneath her [that] radiated heat. The result was a mother, soft, warm, and tender," suggesting that physical warmth may be part

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and parcel of social connection. In follow-up studies, the warmth of the cloth surrogate was directly manipulated to show that warmth, rather than the softness of the cloth, drove preferential behavior (Harlow & Suomi, 1970). In the complete absence of a close social connection, physical warmth may also act as a partial substitute. Indeed, experimental manipulations of early rearing environments show that developmental and behavioral disruptions following separation from a caregiver can be partially restored by reintroducing the physical warmth that the mother provides (Alberts & May, 1984; Blumberg, Efimova, & Alberts, 1992; Stone, Bonnet, & Hofer, 1976).

Results from the animal literature are critical to understanding the causal effects of separation and deprivation on the developing infant and the surprising contribution of the physical warmth of surrogate caregivers to development. An important insight to be gleaned from these findings is the possibility that a warm caregiver is more than merely preferred, but is *necessary* for both the physical development of the infant and the development of mechanisms that support future social connection. Consistent with this hypothesis, follow-up studies of monkeys who had been separated from their caregivers revealed permanent and pervasive social deficits compared with those reared in normal conditions (Harlow, Dodsworth, & Harlow, 1965; Harlow, Harlow, Dodsworth, & Arling, 1966), effects that parallel observational and correlational findings from humans reared in impoverished early care conditions (Bowlby, 1952; Carlson, Hostinar, Mliner, & Gunnar, 2014; Sheridan et al., 2018).

If physical and social warmth are linked because of the copresence of a physically warm caregiver and socially warm caregiver early in life and if this overlap provides the foundation for future social connection, physical warmth should most strongly affect social connection to those in which a relationship already exists. That is, inherent in theories emphasizing the physiological regulation of social connection is the modulating role of closeness toward the social target. It follows that physical warmth might potentiate an experience of social connection with close others, but might not affect the same experience with an unknown stranger with whom there is no established social connection. However, no studies have explicitly examined this possibility. Further, it remains largely unknown what neural mechanisms contribute to physical warmth's direct effects on social connection.

Perceptions of physical warmth and the mechanisms that keep the body at a relatively warm temperature (i.e., thermoregulation) occur, in part, via afferent signals that bring the physiological condition of the body to the brain (Craig, 2003; Morrison & Nakamura, 2019; Raison, Hale, Williams, Wager, & Lowry, 2015). Interestingly, the neural regions associated with the pleasurable experience of physical warmth in humans overlap with regions associated with social connection, principally the ventral striatum (VS) and middle-insula (MI; Inagaki & Eisenberger, 2013; Inagaki, Hazlett, & Andreescu, 2019). Thus, the middle and posterior insula activate to physical warmth (Becerra et al., 1999; Davis, Kwan, Crawley, & Mikulis, 1998; Olausson et al., 2005; Rolls, Grabenhorst, & Parris, 2008; Verhagen, Kadohisa, & Rolls, 2004). Further, subjective feelings of pleasure to physical warmth is associated with more activity in the pregenual cingulate cortex (PACC), ventromedial prefrontal cortex (VMPFC), and VS in response to the same stimulus, suggesting these regions code for the affective experience surrounding physical warmth (Rolls et al., 2008). Finally, as evidence of the causal contribution of the insula to physical warmth, lesions to the insula can result in selective loss of warm sensation (Cattaneo, Chierici, Cucurachi, Cobelli, & Pavesi, 2007).

Separately, images or other cues of close others consistently activate the VS and MI (Acevedo, Aron, Fisher, & Brown, 2012; Aron et al., 2005; Bartels & Zeki, 2000, 2004; Inagaki & Eisenberger, 2013), and activity in the VS and MI in response to loving messages from close others is associated with greater feelings of social connection (Inagaki et al., 2019). In animals, lesions to the VS (vs. sham lesions) also reduce social connection behavior (licking, retrieving, nest building in mothers; Hansen, 1994; Lee, Clancy, & Fleming, 1999). Given the similarities between the neural patterns of physical warmth and social connection and existing human literature showing a causal effect of physical warmth on socioemotional responding (Fay & Maner, 2018; IJzerman & Semin, 2009; Inagaki & Eisenberger, 2013; Inagaki et al., 2019; Inagaki, Irwin, & Eisenberger, 2015; Janssen et al., 2016; Kang, Williams, Clark, Gray, & Bargh, 2011; Williams & Bargh, 2008), it is possible that physical warmth causally influences the brain's response to social connection with close others. To date, no studies have assessed this possibility.

The Current Study

Following the theory that physical warmth is an important contributor to social connection and that physical warmth's causal influence on social connection is through the brain, we tested the hypothesis that physical warmth would increase feelings of social connection and brain activity (focusing principally on the VS and MI) to images of a close other. To investigate the unique contribution of physical warmth to the experience of social connection with close others, participants held warm, cold, and neutral temperature objects while viewing images of a close other and strangers in the MRI scanner. Following the scan, feelings of social connection in response to each of the temperature conditions were collected. Feelings of social connection induced by physical warmth could be attributed to increases in general positive affect. Therefore, feelings of pleasure in response to each of the temperature conditions were also assessed as a covariate.

Method

Forty-two participants (*M* age = 26.640, *SD* = 5.565, range 19–40 years, 22 female), screened for safety in the MRI environment and general health, took part in the current study. Specifically, the presence of nonremovable metal, claustrophobia, pregnancy, weight above 400 pounds, current mental or physical illness, or prescription medication other than birth control were screened out. Self-identified ethnic identification of the sample was 59.5% White, 21.4% Black, 14.3% Asian, and 4.8% Other.

Sample size was determined via a power analysis in fMRIpower (fmripower.org; Mumford & Nichols, 2008) using the comparison of viewing images of close others > strangers from a previously completed study (Inagaki et al., 2019) and the same VS and MI ROIs as used in the present study, we determined that with between 35 and 45 participants, we would have at least 80% power to detect a medium effect size (Cohen's $d = .40$) in the VS and MI at a $p < .005$. Data collection ended once 40 participants with complete data (imaging scans and postscan self-report) had been obtained. Participants were run in accordance with the University of Pittsburgh's Human Research Protection Office. All participants provided written consent prior to completing the following procedures.

Neuroimaging Measure

To assess the effect of physical warmth on social warmth, brain activity was measured by modifying a commonly used scanner paradigm to assess the neural correlates of close social relationships that also reliably increases activity in the VS, one of the two primary regions of interest (Acevedo et al., 2012; Aron et al., 2005). Participants viewed images of a close other and strangers while holding different temperature objects in a 3 (warm therapeutic pack vs. cold therapeutic pack vs. room temperature, neutral, therapeutic pack (i.e., a previously activated therapeutic pack that had since lost its temperature); Dynarex Single Use Instant Therapeutic Packs) $\times$ 2 (close other vs. strangers) within-subjects block design. Prior to entering the scanner, participants were told that they would be shown pictures of people and that the experimenters would be placing different temperature objects in their hand under the guise that they were completing a product evaluation task following previously established procedures (Williams & Bargh, 2008). The task was also presented as a secondary study to another task presented in the scanner (reported in separate publication).

Once in the scanner and prior to each condition, a 2-s cue indicated whether the participant would hold a warm, cold, or neutral object. Images were then presented for 6 s each (2 images per block). During the close other blocks, participants viewed two different pictures of a self-identified close other. During the stranger conditions, participants viewed two pictures of strangers (one silhouette of a man and one silhouette of a woman). Conditions were presented in counterbalanced order with each scan beginning with the neutral room temperature object. No temperature appeared twice in a row. To reduce movement in the scanner, an experimenter stood next to the participant in the scanner and placed each object in the participant's left hand for the 12 s that a participant was viewing images of social targets. Participants practiced the procedure in the mock scanner prior to the MRI scan to reduce movement during the actual scan. Blocks were separated by 7 s of fixation crosshair, during which time the object was removed from the participants' hand.

Prescan Measures

In the current study, close others were rated as very close (M = 9.702, SD = .456, using the question "How would you rate this person on a scale of 1 (*not very close*) to 10 (*very close*)?" asked after screening, but before the imaging session); 42.8% of participants sent images of a spouse or romantic partner, 38.1% of a family member, and 19% of a friend. Prior to the start of the scanner task, the temperature of the warm and cold objects was also measured with a laser infrared thermometer (Etekcity Lasergrip 774) to ensure that the objects were warm and cold, respectively. The warm object was indeed warmer than the cold object (M warm object = 95.121°F, SD = 3.507; M cold object = 49.909°F, SD = 2.416; $t(32) = 54.396$, $p < .001$).[1] Although not measured for each participant, the temperature of the neutral object was both colder than the warm object and warmer than the cold object (72°F).

Postscan Measures

Following the scan, participants reported on their experience while in the scanner. Specifically, participants rated the thermal intensity and pleasantness of holding the three objects (manipulation checks), and their feelings of social connection and social pleasure in a single questionnaire packet. Instructions were to "Please answer the following questions about the [warm pack/cool pack/neutral pack]. When you were holding the [warm pack/cool pack/neutral pack], ..." A 1 (*not at all*) to 7 (*very*) scale was used for all ratings. In addition to the items described below, participants were also asked "how likely are you to recommend this product to a friend?" to enhance the cover story that the task was a product evaluation task.

Manipulation Checks

As a manipulation check for the temperature manipulation, participants were asked to rate the thermal intensity of the objects (how warm did the item feel?; how cool did the item feel?-reversed). As an additional manipulation check that the warm pack was experienced as pleasant, participants rated how pleasant the objects were ("How pleasant was it to hold?"; "How unpleasant was it to hold?" reverse-scored). Responses to each of the two items used to assess thermal intensity and pleasantness were averaged separately for analyses.

Feelings of Social Connection

Feelings of social connection to the three temperature conditions were assessed with the following items: How warm did you feel while holding this item?; How connected did you feel to the person in the photo when holding this item? Items were obtained from our previous work on social connection and physical warmth (Inagaki & Eisenberger, 2013). Instructions did not specify whether participants should report on feelings in response to a specific social target to avoid participant response bias for the current hypotheses that physical warmth might influence feelings toward the close other.

Feelings of Pleasure

It is possible that physical warmth alters the global affective experience of the images, beyond feelings of social connection. Therefore, questions aiming to assess the more general affective experience of viewing the images were assessed with the following two items: How aversive did you find the pictures during this time?; How pleasant did you find the pictures during this time? (worded based on theories of affective perception of emotional pictures; Bradley, Codispoti, Cuthbert, & Lang, 2001). Across the three temperature conditions, feelings of social connection and pleasure were statistically related to one another, though the rela-

[1] The temperature of the objects was added part of the way into the study and obtained from a total of 33 participants.

tionship was modest, suggesting they are separable constructs, r = .323, p = .037.

fMRI Data Acquisition

MRI scans took place on a Siemens MAGNETOM Verio 3T MRI Scanner housed at the Scientific Imaging & Brain Research Center (SIBR) located at Carnegie Mellon University. A Magnetization Prepared Rapid Gradient Echo (MPRAGE) structural scan was collected followed by functional scans (TR/TE = 2300/1.97 ms, flip angle = 9°, 256 × 256 matrix, 176 sagittal slices, Field of View (FoV) = 256; 1 mm thick). Participants completed two runs of the task (4 mins, 30 s, $T_2{}^*$ weighted gradient-echo covering 51 axial slices, TR/TE = 2000/25 ms; flip angle = 79°; 70 × 70 matrix; FOV = 210 mm; 2 mm thick). Participants also completed a separate task as part of a separate study that asks a theoretically different question.

Data Analyses

Neuroimaging data. Imaging data were preprocessed with the Diffeomorphic Anatomical Registration through Exponentiated Lie Algebra (DARTEL) procedure in SPM12 (Wellcome Department of Imaging Neuroscience, London). Images were motion corrected, realigned, normalized to the MPRAGE, warped into Montreal Neurologic Institute (MNI) space, and then smoothed with a 6-mm Gaussian kernel, full width at half maximum (FWHM). Contrasts for the main comparisons of interest (warm close other > cold close other; warm strangers > cold strangers; warm close other > warm stranger; cold close other > cold stranger) were computed at the single-subject level and were then brought to the group-level for analyses.

Region-of-interest (ROI) analyses. Our previous research on social and physical warmth shows that the only two neural regions to show overlapping activity to the two experiences are the VS and MI (Inagaki & Eisenberger, 2013; Inagaki et al., 2019). As such, an a priori, independently defined structural mask of the VS and MI was created. The ROIs were structurally defined from the Automated Anatomical Labeling Atlas (Tzourio-Mazoyer et al., 2002). The VS ROI was constrained at $-10 < x < 10$, $4 < y < 18$, $-12 < z < 0$ (Inagaki et al., 2016; Inagaki, Muscatell, et al., 2015). The MI ROI was constrained at $-5 < y < 15$ based on coordinates from previously published papers on the neural correlates of social connection (Bartels & Zeki, 2004; Inagaki & Eisenberger, 2013; Strathearn, Li, Fonagy, & Montague, 2008). To reduce comparisons among the conditions, ROIs were combined into a single mask.

Mean parameter estimates from each of the six conditions were then pulled using the MarsBar toolbox in SPM (Brett, Anton, Valabregue, & Poline, 2002) and entered into a 3 (temperature: warm vs. cold vs. neutral object) × 2 (social target: close other vs. stranger) repeated measures ANOVA. Significant interactions were further interrogated with paired samples t tests. Significance was determined as $p < .05$, two-tailed, and a 95% confidence interval (using the bias corrected and accelerated percentile method (BCa) with 1,000 samples with replacement) excluding 0.

Whole-brain analyses. As confirmation of the results at ROI correction and to evaluate the effect of the current task on brain activity beyond the structural mask, brain activity across the whole brain was also examined for any significant interactions from the brain data at ROI correction. Results from whole-brain analyses are corrected for multiple comparisons at a false discovery rate (FDR) of .05, 300 voxels.

Postscan ratings. Manipulation checks for the temperature manipulation (thermal intensity, pleasantness) were evaluated with paired-samples t tests in SPSS v.26. The primary hypotheses are that (a) feelings of social connection will be greater in response to holding a warm than cold object and (b) than holding a neutral object. Therefore, feelings to holding the warm object compared with each of the other temperature conditions were evaluated. Feelings of pleasure were evaluated similarly.

Raw data and syntax for the postscan ratings and ROI analyses can be found on the Open Science Framework: https://osf.io/vjr7b/?view_only=9728d3c881db4d09a428751a932cc34f

Results

Manipulation Checks

To ensure that the warm condition was experienced as both warm and pleasant, manipulation checks for thermal intensity and pleasantness were evaluated first. As expected, the warm object was rated as warmer (M = 5.762, SD = .899) than the cold object (M = 1.893, SD = .793; $t(41)$ = 18.118, $p < .001$, 95% BCa CI [3.438, 4.300]) and neutral object (M = 4.060, SD = .607, $t(41)$ = 9.988, $p < .001$, 95% BCa CI [1.358, 2.047]). In addition, the warm object was rated as more pleasant (M = 5.810, SD = 1.273) than the cold object (M = 3.583, SD = 1.168; $t(41)$ = 6.799, $p < .001$, 95% BCa CI [1.565, 2.887]) and the neutral object (M = 4.800, SD = .749, $t(41)$ = 4.747, $p < .001$, 95% BCa CI [.581, 1.442]). The neutral object was also rated as warmer, $t(41)$ = 14.522, $p < .001$, 95% BCa CI [1.865, 2.468] and more pleasant than the cold object, $t(41)$ = 5.721, $p < .001$, 95% BCa CI [.786, 1.643]. Therefore, each temperature condition induced the intended experience.

Effect of Physical Warmth on Feelings of Social Connection

In a replication of previous findings (Inagaki & Eisenberger, 2013; Inagaki et al., 2019; Inagaki, Irwin, et al., 2015) and in line with the current hypotheses, the warm object increased feelings of social connection as compared with the cold, $t(41)$ = 12.797, $p < .001$, 95% BCa CI [2.126, 2.922], Cohen's d = 1.974, Figure 1 and neutral object, $t(41)$ = 8.669, $p < .001$, 95% BCa CI [1.361, 2.187], Cohen's d = 1.337. Interestingly, the cold object also decreased feelings of social connection relative to the neutral object, $t(41)$ = 5.008, $p < .001$, 95% BCa CI [.448, 1.052], Cohen's d = .773.

It is possible that physical warmth increased the global positive experience of viewing social images. Indeed, the warm object increased feelings of pleasure (M = 5.988, SD = 1.027) relative to the cold object (M = 4.833, SD = 1.248, $t(41)$ = 5.561, $p < .001$, 95% BCa CI [.735, 1.574], Cohen's d = .858) and the neutral object (M = 5.286, SD = 1.007, $t(41)$ = 5.110, $p < .001$, 95% BCa CI [.425, .980], Cohen's d = .789). Therefore, feelings of social connection to the warm (vs. cold and vs. neutral) object was evaluated when adjusting for feelings of pleasure. The increase in

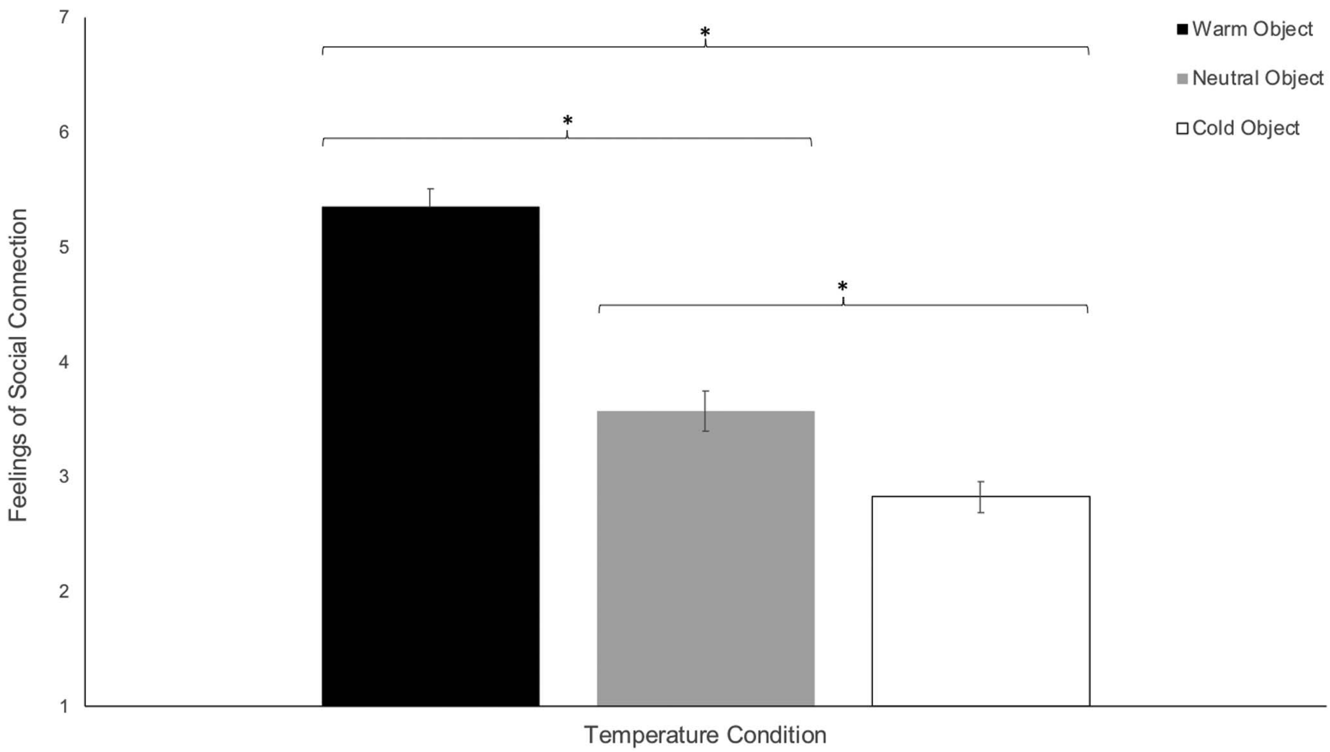

Figure 1. Feelings of social connection in response to the temperature manipulation. Feelings of social connection increased to holding the warm object compared with holding the neutral object and the cold object. Increases in feelings of social connection to the warm object remain after adjusting for feelings of pleasure. Error bars are standard errors. * $p < .05$, two-tailed and a 95% BCa CI excluding 0.

feelings of social connection to holding the warm object remained significant (compared with the cold object: $F[1, 39] = 13.253$, $p = .001$; compared with the neutral object: $F[1, 39] = 7.334$, $p = .010$). The increase in feelings of pleasure to holding the warm object, on the other hand, was no longer present after adjusting for feelings of social connection (compared with the cold object: $F[1, 39] = .011$, $p = .916$; compared with the neutral object: $F[1, 39] = .366$, $p = .549$). Thus, the warm object increased feelings of social connection above and beyond feelings of pleasure, but not vice versa.

Effect of Physical Warmth on VS and MI Activity to Close Others

The effect of the temperature manipulation on VS and MI activity in response to social images was evaluated with a 3 (temperature: warm, cold, neutral) × 2 (social target: close other, strangers) repeated measures ANOVA. There was a main effect of temperature, $F(2, 82) = 9.209$, $p < .001$, but no main effect of social target, $F(1, 41) = 1.383$, $p = .246$. However, the main effects were qualified by an interaction, $F(2, 82) = 3.329$, $p = .041$. The 3-way interaction was further broken down by comparing VS and MI activity to the warm versus cold object, then to the warm versus neutral object, and finally to the cold versus neutral object.

The 2 (temperature: warm vs. cold) × 2 (social target) analysis revealed a main effect of temperature such that VS and MI activity was greater to the warm than cold object, $F(1, 41) = 12.011$, $p = .001$, but no main effect of social target, $F(1, 41) = 1.826$, $p = .184$. Importantly, the main effects were qualified by an interaction, $F(1, 41) = 10.393$, $p = .002$, Figure 2 which was further interrogated with paired samples t tests to assess the direction of the effects.

Evaluating differences between temperature conditions revealed that a warm close other increased VS and MI activity more than a cold close other, $t(41) = 5.110$, $p < .001$, 95% BCa CI [.162, .374], Cohen's $d = .789$. There was, however, no difference in VS and MI activity between warm strangers and cold strangers, $t(41) = .766$, $p = .448$, 95% BCa CI [−.077, .170], Cohen's $d = .118$. That is, there was a specific effect of physical warmth on brain activity to close others, consistent with the notion that physical warmth is particularly important for social connection with close others.

As further evidence for the specificity of physical warmth on close others, the difference in brain activity between a warm close other and warm strangers was not present when holding a cold object. Thus, a warm close other increased brain activity in the VS and MI compared with warm strangers, $t(41) = 2.743$, $p = .009$, 95% BCa CI [.054, .354], Cohen's $d = .423$. In contrast, there was no difference in VS and MI activity between a cold close other and cold strangers, $t(41) = .214$, $p = .832$, 95% BCa CI [−.179, .144], Cohen's $d = .033$. Further, there was no difference between a cold close other and warm strangers, $t(41) = .692$, $p = .493$, 95% BCa

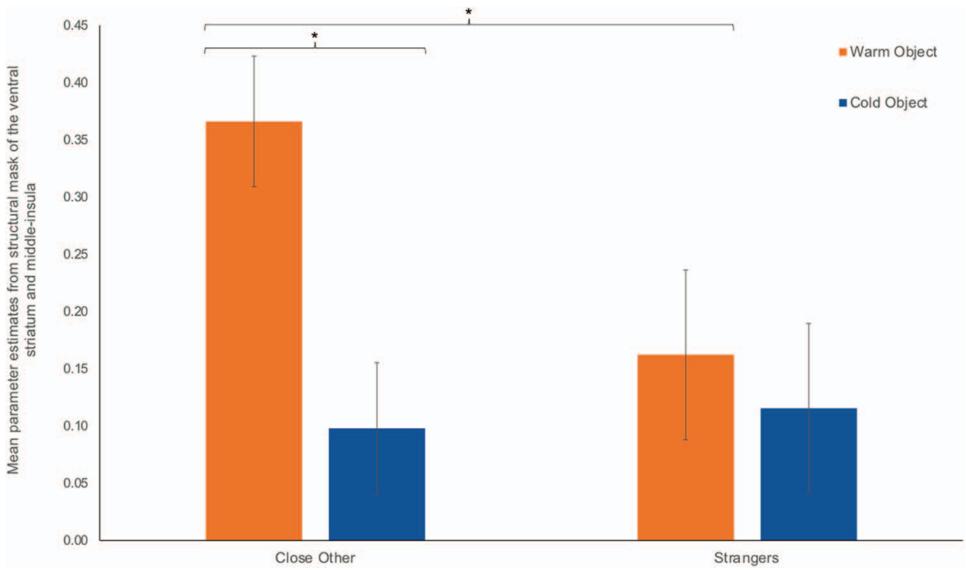

Figure 2. Results from VS-MI mask. An interaction between temperature condition (warm vs. cold) and social target (close other vs. stranger) emerged such that a warm close other increased VS and MI activity compared with a cold close other. There was no such difference in brain activity between warm and cold strangers, nor between a cold close other and warm strangers. Further, the increase in VS and MI activity to a warm close other (vs. warm strangers) was not present when holding a cold object. Error bars reflect standard errors. * $p < .05$, two-tailed and a 95% BCa CI excluding 0. See the online article for the color version of this figure.

CI [−.250, .122], Cohen's $d = .107$, once again suggesting physical warmth is showing a specific effect on brain activity to a close other.

The interaction between temperature and social target when comparing the warm object to the neutral object was not significant, $F(1, 41) = 2.726$, $p = .106$, but the pattern of the interaction was in the same direction as those described previously when comparing the warm object to the cold object. In particular, there was no difference in VS and MI activity between a neutral close other ($M = .069$, $SD = .401$) and neutral strangers ($M = .033$, $SD = .423$) nor between a neutral close other and warm stranger. The interaction between temperature and social target when comparing the cold to neutral object was not significant, $F(1, 41) = .310$, $p = .580$. There were no significant associations between post scan feelings of social connection and VS and MI activity (warm close other > cold close other, warm close other > neutral close other, warm close other > warm stranger, or warm close other > implicit baseline; *r*s between .006 and −.208; *p*s >.140).

Effect of Physical Warmth on Brain Activity to Close Others Across the Whole Brain

To elucidate activity beyond the a priori predicted regions, imaging data was also evaluated across the whole brain. The main effects for temperature (warm vs. cold object) and social target (viewing images of a close other vs. strangers) and the interaction between temperature condition and social target that was present for results at ROI-correction (i.e., warm vs. cold object) are reported in the online supplemental materials. Briefly, the interaction between temperature and social target revealed activity in the mid cingulate cortex (MCC), dorsal anterior cingulate cortex (DACC), primary (S1) and secondary somatosensory cortex (S2), and middle and posterior insula.

The simple effects mirrored results at ROI correction. Thus, a warm close other (vs. cold close other) increased activity in the VS and MI. In addition, a warm close other elicited greater activity in the VMPFC, pregenual cingulate cortex (PACC), and a large cluster encompassing the hippocampus and amygdala (see Table 1 for full list of activations). There were no differences in brain activity, however, between warm and cold strangers.

A warm close other (vs. warm strangers) led to activity in the VS, VMPFC, dorsomedial prefrontal cortex (DMPFC), PACC, and posterior cingulate cortex (PCC; Table 1; Figure 3). There were no peaks in the MI at the current or lower thresholds. But, consistent with the brain results at ROI correction, the cold object resulted in no differential activity in these regions. The only difference to emerge between a cold close other and cold strangers was activity in the occipital cortex.

Discussion

Social connection with close others is a primary need for humans. However, the mechanisms that contribute to experiences of social connection, especially closely bonded others, are less well understood. The current results add to a growing body of evidence showing that physical warmth causes feelings of social connection and activity in the neural regions that support social connection (Inagaki & Eisenberger, 2013; Inagaki et al., 2019; Inagaki, Irwin, et al., 2015). This research also contributes to a long-standing tradition postulating a causal influence of bodily sensation on the mind and brain (Barrett, 2017; Critchley & Garfinkel, 2017; Darwin, 1872; James, 1884; Lindquist, 2013; Panksepp, 2004;

Table 1
Brain Regions More Active to the Primary Condition of Interest (Close Other) Compared With Each of the Respective Control Conditions

Anatomical region	L/R	BA	*x*	*y*	*z*	*t*	*k*	Anatomical region	L/R	BA	*x*	*y*	*z*	*t*	*k*
warm close other > cold close other								warm close other > warm stranger							
Cerebellum	L		−27	−36	−18	6.65	3276	No significant clusters							
Occipital cortex	L	19	33	−78	−12	6.01									
Hippocampus	R		24	−15	−15	5.91									
Amygdala	R		18	−3	−15	5.39									
	L		−18	−3	−15	4.55									
VS	L		−9	9	−9	4.51									
	R		6	9	−9	4.34									
MI	L		−36	−3	−9	4.95									
PACC	R	25	3	33	9	5.41	413								
VMPFC	R	11	3	57	−9	4.05									
Occipital cortex	L	19	−33	−81	42	4.57	302								
warm close other > warm stranger								cold close other > cold stranger							
Occipital cortex	L	19	−30	−84	−12	10.91	4586	Occipital Cortex	L/R	18	30	−93	0	12.80	2388
VMPFC		11	0	48	−15	5.76	1811								
	L	11	−6	39	−15	4.44									
DMPFC	L	8	−9	33	57	5.21									
PCC	R	23	3	−54	21	5.07									
PACC	L	25/11	−3	39	3	4.45									
VS	L		−3	9	−6	4.39									
	R		6	9	−6	4.20									
Parietal cortex	L	39	−42	−60	30	5.31	315								

Note. Activations significant at FDR .05, 300 voxels. L/R = left and right hemispheres; BA = Brodmann's area; *x*, *y*, and *z* = Montreal Neurological Institute (MNI) coordinates; *t* = *t* statistic value at peak coordinates; *k* = cluster voxel extent. Activations that do not include a *k* value extend from the larger cluster listed above those activations. DMPFC = dorsomedial prefrontal cortex; MI = middle insula; PACC = pregenual anterior cingulate cortex; PCC = posterior cingulate cortex; VMPFC = ventromedial prefrontal cortex; VS = ventral striatum.

Schachter & Singer, 1962). The current study manipulated bodily information to show that physical warmth potentiates feelings of social connection and neural responses to close others, but not strangers. Further, images of close others did not have any effects on brain activity at colder temperatures (both room temperature and cold). Taken together, these results suggest physical warmth may amplify our connection to close others.

Physical warmth influenced feelings of social connection in a graded pattern: As the objective and subjective warmth of the three objects increased, so too did feelings of social connection. That is, the warm object increased feelings of social connection more than the neutral object, but the neutral object (which was rated as less warm than the warm object, but as warmer than the cold object) increased feelings of social connection more than the cold object. Importantly, the effects of warmth on feelings of social connection remained after adjusting for feelings of pleasure, but not vice versa. These findings are consistent with previous findings showing that another pleasant physical experience (i.e., soft stroking to the forearm) does not share overlapping neural activity with social warmth (Inagaki & Eisenberger, 2013). Thus, although it may feel pleasurable to experience physical warmth, general positive feelings are not driving the current findings. Instead, physical warmth appears to preferentially increase subjective feelings of social connection. An interesting future direction would be to assess whether physical warmth can help maintain feelings of connection over time or potentially repair a struggling close relationship.

Despite its recent controversy in the social psychological literature (Chabris et al., 2019; Lynott et al., 2014; cf. Bargh & Melnikoff, 2019), these results are consistent with previous findings from the animal and human literature that show selective effects of physical warmth on social connection. In addition, they emphasize the importance of physical warmth over other less-warm temperatures for pro-social behavior (e.g., Hofer, 1973). From the human social psychological literature, cold (vs. warm) temperatures reduce trust behavior toward an anonymous partner (Kang et al., 2011). In the opposite direction, uncomfortably hot environmental conditions are associated with increases in antisocial behavior (Anderson, Anderson, Dorr, DeNeve, & Flanagan, 2000). Even within non-noxious levels, optimal warmth shows the largest increases in pleasant feelings (relative to other temperatures; Ackerley et al., 2014). Though not an experimental manipulation of warmth, associations between internal body temperature and feelings of social connection also suggest an optimal level of warmth: Within a person, warmer body temperature is associated with greater feelings of social connection whereas colder body temperature is associated with lower feelings of social connection (Inagaki & Human, 2019). Thus, an emerging picture from the animal and human literature, that could be directly tested in future research, suggests there might be a Goldilocks effect such that, within a person, warm temperatures increase social connection, but temperatures that are either too warm or not warm enough have different or no effects on social connection.

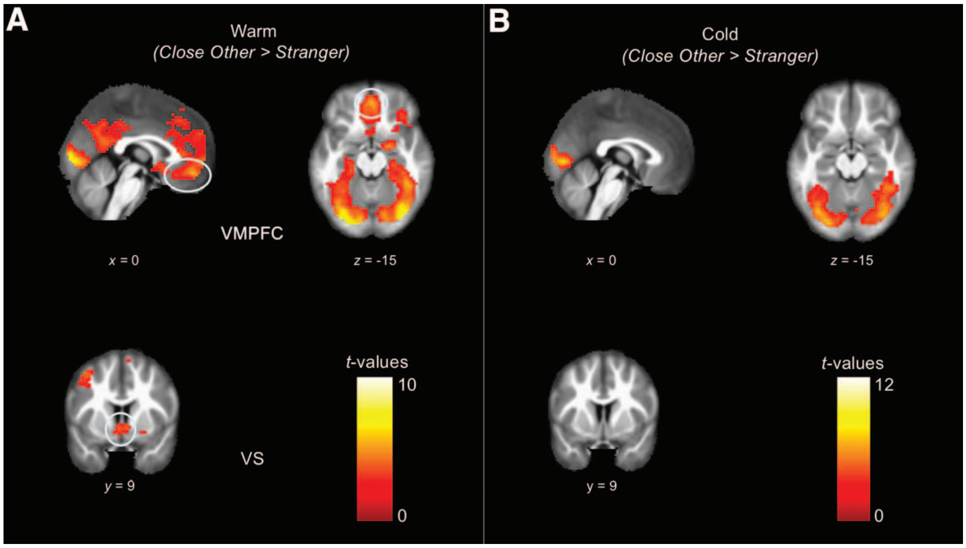

Figure 3. Effect of temperature on brain activity in response to viewing a close other compared with strangers across the whole brain. (A) A warm close other (vs. warm strangers) lead to greater activity in the ventromedial prefrontal cortex (VMPFC), ventral striatum (VS), and other regions (see Table 1). (B) In contrast, a cold close other (vs. cold strangers) only increased activity in the occipital cortex. Results are corrected for multiple comparisons at a false discovery rate (FDR) of .05, 300 voxels. See the online article for the color version of this figure.

In addition to the specific effect of warmth on feelings of social connection, there was also a specific effect of warmth on brain activity to viewing images of a close other (at both ROI correction and whole brain correction). Results from the a priori defined anatomical mask of the VS and MI showed that holding a warm object increased brain activity in response to viewing images of a close other relative to viewing the same images when holding a cold object. In other words, a physically warmed close other increased VS and MI activity more than the same cooled close other. However, temperature had no effect on brain activity to strangers. Although one can feel warmly toward strangers, physical warmth may be particularly relevant for existing, close social connections (Inagaki et al., 2019). Outside of studies including a temperature manipulation, the modulation of the VS by social factors is established (closeness to a social target, Fareri, Chang, & Delgado, 2015; positivity of social feedback, Izuma, Saito, & Sadato, 2008). Similarly, activity in the insula is correlated with the intensity of thermal stimuli (Becerra et al., 1999; Rolls et al., 2008). The current findings extend these literatures by showing that even in response to the same close other, VS and MI activity can be further modulated by thermotactile stimulation.

The interaction pattern between temperature and social target also revealed that the cold object dampened the increase in VS and MI activity to a close other (vs. strangers). A similar pattern emerged for the neutral, room temperature object, but the interaction between temperature and social target was not statistically significant. That is, a cold (or neutral) close other was no different from a cold stranger or a warm stranger. To understand why brain activity in response to close others might be particularly susceptible to temperature, we return to the theorized origins of the link between physical and social warmth, namely experiences of social connection in infancy and early development (Bowlby, 1952; Hofer, 1994). Social experiences in early life are largely isolated to interactions with close others such as caregivers, family, and other close friends. If these interactions co-occurred with physical warmth via physical contact, feeding, or other means, one would expect a stronger, and specific link between physical warmth and close others later in life. Owing to these specific early social experiences, effects of physical warmth may or may not generalize to interactions with strangers in which no social connection has been established.

An additional, complimentary explanation for the specific effects of physical warmth on brain activity to close others is that cooler temperatures reduce a general motivation to approach others. The motivation to approach close others may already be high, as close others are salient, instrumental, rewarding targets of social interaction. Approach toward strangers, on the other hand, may be lower and context-specific. Therefore, the reason why the cold object is reducing activity to close others, but not strangers, is because there was little to no motivation to approach the strangers in the first place. This possibility aligns with the colloquial use of nonwarm language (cold and distant, cold-blooded, lukewarm, or simply cold), synonymous with distant strangers and antisocial, negative social interaction.

At whole brain correction, additional regions beyond the VS and MI also increased to warm close others. As compared with the cold object, warm close others increased activity in regions previously associated with general affective responding (VMPFC, PACC, and amygdala; Lindquist, Wager, Kober, Bliss-Moreau, & Barrett, 2012). Additionally, warm close others (vs. warm strangers) led to increased activity in regions previously associated with mentalizing (DMPFC, PCC; Lieberman, 2010). The robust VMPFC activation as a result of holding a warm object is particularly notable as the VMPFC, along with the PACC, VS, amygdala, and MI, are theorized to contribute to innocuous thermal processing, particularly the affective experience of physical warmth (Larson, Pardo, & Pasley, 2014; Raison et al., 2015). Information from the skin, as manipulated in the current study, may reach these regions through the somatosensory cortex (present in the interaction contrast at whole-brain correction) and insula, both of which project to the medial OFC (Carmichael & Price, 1995). Interestingly, the VMPFC is also a well-known visceromotor region that regulates autonomic nervous system responding (Barrett, 2017; Gianaros & Wager, 2015), potentially also including body temperature. However, this possibility has yet to be directly tested.

Separately, the VMPFC has been highlighted as particularly relevant for close social connection such that the presentation of close others (images or messages from these individuals, relative to respective control conditions) leads to an increase in VMPFC activity (Eisenberger et al., 2011; Inagaki et al., 2019; Younger, Aron, Parke, Chatterjee, & Mackey, 2010). VMPFC activity in response to images of a close other is also associated with longer relationship length and greater feelings of support (Eisenberger et al., 2011). Thus, the specific increase in VMPFC activity in response to warm close others suggests physical warmth is not merely increasing the reward value of the stimuli, but potentially increasing the *social* warmth with which the close other images are experienced (consistent with Harlow's original interpretation of the cloth mother; Harlow, 1958). This pattern of activity is also consistent with the hypothesis that the VMPFC helps the brain make predictions about the affective meaning of bodily sensation by using prior experience to contextualize the sensation (Lindquist, 2013). That is, only physical warmth during matching social contexts in which warmth would have previously been experienced (close others) rather than mismatched social contexts (strangers) should produce social connection (MacCormack & Lindquist, 2019). Indeed, activity in the same set of regions was not found for cold close others or strangers at any temperature. Instead, only activity in the occipital cortex, responsible for processing visual information, remained to a cold close other (vs. strangers). Therefore, physical warmth selectively enhanced activity in regions traditionally associated with affective experience, suggesting the more objective perception of social stimuli can be separated from the more subjective, affective experience surrounding the stimuli.

It is no accident that sensory processes for physical warmth overlap with those of social connection. A long intellectual tradition in the study of emotion, including more recent theories of constructed emotion, suggest emotion occurs via a mixture of internal and external bodily sensation and psychological experience (i.e., conceptual knowledge; Barrett, 2017; Lindquist, 2013). In addition, the notion that the brain serves multiple purposes in the service of predicting the most likely emotional experience, in this case social connection with close others, is consistent with current perspectives and findings. Thermoregulation and the internal processing of physical warmth have not been highlighted in theories of constructed emotions yet. However, cutaneous warmth and internal body warmth may prove fruitful future research directions for greater understanding of the ingredient list of core affect. In addition, the processing of bodily sensations during different social situations, such as during interactions with a variety of social targets (close others, enemies, strangers, outgroup members, etc.), may also clarify the contribution of physical warmth to socioemotional experience.

Limitations and caveats to interpreting the findings are noted. Although VS and MI activity in response to cues from close others have previously been associated with feelings of social connection (Inagaki et al., 2019), there were no significant associations between feelings of social connection and brain activity to images of close others in the current study. It is possible that passive image viewing is not a strong enough manipulation to induce deep feelings of social connection. In addition, participants were not asked whether their feelings were specific to a social target (i.e., the close other or the strangers), rather feelings were rated in response to holding the different temperature objects. The choice not to have participants report on specific social targets was made to avoid demand characteristics for the current hypotheses. However, this choice may have disrupted the correspondence between what was occurring in the scanner and retrospective reporting. A second limitation was the use of silhouettes for the stranger images in the current scanner task. Future research interested in the effects of physical warmth on responses to social stimuli may wish to include additional stimuli, such as familiar others that one is not close to or pictures of other strangers, to further assess the specificity of physical warmth to close others. Finally, it is important not to generalize the current theory regarding the internal processing of physical warmth and social connection to any potential effects of weather or ambient environmental temperature on social connection. The body maintains its physical warmth despite wide variability in environmental temperature and so the warmth of the surrounding environment should not influence social connection in the same way as thermoregulatory pathways. In other words, simply living in warmer (vs. cooler) environments should not alter social connection.

In conclusion, the present study shows a specific effect of physical warmth on feelings of social connection and brain activity to a close other. The results are consistent with previous theoretical accounts of the body's contribution to emotional experience and empirical research on physical warmth's contribution to social connection. Future research endeavors on social connection with close others may wish to consider afferent feedback from the body to understand why and how social connection is such a critical need for humans.

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