SOCIAL CLOSENESS MODULATES THE NEURAL REPRESENTATION AND

PERCEPTION OF THE SELF AND OTHERS

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Abstract

Forming close social relationships is a fundamental human motivation. In fact, some have suggested that self and other identities merge with increasing social closeness, giving rise to overlapping mental representations of the self and close others. Though neural activation in the medial prefrontal cortex (MPFC) has previously been associated with reflecting on the self and close others, whether or not this activation reflects shared mental representations was unknown. The current set of studies demonstrate that 1) social closeness modulates the neural representation and perception of the self and others, 2) perceived social closeness can be motivated by a social connection manipulation, and 3) social closeness relates to well-being. Study 1 used an fMRI paradigm in which participants made personality trait judgments for themselves and a series of personally familiar targets. Response magnitudes in the MPFC linearly increased with social closeness to the self. Moreover, using representational similarity analysis (RSA), I found that representation in the MPFC appeared to cluster targets into personally familiar others, strangers, and the self. However, social brain areas, including the MPFC, reflected an additional graded similarity in brain activation patterns across targets that increased with social closeness to the self. In Study 2, using face morphs I demonstrated that the presence of close others in an image biased the perception of the self. In Study 3, I found that a social connection manipulation shifted perceived social closeness to acquaintances but not close others. Finally, trait loneliness was associated with decreased social closeness to nominated close others. Taken together, these results suggest that close others may share mental and neural representation with the self, and that perceptions of

social closeness with specific close others and acquaintances may be sensitive to general

social connectedness.

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General Introduction

Humans are an innately social species. Because of the evolutionary advantage of living in large social groups, the human brain has evolved to support and prioritize social functioning (Dunbar & Shultz, 2007; Parkinson & Wheatley, 2015). In fact, social and self-relevant processing occurs reflexively and preferentially. Even before babies develop a sense of self, around eighteen months, they have heightened awareness of and fascination with other people—particularly with attachment figures.

In the modern world, social circles are quite fluid and social information abounds. Our acquaintances and everyday contacts change when we move or begin a new job, and we are constantly learning new information about the people around us that we are obligated to access on demand. Balancing the benefits and demands of social relationships, evolution has optimized a social network size—around 150 people (Hill & Dunbar, 2003)—that can be successfully navigated. However, our innermost circle of close others, around 3-5 of our most intimate contacts, remains relatively stable and robust to circumstantial changes. The brain systems that have evolved to support this social lifestyle seem to confer an additional advantage on these close relationship partners. Close others are recognized more easily (Gobbini et al., 2013; Ramon & Gobbini, 2017) and recruit additional social and emotional brain systems (Leibenluft, Gobbini, Harrison, & Haxby, 2004; Moran, Lee, & Gabrieli, 2011). In fact, certain aspects of close others, including their personalities, elicit similar levels of activation in a brain region canonically associated with self-related activation, the medial prefrontal cortex (MPFC).

This and other work suggests that close others may, in fact, become incorporated into our identity so that accessing one cognitive structure activates information associated with the other (Andersen & Chen, 2002; Aron, Aron, & Smollan, 1992; Mashek & Aron, 2004). The apparent overlap between self and close other identities has been associated with successful relationship outcomes (Mashek & Aron, 2004). However, the extent to which this social closeness is mirrored in the neural representation of the self has not been adequately studied in the field of social neuroscience. The purpose of the present dissertation is to use behavioral and neuroimaging methods to investigate whether social closeness modulates the perception and neural representation of the self and others, and whether it relates to social well-being.

Social Connection and Well-being

The need to belong by forming meaningful social relationships is a fundamental human motivation that prepares us for life in a social group (R. F. Baumeister & Leary, 1995). People form social bonds naturally and resist threats to these bonds. In fact, social connection is so central to human nature that failing to form social bonds is associated with poor mental and physical health, including higher rates of depression, anxiety, and mortality (Baumeister & Leary, 1995; Baumeister & Tice, 1990; Cacioppo, Hughes, Waite, Hawkley, & Thisted, 2006). The health risks associated with social isolation is on par with the risks of cigarette smoking (Brummett et al., 2001). Consequently, social threats, like that of group exclusion, elicit physiological stress responses akin to survival threats (Eisenberger, 2013). This stress-related response to social exclusion may explain the relationship between social disconnectedness and poor health outcomes. By contrast,

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having support from social partners with whom we frequently and meaningfully interact mitigates these threats to personal well-being and predicts increased happiness and diminished responses to other threats (Coan, Schaefer, & Davidson, 2006; Diener & Seligman, 2002; Holt-Lunstad, Smith, & Layton, 2010). Even holding a spouse's hand during threat of an electric shock has been shown to reduce threat-related neural responding (Coan et al., 2006).

Indeed, independent of actual social contact, perceptions of social connectedness are predictive of well-being (Holt-Lunstad, Smith, Baker, Harris, & Stephenson, 2015). Loneliness is a condition of perceived social isolation, in which existing social connections fail to meet one's need for social connection. This can occur when existing connections are too shallow, or when one's need for social connection is exceedingly high. In fact, there is a discrepancy between loneliness and the objective social connections within a network (Berscheid & Reis, 1998), and both perceived and actual social connectedness predict physical and mental health outcomes (Cornwell & Waite, 2009).

Brain Systems Supporting Social Cognition

The brain may have evolved specifically to support our social lifestyle and the additional cognitive demands that it requires. The neocortex increased in size proportionate to the increased information processing required by living in large social groups (Dunbar, 1998), and other brain systems have been repurposed to serve social functions (Parkinson & Wheatley, 2015). Flexible navigation of social circles requires the ability to detect and identify social cues, maintain and manipulate social information,

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understand social norms, and predict the behavior of others. Some of these tasks are supported by specialized neural and cognitive systems, including social working memory (Meyer, Spunt, Berkman, Taylor, & Lieberman, 2012) and face processing systems (Haxby, Hoffman, & Gobbini, 2000). Social brain systems also organize fine-grained social information, like the social hierarchy (Parkinson, Kleinbaum, & Wheatley, 2017) and person knowledge (Thornton & Mitchell, 2017a), in brain activation patterns. This information is useful for understanding and predicting other people's behavior (Tamir & Thornton, 2018). In fact, a collection of brain regions credited with supporting various aspects of social cognition, including the posterior superior temporal sulcus (pSTS), temporo-parietal junction (TPJ), amygdala, temporal poles, medial prefrontal cortex (MPFC), the anterior cingulate cortex (ACC), and the extrastriate body area (EBA), has been referred to as the social brain (Adolphs, 2009; Frith, 2007; Van Overwalle, 2009). These regions broadly support mentalizing, understanding and abiding by social scripts, the detection of animacy, bodies, and biological motion, emotion processing and empathy (Frith, 2007; Saxe, 2006).

Critically, the brain appears to engage in social thought by default, when unengaged with external stimuli but without explicit reason to consider other minds. In fact, the default mode network, a system of brain regions whose activation increases in the absence of external stimuli, has extensive overlap with social brain regions, suggesting that social thought might be a default state for the human brain (Schilbach, Eickhoff, Rotarska-Jagiela, Fink, & Vogeley, 2008). Moreover, the extent to which a person reflexively indulges in social thought may predict his or her social cognitive proficiency and social behavior (Meyer & Lieberman, 2018; Powers, Chavez, &

Heatherton, 2015; Spunt, Meyer, & Lieberman, 2015; Wagner, Kelley, & Heatherton, 2011). Individual differences in the spontaneous processing of social cues has been related to perspective-taking ability (Wagner et al., 2011) and social interaction in the real world (Powers et al., 2015). Recent research has suggested that this default activation may support social information processing and consolidation (Meyer, Davachi, Ochsner, & Lieberman, 2018). For example, the connectivity of social brain regions, including the medial prefrontal cortex (MPFC) and the temporo-parietal junction (TPJ), during a rest period following social encoding predicted subsequently enhanced memory for social information.

Similarly, baseline activation in the MPFC, a region associated with self-referential processing (Kelley et al., 2002), may support self-focused thought. Self-related tasks elicit less MPFC activation than the baseline state, suggesting that these tasks are more cognitively demanding but no more self-focused than the default state (Gusnard, Akbudak, Shulman, & Raichle, 2001). Moreover, individual differences in MPFC activation during rest has been associated with performance enhancement on a self-related task (Meyer & Lieberman, 2018). Participants who recruited the MPFC by default were quicker to make trait judgments for the self. Collectively, these results suggest that self-related and social thought may occur naturally and when unengaged in externally-focused thought. Moreover, this default social processing may enable more efficient processing of social information.

Close and Familiar Others are Privileged

Finally, these social brain systems confer an additional advantage on close relationship partners. We are quicker to detect a friend's face than a stranger's face, even under limited attentional resources (Gobbini et al., 2013; Keyes & Zalicks, 2016; Ramon & Gobbini, 2017). Moreover, familiar faces are more photograph and view invariant than unfamiliar faces (Freiwald, Duchaine, & Yovel, 2016; Jenkins & Burton, 2011). This is due in part to spontaneous activation of person knowledge and social processing by familiar faces (Gobbini, Leibenluft, Santiago, & Haxby, 2004). Because familiar faces are tagged with additional semantic and emotional cues, they may be more deeply encoded and robust to small perceptual changes. In fact, all faces are more recognizable when attending to holistic, abstract knowledge about the person than about any single physical feature (Courtois & Mueller, 1979).

Because of the added social and emotional associations, familiar faces recruit a broad, distributed network of brain areas. Familiar face recognition requires the cooperation of the canonical face processing system (pSTS and fusiform gyrus), as well as systems responsible for representing the emotional attachment (amygdala, insula, striatum) and person knowledge (anterior paracingulate, pSTS/TPJ, anterior temporal cortex, and precuneus/posterior cingulate cortex) associated with familiar others (Leibenluft et al., 2004). Broader knowledge about personally familiar others is also represented in distributed activation patterns across the social brain, including the MPFC, posterior cingulate cortex (PCC), and TPJ (Thornton & Mitchell, 2017a). These person-specific activation patterns reflect richly coded person knowledge and contribute to the richness of mental simulation of the other person's mind.

However, familiarity alone does not elicit the richness of emotional and social processing that social closeness does. Famous familiar identities are facilitated in perception and are consequently easily recognized, but they are not associated with the same emotional attachment that personally familiar people are (Gobbini & Haxby, 2007). Accordingly, personally familiar faces, like that of one's child, elicit more activation in regions associated with theory of mind than famous familiar faces do (Gobbini & Haxby, 2007; Gobbini et al., 2004; Leibenluft et al., 2004).

Some have suggested that close relationships comprise a separate but integral aspect of the self (Andersen & Chen, 2002; Aron, Aron, & Smollan, 1992; Mashek & Aron, 2004), with social closeness reflecting the degree of overlap between the self and the close other (Aron, Aron, Tudor, & Nelson, 1991). This overlap is believed to reflect the resources, perspectives, and characteristics that are shared between a person and their relationship partner. Importantly, the degree of overlap is an important predictor of relationship success, with reported overlap among spouses predicting marital satisfaction and duration (Aron et al., 1992; Mashek & Aron, 2004). In fact, self and other identities may actually merge with increasing social closeness, giving rise to overlapping cognitive representations of close others and the self (Andersen & Chen, 2002; Aron et al., 1991). Accessing one cognitive structure may activate information associated with the other. Indeed, one study found that an individual's self-evaluations were predicted by his or her evaluations of close others (Dehart, Pelham, Fiedorowicz, Carvallo, & Gabriel, 2011). If social closeness promotes an overlap between the self and close others it may be detectable at the level of the neural representation of the self.

Neural Representation of the Self

Activation in the medial prefrontal cortex (MPFC) has been reliably associated with self-referential processing (D'Argembeau et al., 2007; Kelley et al., 2002; Northoff & Bermpohl, 2004; Schmitz & Johnson, 2007; van der Meer, Costafreda, Aleman, & David, 2010). Critically, although self-directed thought has classically been induced with a trait attribution paradigm (Kelley et al., 2002; Wagner et al., 2011), both implicit and explicit self-referential tasks, and even undirected self-focus, elicit similar activation in the MPFC (D'Argembeau et al., 2005; Gusnard et al., 2001; Moran, Heatherton, & Kelley, 2009; Whitfield-Gabrieli et al., 2011). This effect is so robust that the prominence of MPFC activation during rest has been taken to indicate that self-referential or introspective thought is a default state of being.

Commonly, MPFC activation in response to self-focused thought has been defined from its contrast with other-focused thought. In fact, a functional dissociation within the MPFC was observed, whereby self-referential thought activates ventral aspects of the MPFC (vMPFC), and conversely, other-referential thought, or perspective taking, activates dorsal aspects of the MPFC (dMPFC) (D'Argembeau et al., 2007; van der Meer et al., 2010). There have been some nuanced exceptions to this rule. Specifically, thinking about similar others or close others has been shown to elicit similar or only slightly attenuated levels of activation in the vMPFC when compared to the self. Moreover, recent meta-analytic evidence points to a more distributed functional organization in the MPFC that abides by a spatial gradient, rather than a strict dissociation—with observations of self-relating processing occurring more frequently but not exclusively in

ventral portions of the MPFC (Denny, Kober, Wager, & Ochsner, 2012; Wagner, Haxby, & Heatherton, 2012).

Making opinion judgments for a similar person engaged the vMPFC, whereas making similar judgments for a dissimilar person engaged the dMPFC (Mitchell, Neil Macrae, & Banaji, 2006). During mental simulations for which the self is an appropriate model for the other person (i.e., for similar others), the vMPFC is engaged in making judgments—suggesting the use of self-referential thought when mentalizing about these people. Consistent with this notion, one study found repetition suppression of vMPFC activity following self-thought and the simulation of a similar other but not following the simulation of a dissimilar other (Jenkins, Macrae, & Mitchell, 2008). Overall, these results suggest that self-referential processing occurs in the vMPFC and mental simulations of other minds occur in the dMPFC, unless the other person is sufficiently similar to the self to be simulated using self-referential processing. For tasks that do not require mentalizing, similarity does not appear to engage the vMPFC (Krienen, Tu, & Buckner, 2010).

However, distinctions between the self and close others in the vMPFC are less clear. Although self remains dissociable from close others during trait attributions (Chen, Wagner, Kelley, Powers, & Heatherton, 2013; Heatherton et al., 2006; Sui & Han, 2007), close others often recruit the vMPFC to an intermediate degree (Krienen et al., 2010; Moran et al., 2011; Seger, Stone, & Keenan, 2004). Further, one meta-analysis found no unique MPFC activation for the self relative to close others, but rather a difference in the anterior cingulate (Murray, Schaer, & Debbané, 2012), and yet another found that all

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studies involving either the self or close others were localized in the vMPFC/BA 10 (below z-coordinate 22; Figure 1; Van Overwalle, 2009).
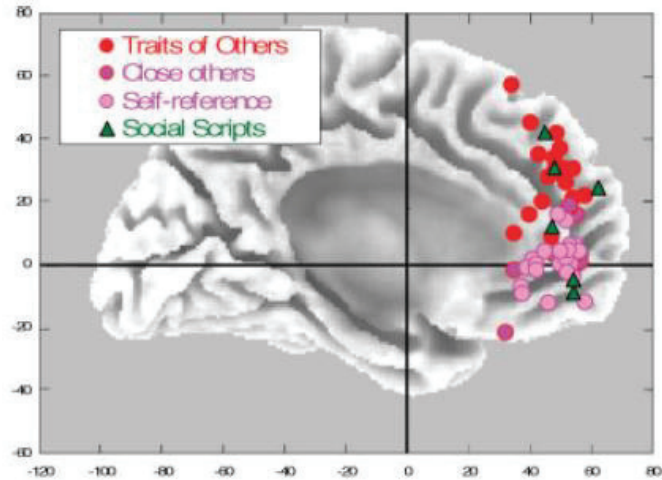
Figure 1. Peak coordinates associated with trait judgments for the self and close others were localized to the ventral MPFC/BA 10 in a meta-analysis of social cognition (Van Overwalle, 2009).

Importantly, these responses are robust to similarity between friends. Our friends are both personally familiar and more similar to us (McPherson, Smith-Lovin, & Cook, 2001), creating difficult confounds to address when studying social closeness. However, friends have been shown to elicit similar levels of activation in the vMPFC as the self, even after controlling for the similarity of the friend (Krienen et al., 2010). Moreover, specific aspects of close others, such as a mother's personality but not her appearance, appear to be processed much more similarly to the self, suggesting that this region is sensitive to close others because of a deeper connection rather than mere familiarity or similarity (Moran et al., 2011).

One limitation of these studies is that they tend to dichotomize others as either close/distant (Heatherton et al., 2006) or similar/dissimilar (Mitchell et al., 2006), though the category of close others is likely to reflect a range of social closeness. Although

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categorizations such as these tend to increase the psychological distance between experimental conditions and increase power for detecting group differences in activation, there is information lost that may be detected using a richer, more graded sampling of stimuli. Moreover, these univariate neuroimaging approaches have demonstrated the involvement of particular regions, namely the MPFC, in thinking about the self and close others, but they have not shed light on the representation of self and others in these regions. Conversely, by comparing the similarity in multivariate (or multi-voxel) patterns across conditions, which has been interpreted as reflecting their shared informational content, we can better approximate the question of whether the underlying mental representations of the self and close others share information.

The present projects used multivariate pattern analysis (MVPA; Norman, Polyn, Detre, & Haxby, 2006), to explore the neural representation of social closeness between the self and close others. To the extent that close others are represented as an extended part of the self, brain activation should mimic this pattern and track social closeness. That is, condition-specific (e.g., self vs. close others) patterns of fMRI blood-oxygen-level-dependent (BOLD) activation across voxels should be more similar for close others than for acquaintances, and this difference should increase with self-reported social closeness. These projects further explored whether the structure of self-representation (e.g., representational distance of self from close other) and self-reported social closeness relate to social well-being.

General Aims of the Present Research

The present research projects investigated the distinctiveness of self and close other identities at the level of neural representation, measured by neural activation patterns, to specifically probe whether close others are incorporated into self-representation in a pattern consistent with self-other merging. To do so, we employed behavioral tasks and multivariate neuroimaging to characterize the structure of self-other representation and to determine whether the represented distance between self and close others underlies the social well-being of the individual.

Aim 1: To determine how social closeness modulates the neural representation and perception of self and other

Building off of previous research, which demonstrated activation in the MPFC in response to judgments about the self and close others (Heatherton et al., 2006; Kelley et al., 2002; Moran et al., 2011), the present set of studies characterized self-related processing in this region to determine whether information about self and close others reflects a pattern predicted by self-other merging. Specifically, participants made judgments (trait descriptors in Study 1; face morphs in Study 2) for targets that varied in social closeness to the self. Multivariate neuroimaging analyses were used to estimate the underlying representational structure of self and others along the dimension of social closeness. If neural activation patterns associated with self and others are more similar for friends than for acquaintances or if perceptions of the self are biased by the presence of close others, then it supports the idea the self-other merging occurs and depends on social closeness.

Aim 2: To manipulate social closeness of self and other

The second aim was to determine whether the representational distance between self and other could be influenced by motivational changes in the individual. Specifically, social disconnectedness is known to successfully motivate the need to belong (Baumeister & Leary, 1995; Baumeister & Tice, 1990; Cacioppo et al., 2006; Holt-Lunstad et al., 2010), increasing social pursuit and decreasing barriers to social perception (Baumeister & Leary, 1995; DeWall, Baumeister, & Vohs, 2008; Maner, DeWall, Baumeister, & Schaller, 2007; Powers, Worsham, Freeman, Wheatley, & Heatherton, 2014). Aim 2 investigated whether manipulating social disconnectedness changed self-reported social closeness of the self to nominated relationship partners.

Aim 3: To relate social closeness to social disconnectedness

Aim 3 investigated whether self-reported social closeness to relationship partners and the neural representation of the self and others relate to general social disconnectedness, as measured by loneliness. Real social connectedness and perceived social connectedness are known to diverge and independently predict social well-being and related health outcomes (Holt-Lunstad et al., 2015). That is, loneliness reflects perceived social disconnectedness and sometimes fails to reflect true social connections. We explored the possibility that neural representational distance of the self and others could more accurately reflect this implicit representation of a disconnected self than objective measures, like frequency of social contact. That is, if perceived relational distance is distorted from reality, perhaps it is reflected in patterns of neural similarity that may reflect a more isolated representation of the self. Here we related self-reported

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social closeness with specific relationship partners and measures of neural

representational distance between the self and other to levels of trait loneliness.

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Study 1: Representational Similarity of Self and Other Reflects Social Closeness

Study 1 built off of prior research demonstrating reliable MPFC activation in response to making trait attributions about the self. Though the MPFC consistently distinguishes between the self and others, supporting a "self is special" notion, this region has been known to be moderately engaged by people who are close to the self (Krienen et al., 2010; Moran et al., 2011; Murray et al., 2012). Indeed, the "inclusion of other in the self" theory of close relationships (Aron et al., 1991) characterizes relationship closeness as increasing overlap between self and other representation.

To adequately address these theoretical perspectives, representational similarity analysis (RSA; Kriegeskorte, Mur, & Bandettini, 2008) was applied to multivariate activation patterns in MPFC to better characterize the representation of self and others along the dimension of social closeness. A "self is special" model of self-other representation would predict that all other people, regardless of relationship closeness, would be represented as highly distinct from the self. Alternatively, a "self-other overlap" model might predict more graded similarity to the self that increases with social closeness. To permit a more careful investigation into the category of close others, this study more richly sampled from personally familiar others that varied along the dimension of social closeness.

This study aimed to determine whether social closeness would be apparent from neural representations of self and others in the MPFC, and furthermore, whether individual differences in this representational structure would predict anything about the loneliness of the participant. Specifically, this study explored whether social closeness

ratings and neural similarity of others to the self were sensitive to trait-level

connectedness, or loneliness.

Method

Participants

Fifty college students and community members (30 female) between the ages of

18 and 47 (*M*= 20.2, *SD*= 4.6) were recruited for Study 1. All participants were screened

for compliance with MRI safety, reported normal neurological history, and had normal or

corrected-to-normal visual acuity. Each participant provided informed consent in

accordance with the guidelines set by the Committee for the Protection of Human

Subjects at Dartmouth College and received monetary compensation or class credit for

participating in the study. FMRI data were excluded for participants (n = 7) whose

movement during any run of the scan exceeded 3mm in translation or 2 degrees in

rotation. Five participants were missing data for the Revised UCLA Loneliness Scale

(Russell, Peplau, & Cutrona, 1980) and were excluded from analyses requiring that

measure.

Procedure

Prior to the scan, participants completed a short survey in which they provided the

names of five close others and five acquaintances, ranked in the order in which they felt

closest to them. Specifically, for close others they were instructed to choose five people

with whom they had "the closest, deepest, most involved, and most intimate

relationships". They were also instructed to select five familiar acquaintances, such as

classmates, colleagues, or neighbors. These names were later used in the scanner task to elicit activation associated with thinking about close others and acquaintances.

During the scan, participants made judgments about trait adjectives for 16 targets: the self, five nominated close others, five nominated acquaintances, and five well-known celebrities (Ellen Degeneres, Kim Kardashian, Barack Obama, Justin Bieber, and Mark Zuckerberg). Importantly, all targets were familiar to the participants (though celebrities are not personally familiar) but were expected to vary in social closeness. Each trial consisted of one target name (above) and a trait adjective (below) subtending a central fixation cross. The trial lasted for 2000 ms during which the participant was instructed to respond using a button-box with how much the trait describes the person (1= "not at all", 4= "very much"). The task lasted for 10 functional runs (80 trials each, 5 trials per target) for a total of 800 trials (Figure 2).
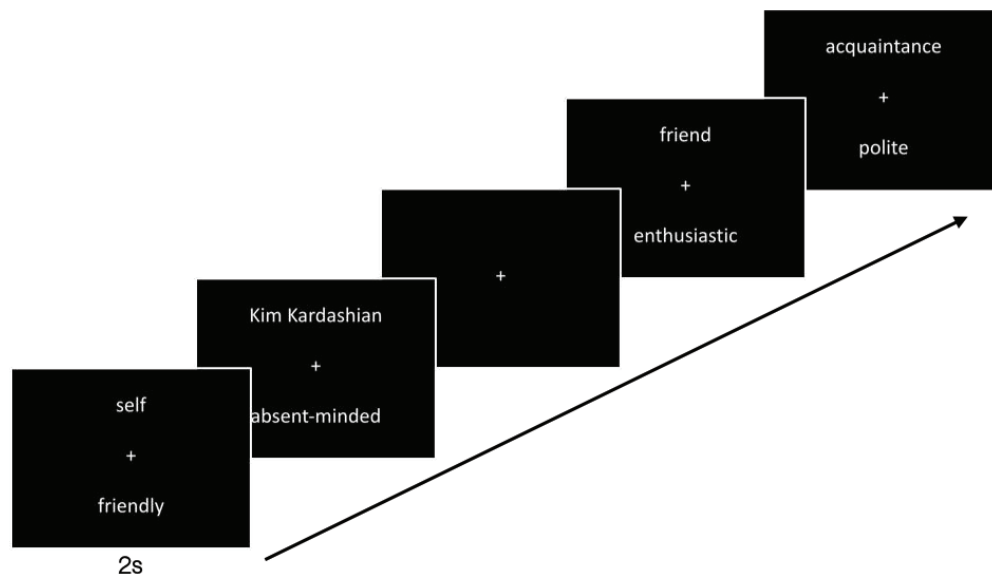
Figure 2. Schematic of Study 1 design. Ten functional runs with 80 2s trials jittered with fixation. Participants made trait attributions for the self, five nominated close others, five nominated acquaintances, and five celebrities.

Following the scan, participants rated their closeness to, familiarity with, and similarity to each of the targets on a 0-100 scale (0= "not at all", 100= "very much"). To permit a comparison of the previous behavioral and neural measures to social well-being, participants additionally completed the Revised UCLA Loneliness Scale (Russell et al., 1980).

Apparatus

Imaging data were acquired on a 3T Siemens MAGNETOM Prisma Scanner (Siemens AG, Munich, Germany) with a 32-channel head coil. Stimuli were presented from a 13-inch Apple MacBook Air laptop computer running PsychoPy v1.85 software (Peirce, 2008). An Epson (model ELP-7000) LCD projector displayed the stimuli on a screen at the head end of the scanner bore. Subjects viewed that screen through a mirror mounted on top of the head coil. An MR compatible keypress interfacing with the Cedrus Lumina Box recorded participant's responses.

FMRI image acquisition

An anatomical (T1) image was acquired using a high-resolution 3-D magnetization-prepared rapid gradient-echo (MPRAGE) sequence (TR=9.9ms; TE=4.6 ms; flip angle=8°; 1x1x1mm^3 voxels). Functional images were collected using a T2*-weighted echo planar imaging (EPI) sequence (TR = 1000 ms, TE = 30ms, flip angle = 59°, bandwidth = 2742, echo spacing = 0.49, 2.5x2.5x2.5 mm resolution) with a simultaneous multi-slice (SMS) of 4 and GeneRalized Autocalibrating Partial Parallel Acquisition (GRAPPA) of 1. Ten functional runs of 250 axial images (52 slices, 130mm

coverage) were acquired for each participant. Sequence optimization was obtained using optseq2 (Dale, 1999) and included 30% jittered trials of fixation for obtaining a baseline estimation of neural activity.

FMRI preprocessing

Univariate functional neuroimaging data were analyzed using SPM12 (Wellcome Department of Cognitive Neurology, London, UK) in conjunction with a suite of preprocessing and analysis tools (https://github.com/wagner-lab/spm12w). Functional data were slice time corrected, realigned within and across runs to correct for head movement and transformed into a standard anatomic space (3-mm isotropic voxels) based on the ICBM 152 brain template space [Montreal Neurological Institute (MNI)]. Normalized data were then smoothed spatially using a 8mm FWHM Gaussian kernel for univariate analyses and a 4mm FWHM Gaussian kernel for multivariate analyses. To further account for motion artifact, participants that demonstrated substantial movement (> 3mm in translation or 2 degrees in rotation) were discarded.

Univariate FMRI analysis

General linear model. A general linear model (GLM) incorporating task effects (modeled as events of interest convolved with the canonical hemodynamic response function) was used to compute beta images estimating task-related effects for every voxel in the brain. The model included nuisance regressors for six motion parameters (x, y, z directions and roll, pitch, yaw rotations), a linear drift, and run constants. The resulting

beta images were used to compute a whole-brain voxel-wise contrast comparing all targets to the baseline condition.

Parametric modulation analysis. Next, a parametric modulation analysis was conducted to identify regions of the brain whose activation magnitude increased with social closeness to the self. A subject-level regressor reflecting the social closeness ratings for each target (from 1-100, with a 100 entered as closeness to the self) were entered into the first-level GLM to identify brain regions whose activity linearly increased with social closeness. Next, a second-level one-sample t-test was conducted and the resulting group-level map was voxelwise thresholded at $p < 0.001$ and cluster corrected to $p < 0.001$ (minimum extent threshold: $k = 66$ contiguous voxels), as recommended by AFNI's 3dClustSim, using the spatial autocorrelation function (Cox, Chen, Glen, Reynolds, & Taylor, 2017; Eklund, Nichols, & Knutsson, 2016).

Multivariate FMRI analysis

Multivariate analyses were conducted using Python tools for neuroimaging, including the PyMVPA toolkit (http://www.pymvpa.org; Hanke, Halchenko, Sederberg, & Hanson, 2009) and SciPy (http://www.scipy.org). Voxel-wise GLM beta images were used to conduct representational similarity analysis (RSA; Kriegeskorte et al., 2008) for the comparison of activation patterns and information overlap across conditions.

ROI analyses. Given our specific predictions about the role of the MPFC and DMPFC in self and social processing, respectively, we defined regions of interest (ROI) masks from which we could to test specific hypotheses about the involvement and

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structure of representation in these regions. To define these ROIs independently of our own data, we downloaded reverse-inference maps generated by Neurosynth (Yarkoni, Poldrack, Nichols, Van Essen, & Wager, 2011) reflecting meta-analytic association with the terms "self" and "social". To ensure that our masks only included voxels in the MPFC that are most involved in self-referential processing (for "self") and social cognition (for "social") these masks were further restricted the coordinates associated with BA 10 and BA 9 (Denny et al., 2012; Meyer & Lieberman, 2018; Wagner et al., 2012). Specifically, the self/MPFC ROI was restricted in the x-dimension from -18 to 18, in the y-dimension from 30 to 80, and in the z-dimension from -12 to 22, for a resulting mask size of 409 voxels (Figure 3a). The social/DMPFC ROI was restricted in the x-dimension from -18 to 18, in the y-dimension from 26 to 74, and in the z-dimension from 22 to 58, for a resulting mask size of 319 voxels (Figure 3b).
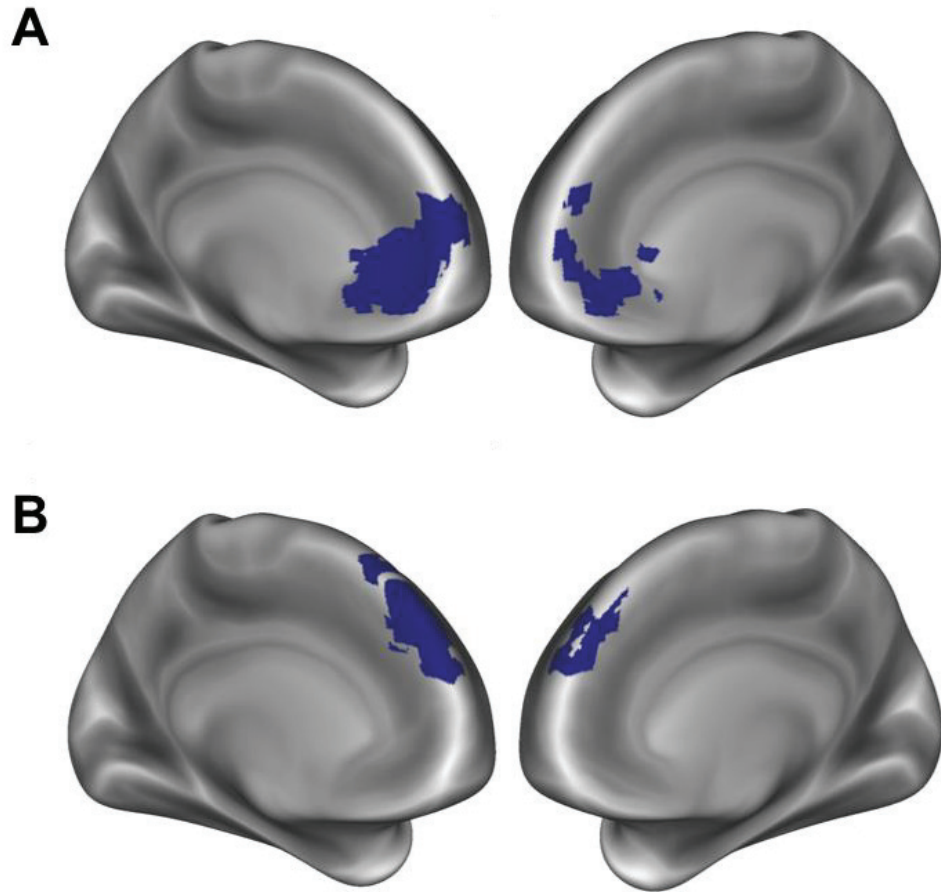
Figure 3. ROI masks of the MPFC (A) and DMPFC (B) created from a meta-analytic search for the terms "self" and "social" and restricted to to BA10 and BA9, respectively (Yarkoni et al., 2011).

Model similarity structures. Next, to help make sense of the extracted structure, the representational similarity structure in the MPFC/"self" ROI was compared to a series of seven theoretically-driven model matrices. These models reflect a theoretical structure according to which the MPFC could represent and cluster the conditions of interest. Specifically, the models included: 1) "all conditions distinct" model, 2) "self vs. other" model in which self is distinct from all others, who are indistinct , 3) "3 cluster" model with self distinct from familiar others (close others and acquaintances) distinct from celebrities, 4) "self and familiar" model with self and familiar others clustered and

celebrities as distinct, 5) "self and close" model with self and close others clustered and familiar and celebrities clustered, and 6) "self and close vs. acquaintance vs. celebrity" model where self and close others are clustered but the other conditions are distinct, 7) "combined 3 cluster-social closeness" model where overall self, familiar others, and celebrities are distinct clusters but where familiar others are represented in a graded fashion based on their social closeness to the self (Figure 4).
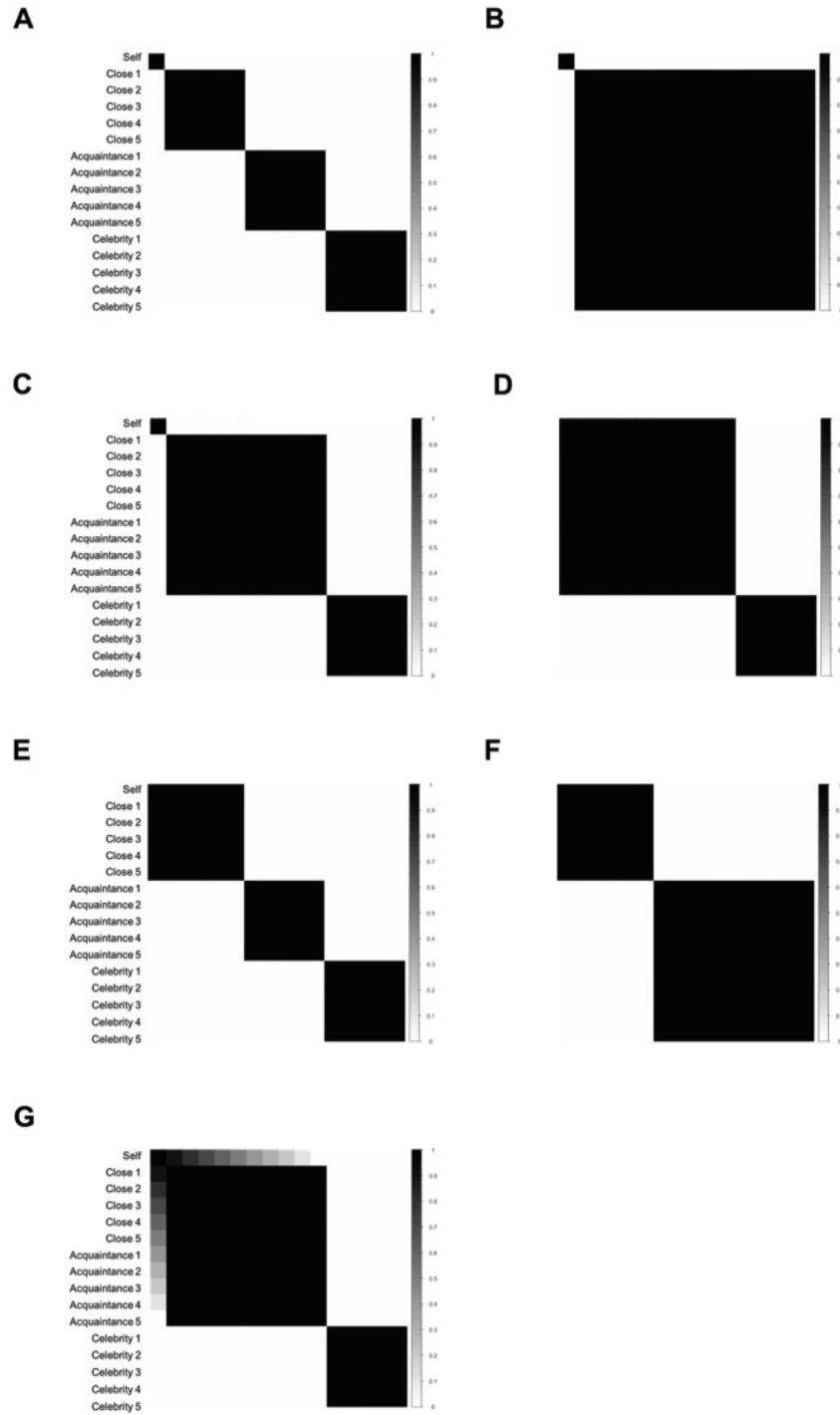
Figure 4. Seven model similarity matrices of self-other representation against which the MPFC representational similarity structure was compared: A) "all conditions distinct" model, B) "self vs. other" model, C) "3 cluster" model, D) "self and familiar" model, E) "self and close" model, F) "self and close vs. acquaintance vs. celebrity" model, G) "combined 3 cluster-social closeness" model.

Searchlight RSA. To isolate the effect of interest and conduct a more complete search for brain response patterns that reflected self-other overlap and the social closeness of the target, a sphere searchlight (3mm radius) was used to conduct four whole-brain RSAs. The first searched only for the pattern associated with social closeness to personally familiar others while allowing all other pairwise relationships to vary (i.e., searching for the vector of closeness-related values alone). This approach identified brain regions whose cross-condition patterns of activation were most similar to the social closeness ratings of all nominated, personally familiar others. These 1-100 ratings were transformed to a 0-1 scale and converted to distances (1 minus the transformed value) to permit correlation with neural representational dissimilarity matrices. The self condition was weighted with a distance of 0 (similarity of 1) and celebrities were weighted with a distance of 1 (similarity of 0) to isolate the relationship within personally familiar others. Similarity in activation patterns was estimated using Pearson correlation and similarity across brain activation patterns and behavioral responses was estimated using Spearman rank correlation. The second searchlight more directly isolated self-other overlap by searching for regions whose activation patterns matched the "self and close" model above, showing similar patterns for the self and close others and similar patterns for acquaintances and celebrities. The third searchlight searched for activation patterns that reflected the "self and familiar" model above, revealing regions where the self and all personally familiar others (close others and acquaintances) were represented more similarly and were distinct from celebrities. Finally, the target dissimilarity matrix for the fourth searchlight reflected the "combined 3 cluster-social closeness" model, combining both the expected similarity structure and

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the effect of interest. For each searchlight, a one-sample t-test was conducted on the voxel-level Fisher-z transformed correlation values representing similarity of the neural and target RDMs. The resulting group-level statistical maps were voxelwise thresholded at $p < 0.001$ and cluster-corrected to $p < 0.001$ (minimum extent threshold: $k = 164$ contiguous voxels for the first analysis, $k = 162$ voxels for the second analysis, $k = 174$ voxels for the third analysis, and $k = 200$ voxels for the fourth analysis).

Relating social closeness and representational structure in MPFC to loneliness

Finally, to relate social closeness ratings and the structure of self-other representation in MPFC to social well-being, loneliness was entered as a predictor (in independent models) of either social closeness ratings or cross-condition similarity (Fisher-z transformed correlation coefficients) of each condition with the self, using the *lme4* (Bates, Maechler, Bolker, & Walker, 2015) and *lmerTest* (Kuznetsova, Brockhoff, & Christensen, 2017) packages in R. Specifically, these models included a random intercept for subject and an interaction with condition (close others, acquaintance, celebrities), with celebrities coded as the reference group for contrasts. An additional whole-brain regression with loneliness was conducted on the statistical map from the second searchlight analysis (for self-other overlap) to reveal regions of the brain where similarity of activation patterns to the target RDM depended on the loneliness of the participant. This statistical map was voxelwise thresholded at $p < 0.05$ and cluster-corrected to 200 contiguous voxels.

Results

Behavioral results

Ratings of closeness (Figure 5) for each target were correlated across subjects with both familiarity, $r(49) = 0.82$, $t(49) = 15.89$, $p < 0.001$, and similarity, $r(49) = 0.84$, $t(49) = 18.06$, $p < 0.001$. Moreover, all ratings were higher for close others than acquaintances than celebrities (Table 1), demonstrating a linear trend, $B_{closeness} = -53.11$, $p < 0.001$, $B_{familiarity} = -35.49$, $p < 0.001$, $B_{similarity} = -38.78$, $p < 0.001$.
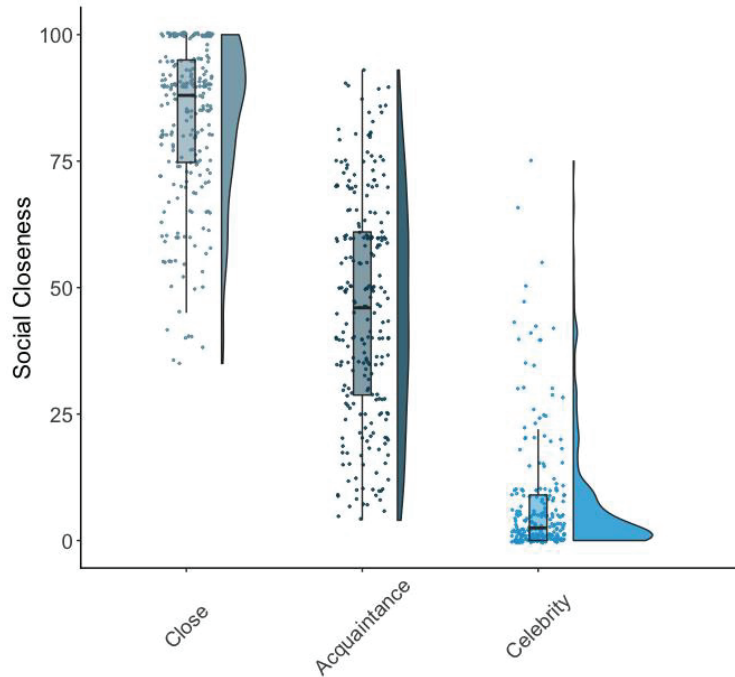
Figure 5. Social closeness ratings (1-100) for five nominated close others, five nominated acquaintances, and five celebrities.

Parametric modulation analysis

The parametric modulation analysis revealed a single cluster in the MPFC (MNI: -3, 33, -9; voxelwise $p < 0.001$, cluster-corrected to $p < 0.001$, Figure 6) whose BOLD

activation during the task linearly increased with the social closeness of the target to the participant.
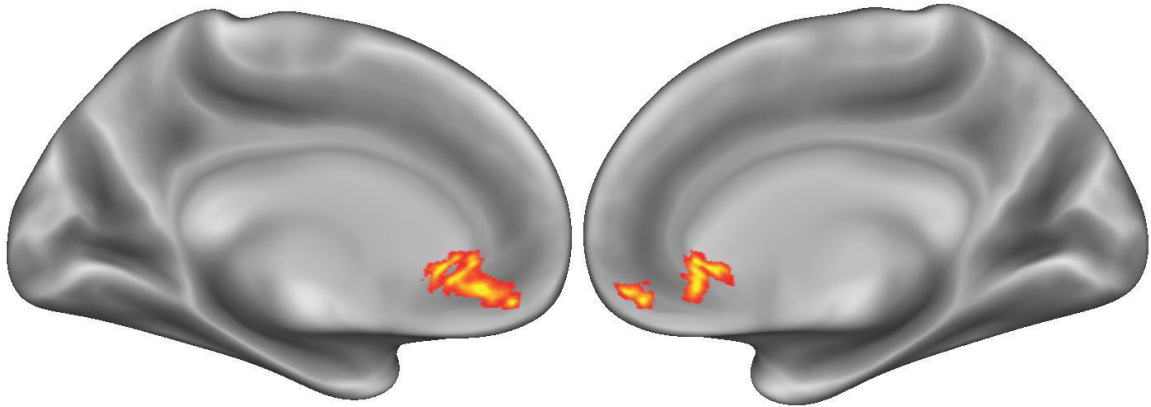
Figure 6. Activation magnitude in a single cluster in the MPFC (-3, 33, -9) linearly increased with the social closeness of the target to the participant (voxelwise p< 0.001, cluster-corrected to p< 0.001).

Multivariate ROI analysis

The representational similarity structure in the MPFC/"self" ROI (Figure 7a) appeared to reflect a structure whereby i) self was distinct from all others and ii) representation of others was clustered such that all personally familiar others (close others and acquaintances) were similarly represented and celebrities were more similarly represented. To better visualize the emergent structure of the matrix, a multi-dimensional scaling solution was derived to depict the similarity of conditions along two dimensions (Figure 7b). This plot more clearly illustrates that three clusters emerge from cross-condition similarity in MPFC activation: self, familiar others (close others and acquaintances) and celebrities. There was a less clear structure to the activation patterns from the DMPFC/"social" ROI (Figure 8).

A

RSA for Self and Other Representation in MPFC

B
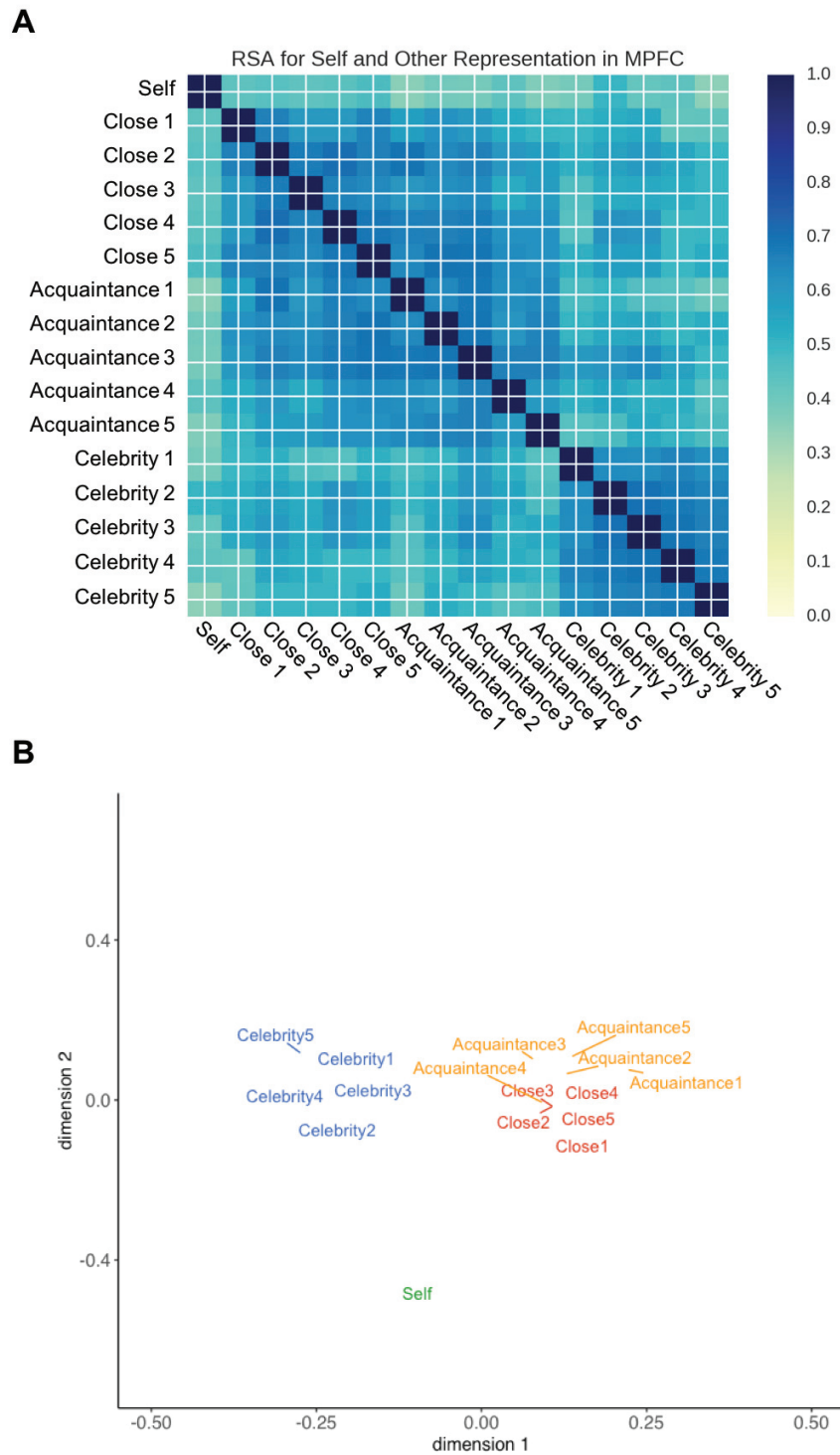
Figure 7. Representational similarity of self and others in MPFC/"self" ROI reflected in a correlation matrix (A) and multi-dimensional scaling plot depicting distances on two dimensions for visualization (B).
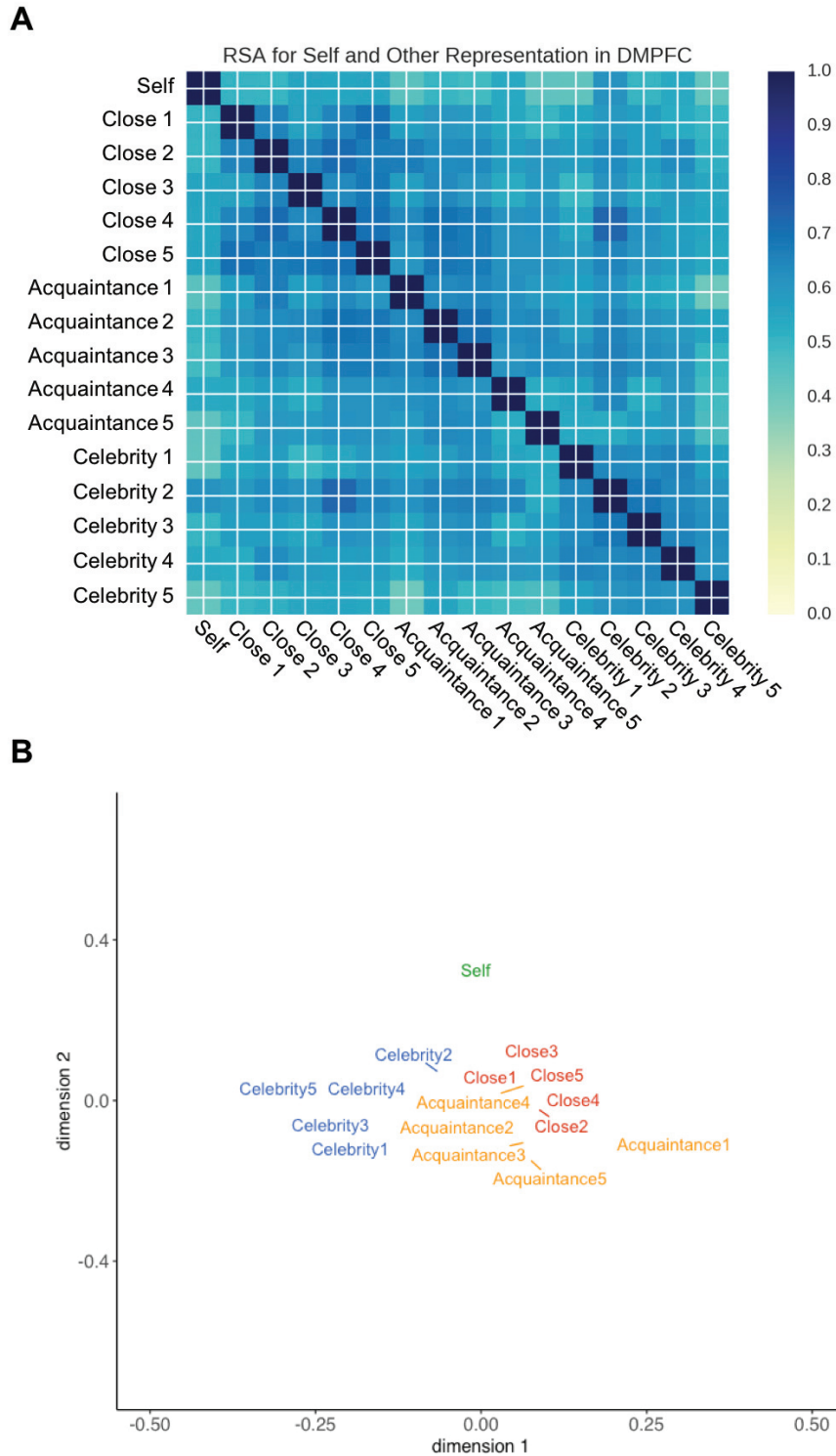
Figure 8. Representational similarity of self and others in DMPFC/"social" ROI reflected in a correlation matrix (A) and multi-dimensional scaling plot depicting distances on two dimensions for visualization (B).

The similarity structure in the MPFC/"self" ROI was correlated with the similarity of closeness ratings (Figure 9) across targets, $r(42)= 0.26$, $t(42) = 9.48$, p< 0.001. It was similarly correlated with the similarity of familiarity ratings, $r(42)= 0.21$, t(42) = 7.65, p< 0.001, and similarity ratings, $r(42)= 0.29$, $t(42) = 9.22$, p< 0.001. The similarity structure in the DMPFC/"social" ROI was also correlated with closeness, $r(42)= 0.13$, $t(42) = 6.07$, p< 0.001, familiarity, $r(42)= 0.11$, $t(42) = 4.93$, p< 0.001, and similarity, $r(42)= 0.14$, $t(42) = 5.64$, p< 0.001, though the relationships were weaker. Moreover, social closeness predicted the similarity of activation patterns for personally familiar targets and the self in the MPFC, $B= 0.0014$, 95% CI [0.0004, 0.002], $t = 2.75$, $p = 0.006$ (Satterthwaite approximated df= 408.8). Because celebrity closeness ratings were quite variable and uninterpretable they were left out of these analyses.
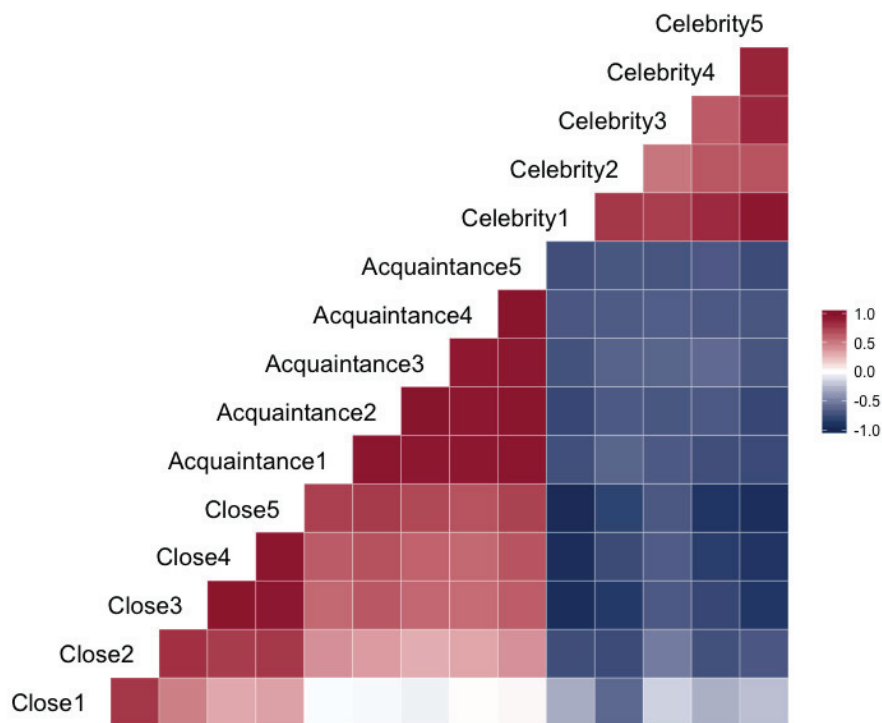
Figure 9. Correlation matrix of closeness ratings for each participant.

Model similarity structures

　　　To more empirically test this structure against theoretically-driven models, the similarity matrices (lower triangular only, excluding the diagonal) from the MPFC/"self" ROI and the DMPFC/"social" ROI were correlated with each model matrix. The similarity structure in both ROIs was significantly correlated with all models (Table 2).

Searchlight representational similarity analysis

　　　The searchlight RSA driven by closeness with familiar others, and allowing other pairwise relationships to vary, revealed regions in the left occipital cortex, middle cingulate cortex, right medial prefrontal cortex (MPFC), and left superior frontal gyrus whose activation patterns reflected social closeness to the self. (Table 3; Figure 10). The second searchlight RSA reflecting self and close other similarity revealed regions of the left occipital cortex, the MPFC/orbitofrontal cortex, the left inferior temporal/fusiform cortex whose activation patterns most highly correlated with the proposed model of self-close other similarity (Table 4; Figure 11). The third searchlight RSA reflecting similarity between the self and personally familiar others revealed regions of the precuneus, right inferior temporal/fusiform cortex, and cerebellum whose activation patterns most highly correlated with the proposed model of self-personally familiar other similarity (Table 5; Figure 12). The fourth searchlight RSA reflecting the combined 3 structure model and social closeness to the self revealed regions in the precuneus and cerebellum whose activation patterns most highly correlated with the model (Table 6; Figure 13).
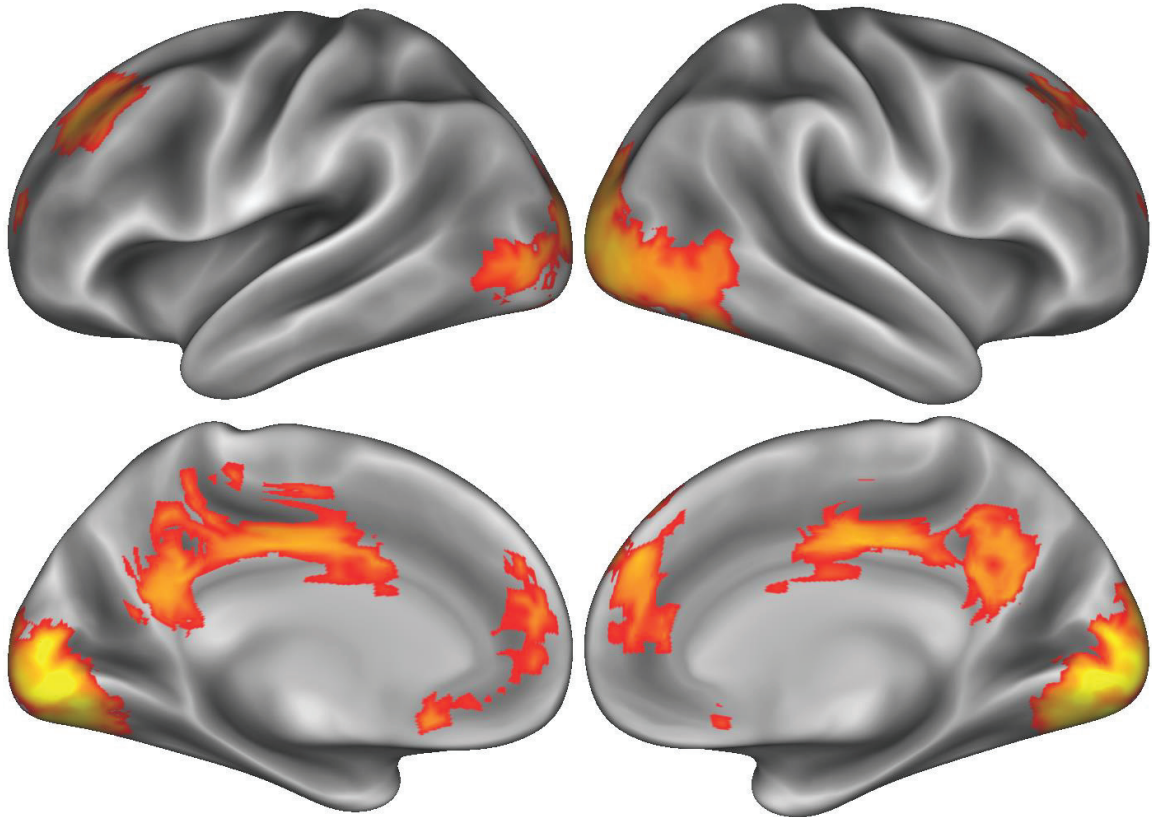
Figure 10. A whole-brain searchlight representational similarity analysis (RSA) revealed brain regions whose similarity structures positively correlated with the social closeness of all close others and acquaintances, allowing other relationships to vary (voxel-wise threshold p< 0.001, cluster-corrected p< 0.001).
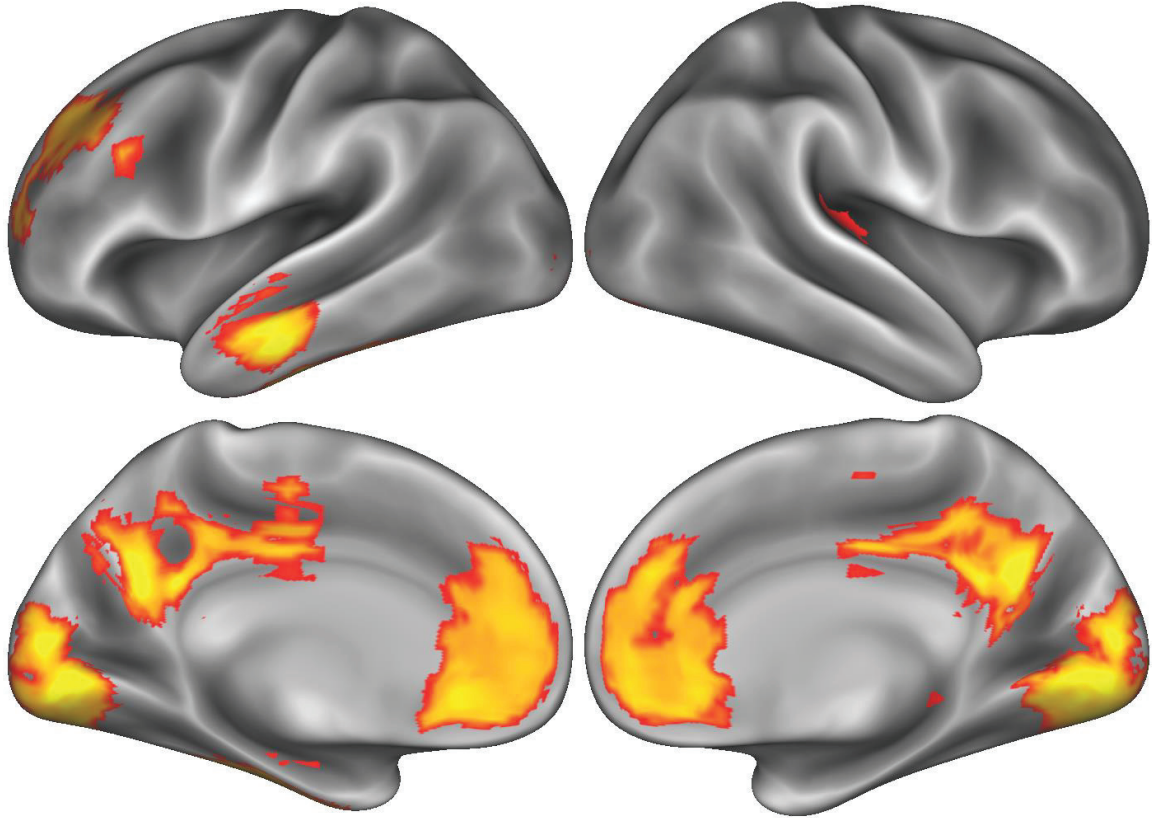
Figure 11. A whole-brain searchlight representational similarity analysis (RSA) revealed brain regions whose similarity structures reflected self-close other similarity and acquaintance-celebrity similarity (voxel-wise threshold p< 0.001, cluster-corrected p< 0.001).
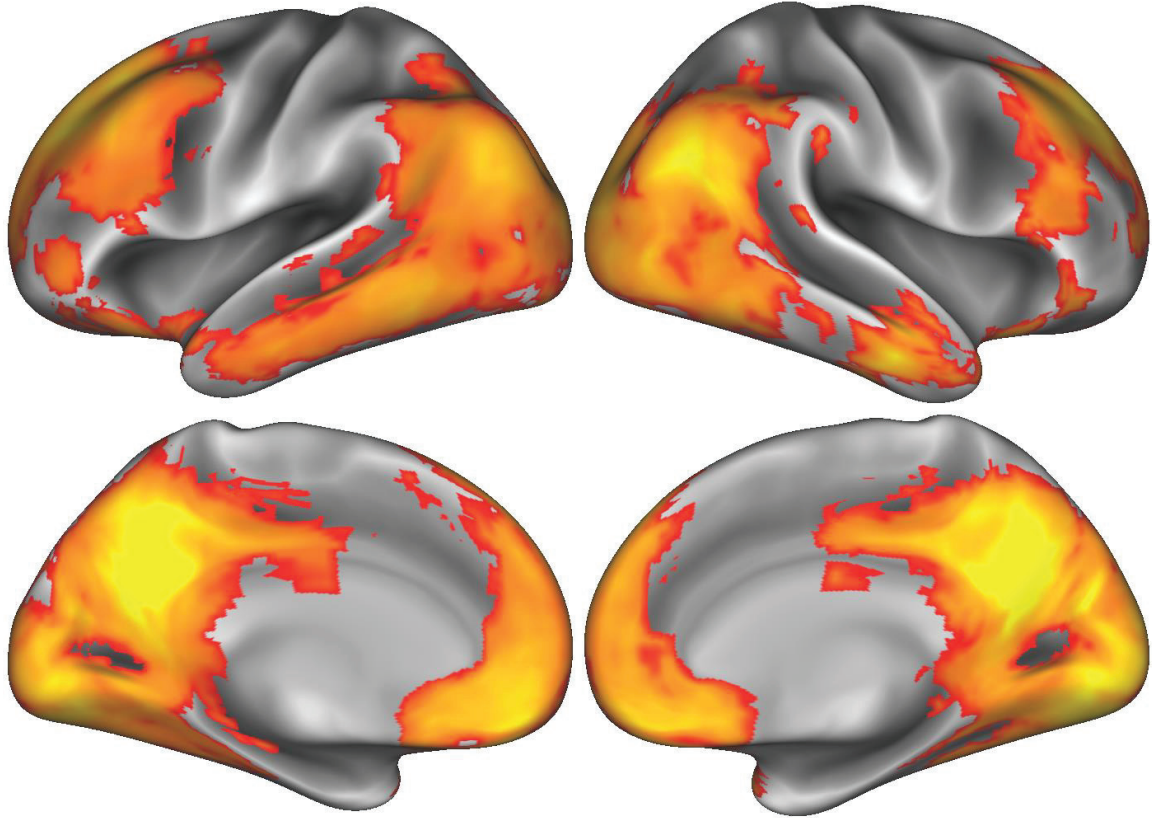
Figure 12. A whole-brain searchlight representational similarity analysis (RSA) revealed brain regions whose similarity structures reflected similarity between the self and personally familiar others (close others and acquaintances; voxel-wise threshold p< 0.001, cluster-corrected p< 0.001).
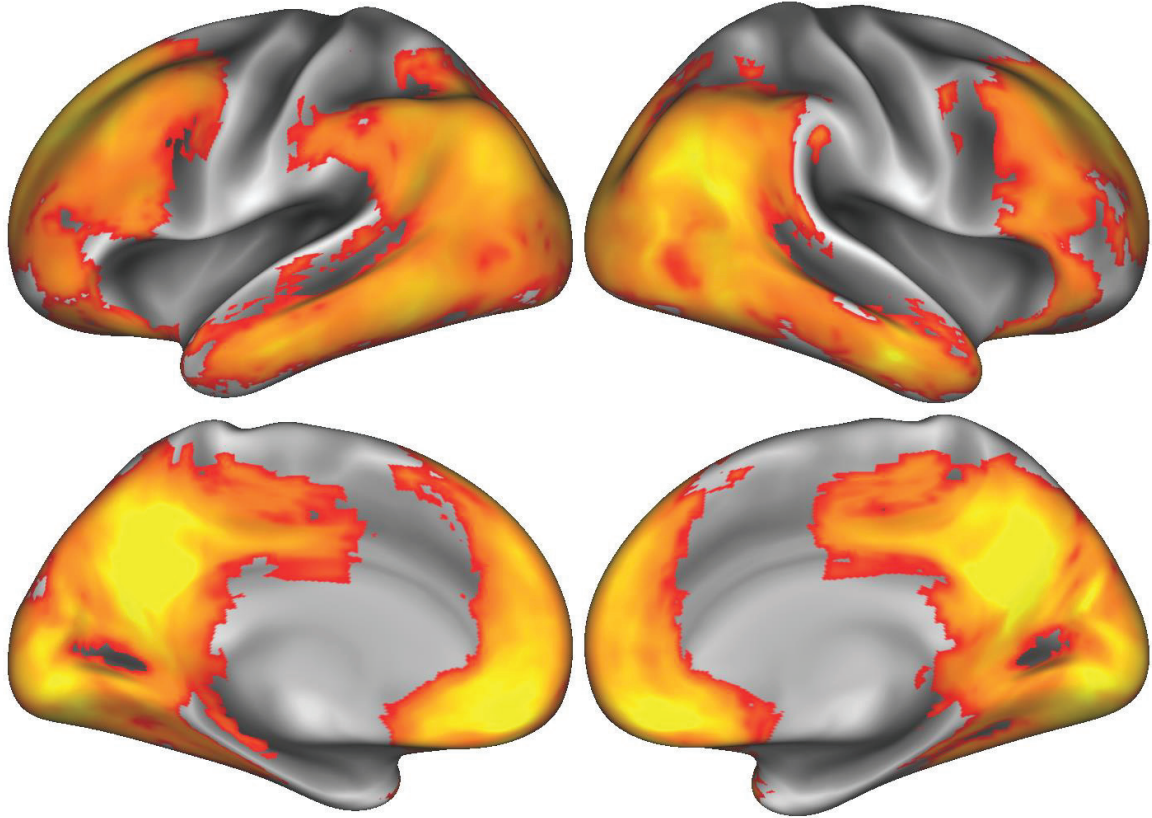
Figure 13. A whole-brain searchlight representational similarity analysis (RSA) revealed brain regions whose similarity structures reflected the "combined 3 cluster-social closeness" model in which self, familiar others, and celebrities were distinct clusters but familiar others were represented in a graded fashion based on social closeness to the self (voxel-wise threshold p< 0.001, cluster-corrected p< 0.001).

Relating behavioral and neural measures of social closeness to loneliness

  Social closeness and loneliness. Loneliness interacted with target condition to predict social closeness ratings. With increasing trait loneliness, both close others, *B*= -0.18, 95% CI [-0.26, -0.11], *t* = -4.69, *p* < 0.001 (Satterthwaite approximated df= 626), and acquaintances, *B*= -0.14, 95% CI [-0.21, -0.06], *t* = -3.55, *p* < 0.001 (Satterthwaite approximated df= 626), were rated as less close (Figure 14).
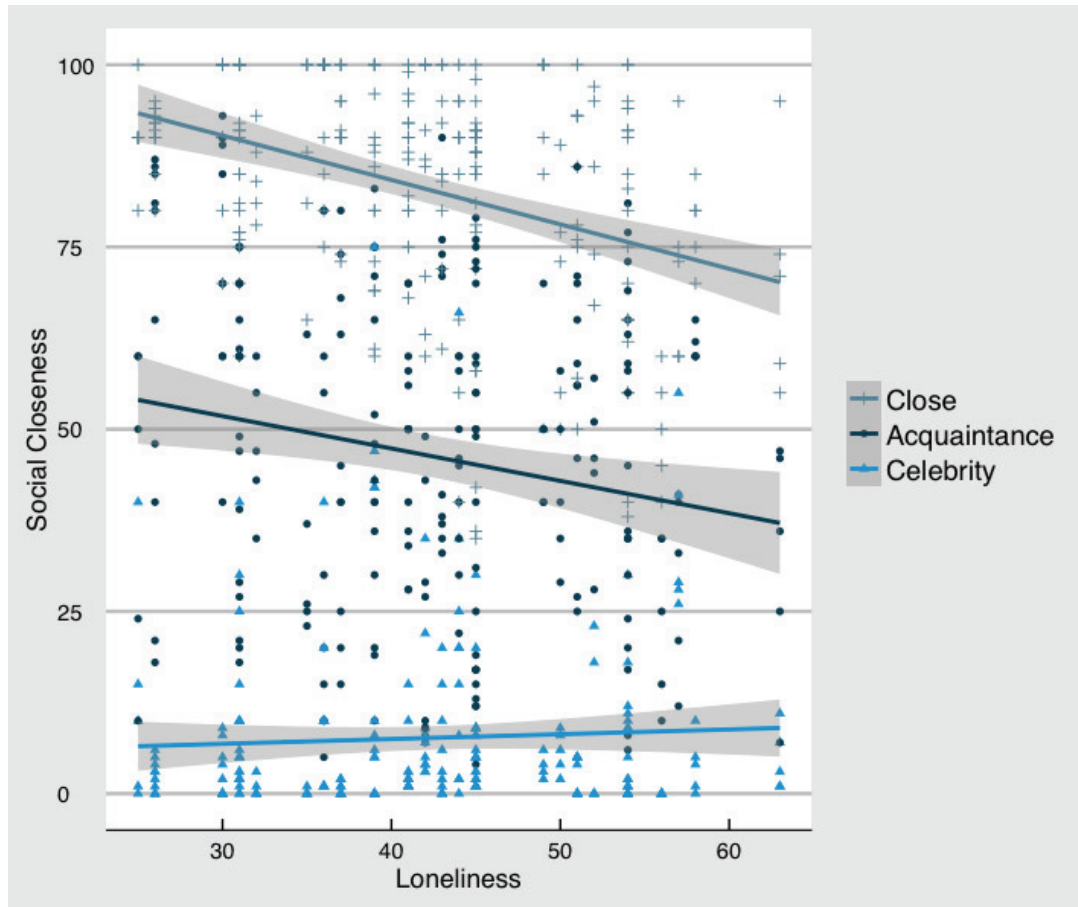
Figure 14. Self-reported social closeness to close others and acquaintances decreased with increasing loneliness, *B*= 0.0014, 95% CI [0.0004, 0.002], *t* = 2.75, *p* = 0.006 (Satterthwaite approximated df= 408.8).

Representational similarity and loneliness. Loneliness interacted with target condition to predict representational distance of others from the self in the MPFC/"self" ROI, *B*= 0.003, 95% CI [0.001, 0.006], *t* = 2.72, *p* = 0.007 (Satterthwaite approximated df= 367), and the DMPFC/"social" ROI, *B*= 0.005, 95% CI [0.001, 0.008], *t* = 2.62, *p* = 0.009 (Satterthwaite approximated df= 367). Specifically, loneliness was associated with marginally decreased similarity between the self and acquaintances, *r*(39) = -0.24, *p* = 0.13, in the MPFC/"self" ROI, but not between the self and close others, *r*(39) = 0.006, *p* = 0.97 (Figure 15). Conversely, it was associated with increased similarity between the

self and close others in the DMPFC/"social" ROI, $r(39) = 0.37$, $p = 0.02$, but not between

the self and acquaintances, $r(39) = 0.08$, $p = 0.63$ (Figure 16).
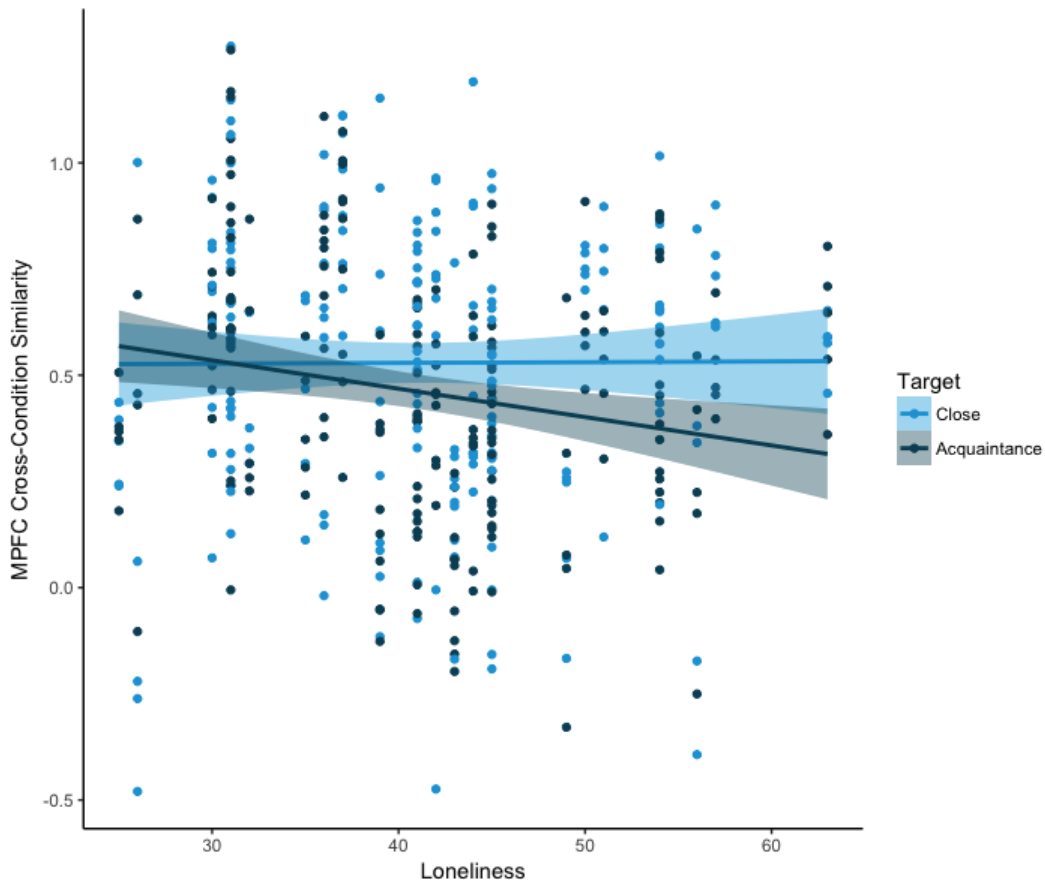
Figure 15. Cross-condition similarity (self and other) in the MPFC/"self" ROI marginally decreased with loneliness for acquaintances, $r(39) = -0.24$, $p = 0.13$, but not close others, $r(39) = 0.006$, $p = 0.97$.
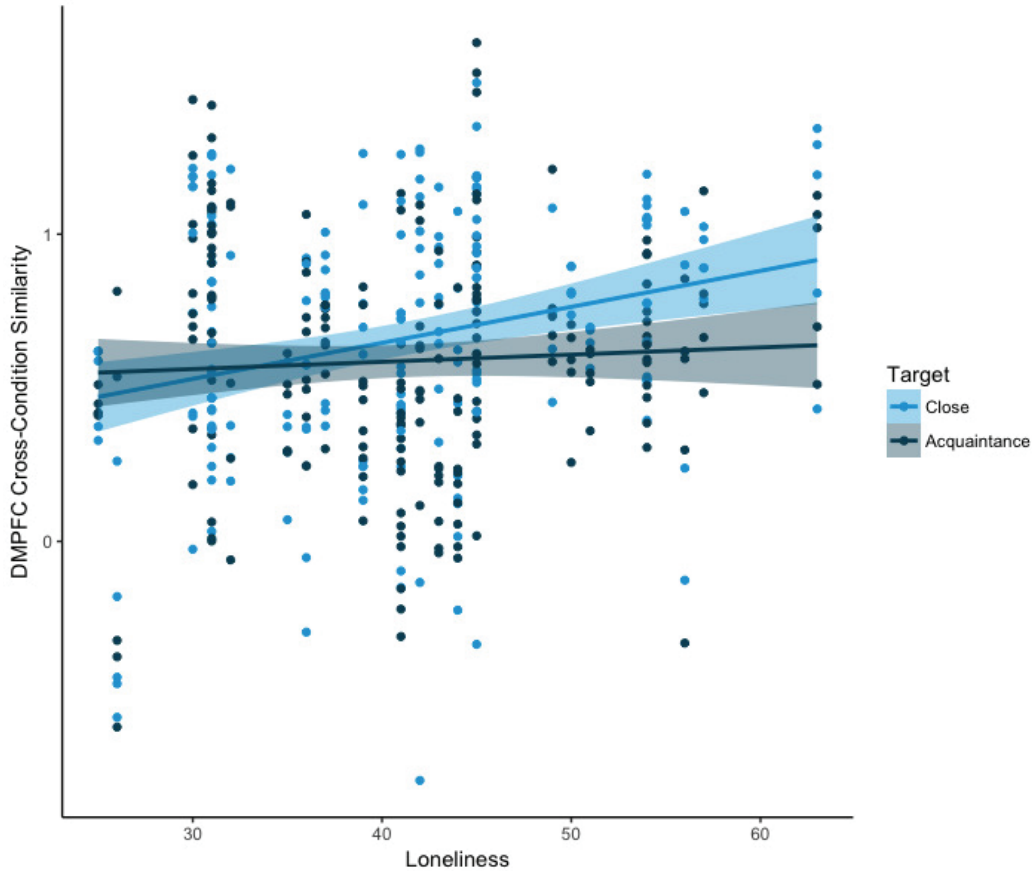
Figure 16. Cross-condition similarity (self and other) in the DMPFC/"social" ROI increased with loneliness for close others, $r(39) = 0.37$, $p = 0.02$, but not acquaintances, $r(39) = 0.08$, $p = 0.63$.

Whole-brain regression of loneliness on searchlight representational similarity. A whole-brain regression of loneliness on the statistical t-map resulting from the second searchlight RSA revealed regions whose similarity to the target self-close other similarity model increased with loneliness, including the MPFC/dorsal anterior cingulate cortex (dACC) and posterior cingulate cortex (PCC; Table 7; Figure 17). The similarity matrices from the *a priori* ROIs (MPFC/"self" and DMPFC/"social") along with these two clusters were extracted and visualized along with their MDS solutions for high and low lonely participants, as defined by a median split (MPFC/"self": Figure 18; DMPFC/"social": Figure 19; MPFC/dACC: Figure 20; PCC: Figure 21). Interestingly, at low levels of

loneliness all personally familiar others appeared to cluster in the MPFC and were more dissimilar to the self, whereas for high loneliness the clusters appeared less distinct. Conversely, in the DMPFC, at high levels of loneliness the personally familiar cluster appeared most distinct and differentiated from the self, and the self was much less differentiated from other targets at low levels of loneliness. In both the MPFC/"self" ROI and the MPFC/dACC peak the cluster of personally familiar others appeared to include even the closest targets at low levels of loneliness, but at high loneliness two targets appeared to cluster separately from the other personally familiar others. In the PCC, self was represented more similarly to personally familiar others at high levels of loneliness.
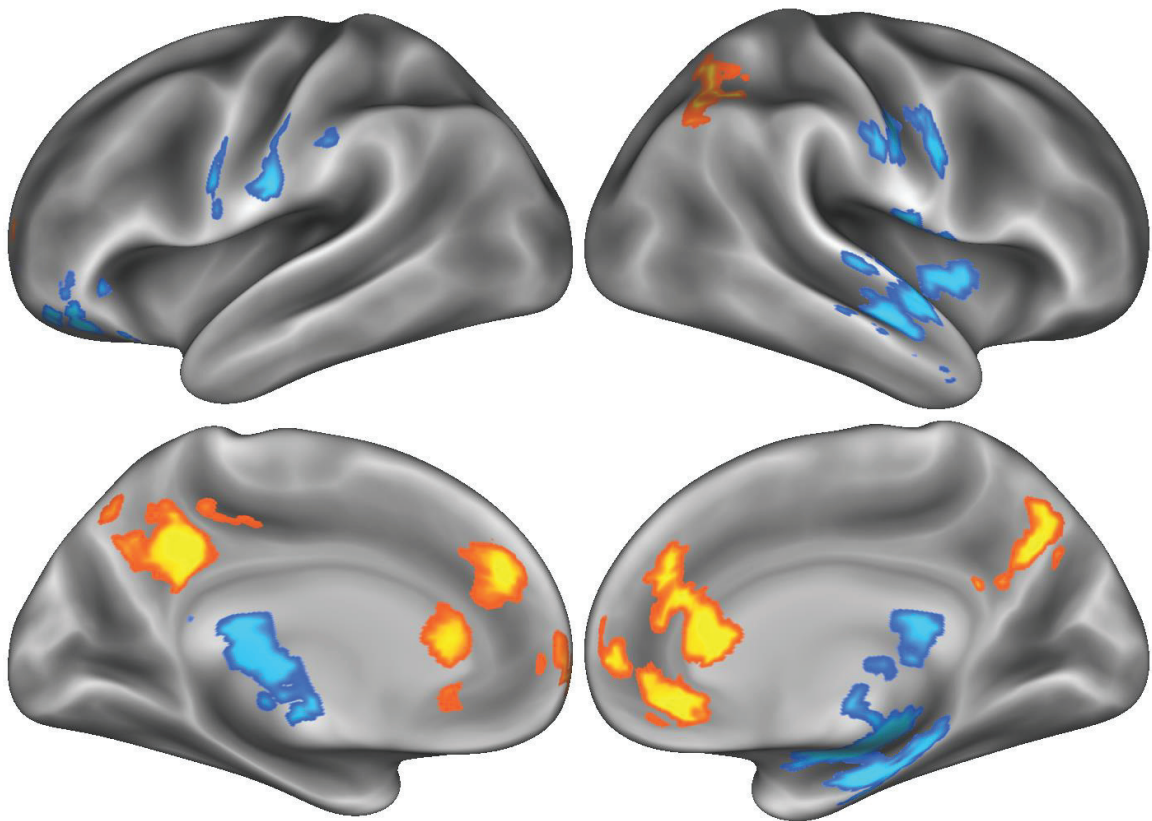
Figure 17. A whole-brain regression revealed regions where loneliness modulated the similarity between cross-condition similarity in activation patterns and the target matrix reflecting self-close other similarity (voxel-wise threshold p< 0.05, cluster-corrected to 200 voxels).
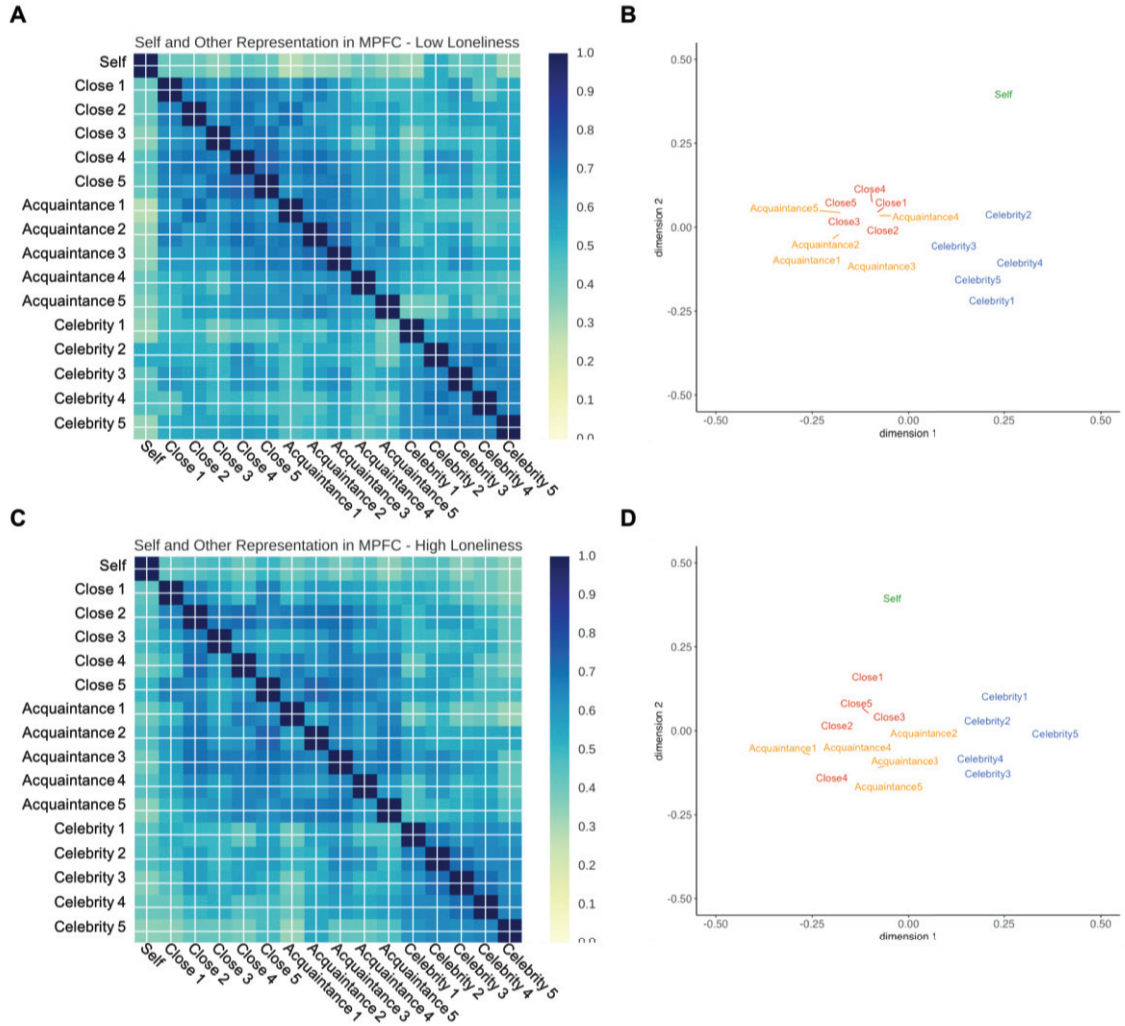
Figure 18. Representational similarity matrices in MPFC/"self" ROI visualized by median split in loneliness. A) Cross-condition similarity matrix in MPFC for low lonely participants, B) MDS solution for similarity in MPFC for low lonely participants, C) Cross-condition similarity matrix in MPFC for high lonely participants, B) MDS solution for similarity in MPFC for high lonely participants.
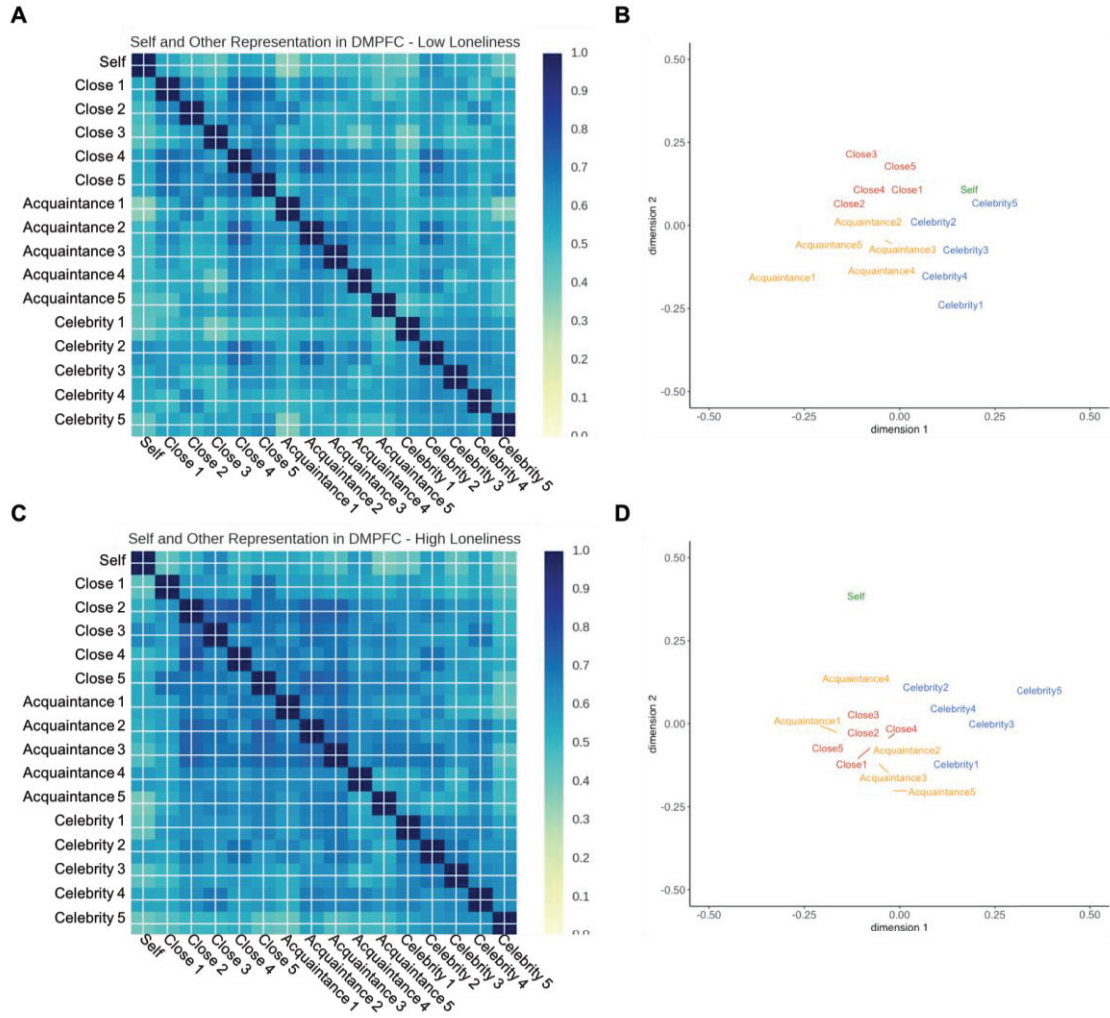
Figure 19. Representational similarity matrices in DMPFC/"social" ROI visualized by median split in loneliness. A) Cross-condition similarity matrix in DMPFC for low lonely participants, B) MDS solution for similarity in DMPFC for low lonely participants, C) Cross-condition similarity matrix in DMPFC for high lonely participants, B) MDS solution for similarity in DMPFC for high lonely participants.
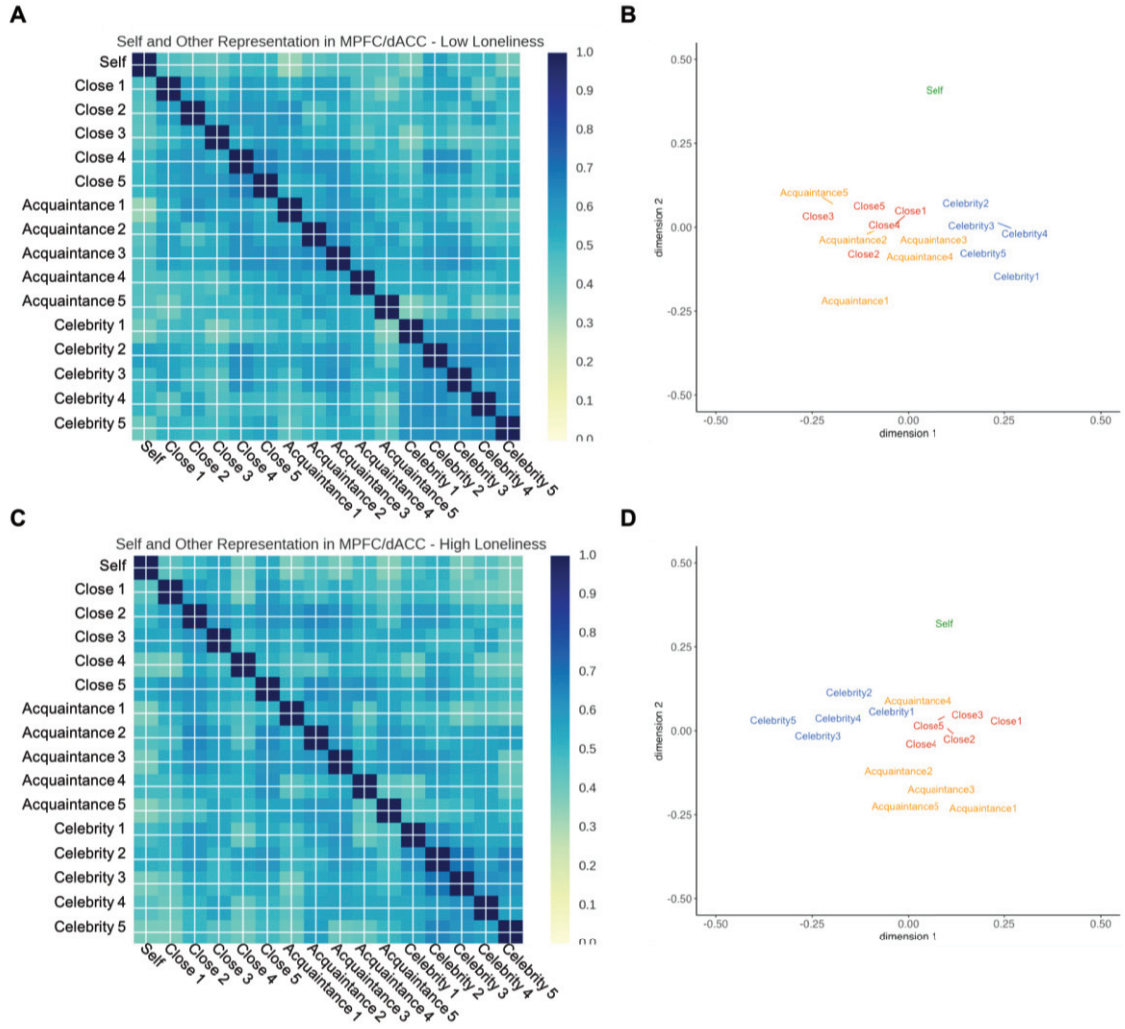
Figure 20. Representational similarity matrices in peak region of the MPFC/dACC from whole-brain regression of loneliness on searchlight RSA similarity map (for self-close other similarity) visualized by median split in loneliness. A) Cross-condition similarity matrix in VMPFC/dACCS for low lonely participants, B) MDS solution for similarity in MPFC/dACC for low lonely participants, C) Cross-condition similarity matrix in MPFC/dACC for high lonely participants, B) MDS solution for similarity in MPFC/dACC for high lonely participants.
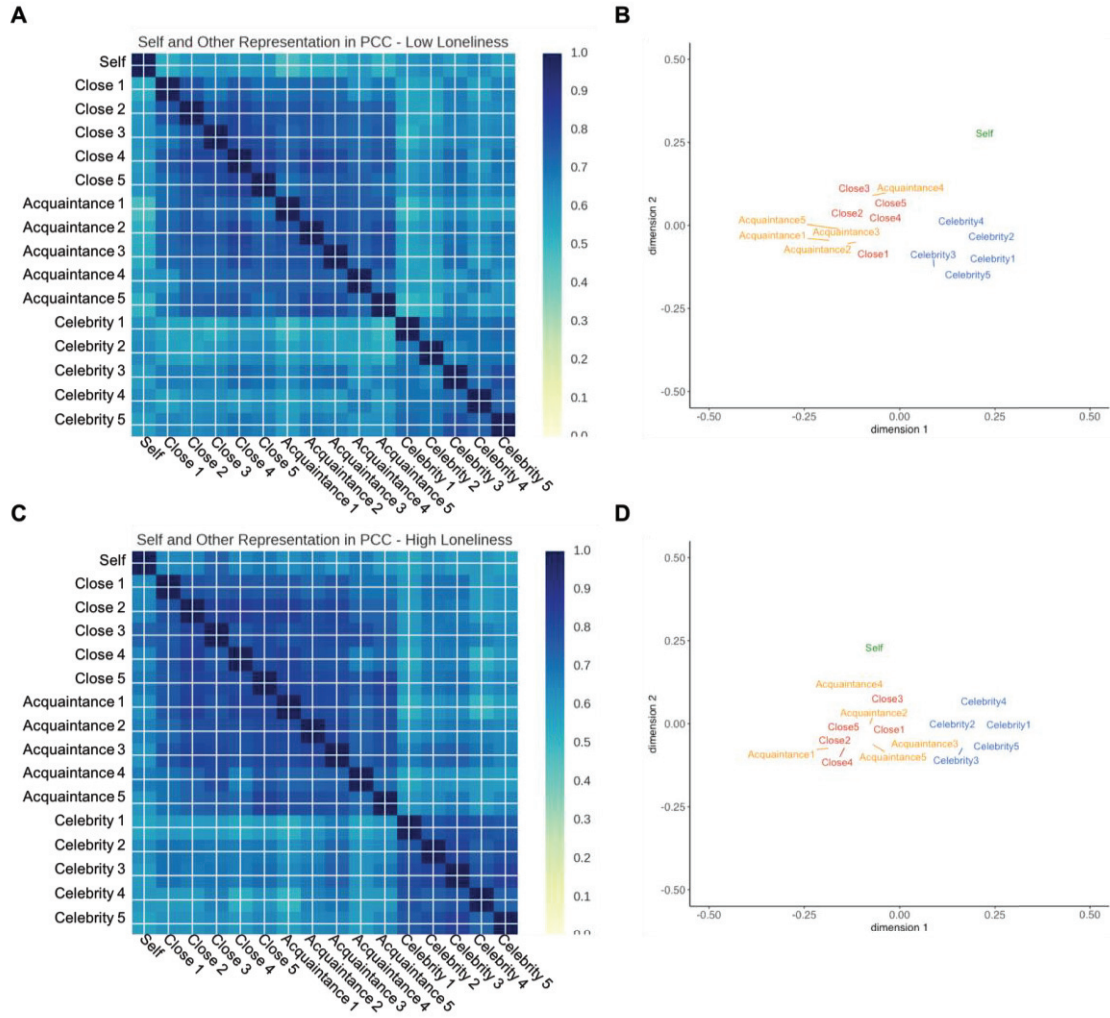
Figure 21. Representational similarity matrices in peak region of the posterior cingulate cortex (PCC) from whole-brain regression of loneliness on searchlight RSA similarity map (for self-close other similarity) visualized by median split in loneliness. A) Cross-condition similarity matrix in PCC for low lonely participants, B) MDS solution for similarity in PCC for low lonely participants, C) Cross-condition similarity matrix in PCC for high lonely participants, B) MDS solution for similarity in PCC for high lonely participants.

Discussion

In this study, social closeness modulated both univariate and multivariate brain responses when thinking about (making trait judgments for) other people, and this occurred in a region of the MPFC classically associated with self-referential processing.

This study provides partial evidence that close others may impinge on self-representation—close others are represented more similarly to the self than distant others in social brain areas. However, the self continues to be distinct and favored in the MPFC.

Another interesting feature of self-other representation in the MPFC is the super-categorization of personally familiar others, where close others and acquaintances were represented similarly. This could be due in part to the constraints of the design: close others and acquaintances were nominated by participants, whereas celebrities were pre-selected. As a consequence, all familiar others could be more similar and even selected from the same social network (e.g., college students at the same university). However, they may in fact be a special category of social targets. In fact, previous research dedicated to identifying brain systems responsible for identifying personally familiar and close others has suggested that familiar others are favored in the social brain. As a result, familiar faces are recognized more easily and in the absence of awareness (Gobbini et al., 2013; Ramon & Gobbini, 2017). This is in part due to the fact that brain systems supporting perception receive inputs from emotion and personal knowledge systems, which convey the saliency of these cues and help to prioritize their detection (Gobbini & Haxby, 2007).

Existing social connections shape both low-level perceptual processes (Powers et al., 2014) and long-term health trajectories (Eisenberger, 2013). Social intimacy is a basic human need and its absence is associated with negative mental and physical health outcomes (Hawkley, Thisted, Masi, & Cacioppo, 2010; Holt-Lunstad, 2017). Replicating previous research, loneliness in this study was associated with weaker feelings of social connection to nominated relationship partners (Inagaki et al., 2016). Loneliness was

associated with feeling less intimacy, even toward close others who were nominated for being the closest and most intimate with the participant, and with shifting the similarity of self to others in the MPFC and PCC—regions associated with both self-related processing and familiarity (Qin & Northoff, 2011). The direction of this relationship is unclear—changes in perceived loneliness may exist as a cause or a symptom of loneliness. If loneliness is a disorder of perception, lonely people may fail to perceive intimacy when it exists, or they may be less likely to form close relationships. Alternatively, a lack of intimacy at the relationship-level may accumulate and accurately contribute to feelings of loneliness. Study 3 will begin to tease it apart the directionality of this relationship by implementing an experimental manipulation of social connection. Interestingly, in the present study, loneliness was related to less perceived social closeness with close others but less representational similarity with acquaintances. These two metrics may tap into slightly different aspects of the condition.

Overall, the current study demonstrated that social closeness modulates the engagement of the MPFC and the representational similarity of self and others in the MPFC. We began to find support for both the notion of the "self as special" and the "inclusion of other in the self", whereby self remains distinct in its representation but social closeness drives increasingly similar representation to the self. Another way to indirectly assess the level of self-other overlap is to determine whether activating the representation of a close other facilitates access to the self, which is the aim of Study 2.

Study 2a: Social Closeness Biases Self-Perception

The perception of social cues can be biased by motivation. That is, context, experience, and desires can alter the perception and interpretation of these cues (Balcetis & Dunning, 2006). In one study, participants who were assigned to an unrelated approach task—pulling a joystick toward themselves—showed an attenuated neural bias (of the P100 response) in response to other-race faces, demonstrating an influence of the approach motivation (Cunningham, Van Bavel, Arbuckle, Packer, & Waggoner, 2012). These biases can result from natural motivations, as well. Because people are motivated to find themselves attractive, one study found that participants were more likely to recognize a modified, more attractive version of their face as the real one; and this advantage was also conferred on their friend (Epley & Whitchurch, 2008).

One way that this plays out in the real world is that individuals with stronger social proclivities demonstrate a stronger advantage for social processing. Indeed, individuals with a higher need to belong show an enhanced sensitivity to social cues, including sensitized detection of vocal and emotional cues (Pickett, Gardner, & Knowles, 2004) and improved memory for social events (Gardner, Pickett, & Brewer, 2000). Another previous study illustrated that social disconnectedness, at both the trait and state levels, biased the detection of animacy in a face morph continuum extending from human to doll faces (Powers et al., 2014).

Similarly, personal relationships might motivate the perception of specific targets. Here we extended this work to determine if social closeness motivates self-perception. If relationship partners share mental representations with the self (Andersen & Chen, 2002; Aron et al., 1991), then we might expect to see biased self-perception in the presence of

close others. In other words, the presence of close others might facilitate access to the self and bias self-perception. The current studies employed a self-face recognition paradigm with images from a morph continuum extending from 100% self to 100% other, in which the target others varied in social closeness to the self.

Method

Participants

Nine current and former graduate students at Dartmouth College (4 female) between the ages of 26 and 35 (M= 29, SD= 2.6) were recruited for Study 2a and 2b. All participants were screened for compliance with MRI safety, reported normal neurological history, and had normal or corrected-to-normal visual acuity. Each participant provided informed consent in accordance with the guidelines set by the Committee for the Protection of Human Subjects at Dartmouth College and received monetary compensation for participating in the study. Participants were selected based on prior participation in the creation of an existing stimulus set (Dartmouth 100), and a subset of these images were used to create subject-specific stimuli for the current set of studies.

Stimuli

The stimuli for the current studies were morphed face stimuli created from photographs of the participant's own face morphed with photographs of other familiar faces (Figure 22; Turk et al., 2002). Stimuli for the current studies were selected from an existing emotional face stimulus set (Dartmouth 100). One photograph of each participant making a calm expression was used to create face morphs between the participant's face

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and a familiar target from the same stimulus set. These photographs were first converted to grayscale and luminance-matched using the SHINE toolbox (Willenbockel et al., 2010). They were then morphed with each of 7 target faces using Norrkross MorphX morphing software (http://www.norrkross.com/software/morphx/morphx.php). A series of images ranging from 0% of the participant's face (100% of the target's face) to 100% of the participant's face (0% of the target's face) in 10% increments were created for a total of 11 images for each of 7 participant-target pairs. The final images were cropped and sized to 2700 x 2700 resolution and were centered and subtended 9° x 9° visual angle at 60cm distance from the screen during the task.

100% other   100% self

Figure 22. Example face morph continuum ranging from 0% of the participant's face (100% of the target's face) to 100% of the participant's face (0% of the target's face) in 10% increments.

Apparatus

The task was conducted on an 11-inch Apple MacBook Air laptop computer running PsychoPy v1.85 software (Peirce, 2008).

Procedure

Participants completed a self-face recognition task where they viewed the morphed face stimuli and categorized the identity (e.g., "me"/"not me") by making binary "me"/"not me" perceptual judgments for a series of morphed images. Following 8 practice trials, participants began 10 blocks of the task. The task was self-timed and

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participants made responses by pressing a "p" or "q" key on the keyboard, according to the location of a response cue, which was counterbalanced across participants. Each trial was followed by a fixation cross which was advanced with a spacebar. Each of 10 blocks consisted of judgments for the 10 morph levels containing some percentage of the target's face for each of 7 targets and one trial of 100% of the participant's face, for 71 trials per block and a total of 710 trials for the entire task. Following this task, participants made closeness, familiarity, and similarity ratings for each of the targets on a 0-100 scale (0= "not at all", 100= "very much").

Data analysis

The face morph categorization judgments were analyzed by fitting the binomial data ("me"/"not me" responses) with a generalized linear model using the *quickpsy* package (Linares & López-Moliner, 2016) in R (R Core Team, 2017). For each participant-target pair, a psychometric curve was fitted using a probit model with a cumulative normal distribution function. By including subject and target as random grouping factors, model parameters (including the threshold and slope) were estimated on the subject and target-level. From the individual psychometric functions, threshold and slope parameters were extracted from each of 63 models from every participant-target combination (Figure 23), allowing for a separate regression of these model parameters with the closeness ratings provided by the participant for each of the targets.

Linear mixed-effects models using the *lme4* package (Bates et al., 2015) in R were used to relate model parameters and closeness ratings while controlling for subject-level differences in the intercept. A random intercept for subject was entered into the

model to account for variability in model parameters attributable to person-level response patterns, or individual differences in the tendency to perceive the self in a morph sequence.
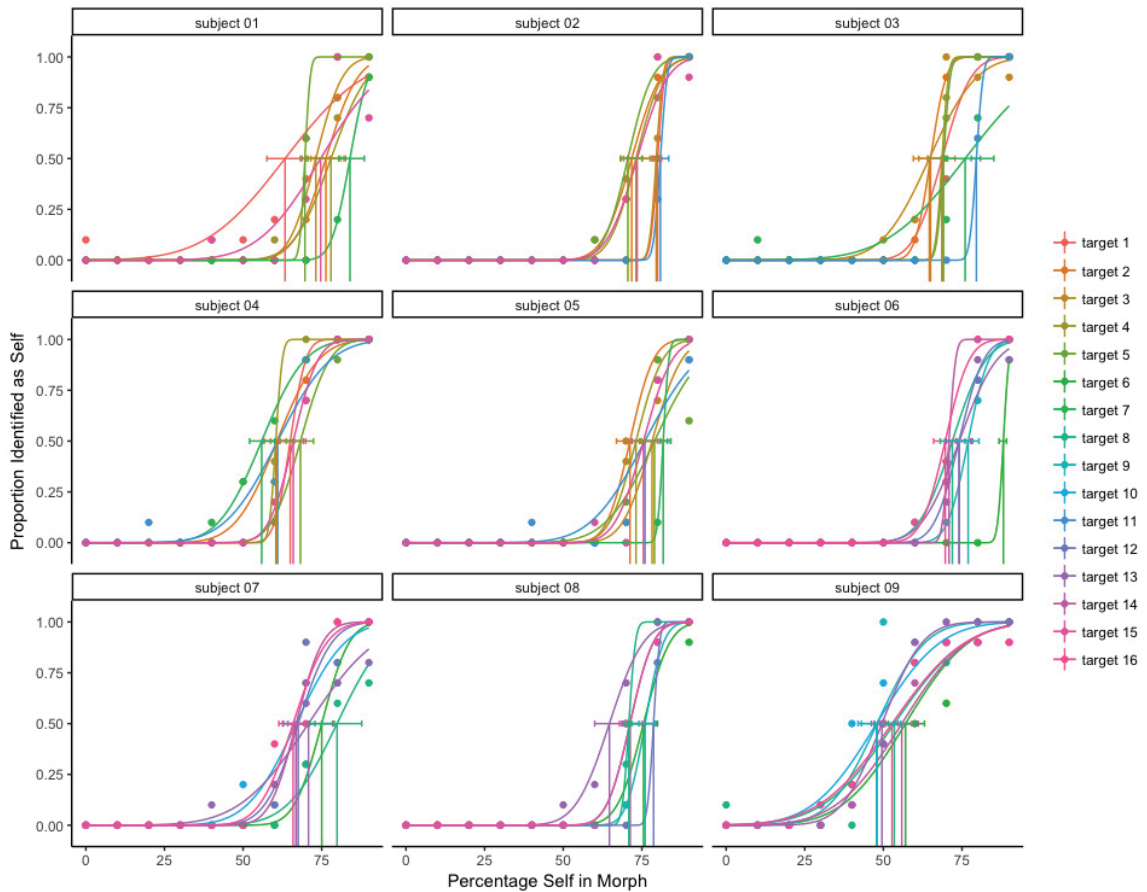
Figure 23. Estimated psychometric curves for each subject-target pair reflecting the proportion of morph stimuli identified as the self for each point along the morph continuum.

Closeness Ratings

Closeness ratings (M = 54.19, SD = 27.87) were highly correlated across subjects with familiarity, $r(8) = 0.77$, $t(8) = 6.10$, p< 0.001, and similarity, $r(8) = 0.82$, $t(8) = 6.00$, p< 0.001.

Face Categorization

The 50% threshold, or the point at which the participant began to consistently respond that the morph was primarily the self, was significantly removed from the midpoint (M = 69.90, SD = 8.85), $t(62)= 25.1$, $p < 0.001$. That is, participants reached threshold significantly closer to the self end of the spectrum, reflecting a somewhat conservative willingness to categorize a face as belonging to the self (Figure 24, Figure 25). Next, the model parameters were compared across targets to determine if social closeness influenced the threshold and slope of the curve. For visualization, the curve is plotted for the three closest targets and the least close targets (of seven total), demonstrating a shift in the curve based on social closeness (Figure 26; though statistics were conducted with the full continuous measure of social closeness).
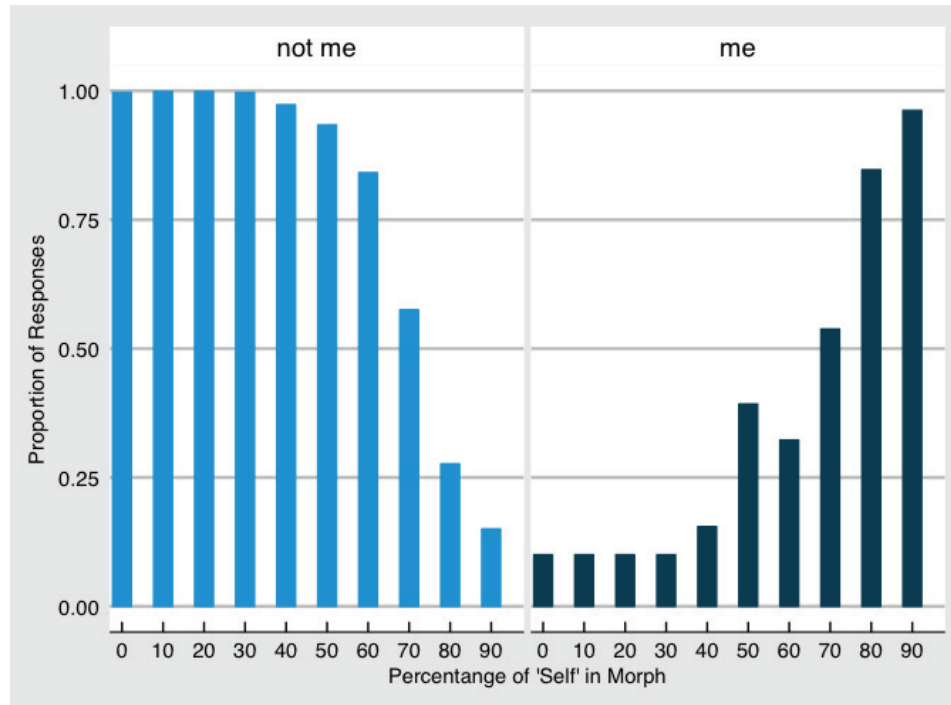
Figure 24. Proportion of "not me" and "me" responses to face morphs at each percentage of the morph continuum.
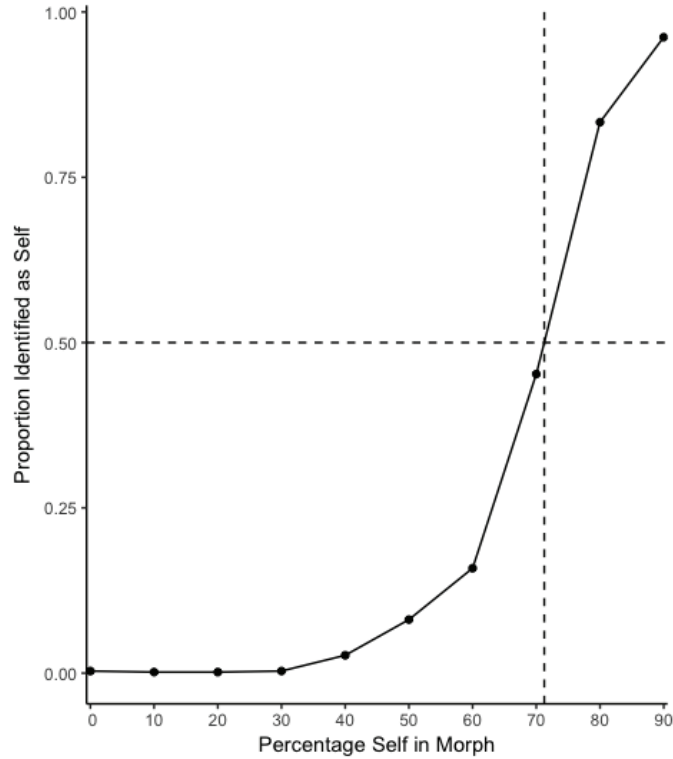
Figure 25. Psychometric curve reflecting the proportion of morph stimuli identified as the self for each point along the morph continuum.

Using a linear mixed-effects model with a random intercept for subject, participant closeness negatively predicted the 50% threshold, B= -0.08, 95% CI [-0.13, -0.04], t= -3.55, p< 0.001 (Satterthwaite approximated df= 54.69; Figure 27). That is, the threshold was lower for close others than for more distant targets. In fact, these two measures were moderately negatively correlated, r(61) = -0.34, p = 0.006, suggesting that threshold for self-identification is lower when one's face is morphed with a close other than a more distant other, and may support the notion that the self-concept is activated by close others. In a similar linear mixed-effects model with a random intercept for subject, participant closeness positively predicted the slope of the psychometric curve, B= 0.06, 95% CI [0.02, 0.10], t= 2.97, p = 0.004 (Satterthwaite approximated df= 59.65; Figure 28). The closer the target was to the participant the steeper the rise of the curve,

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indicating a more rapid shift toward self-detection, or a shift from more "not me" to more "me" judgments as the morphs approached the self end of the continuum. Closeness and the slope of the psychometric curve were moderately positively correlated, $r(61)= 0.38$, $p = 0.002$.
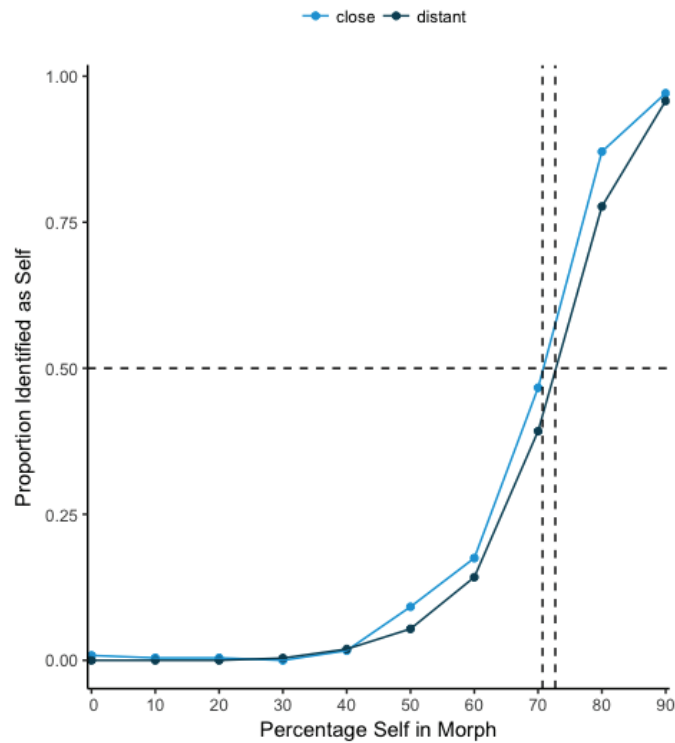
Figure 26. The psychometric functions plotted for the three closest targets (close) and three least close targets (distant) for visualization. Statistics were conducted on the full continuous measure of social closeness.
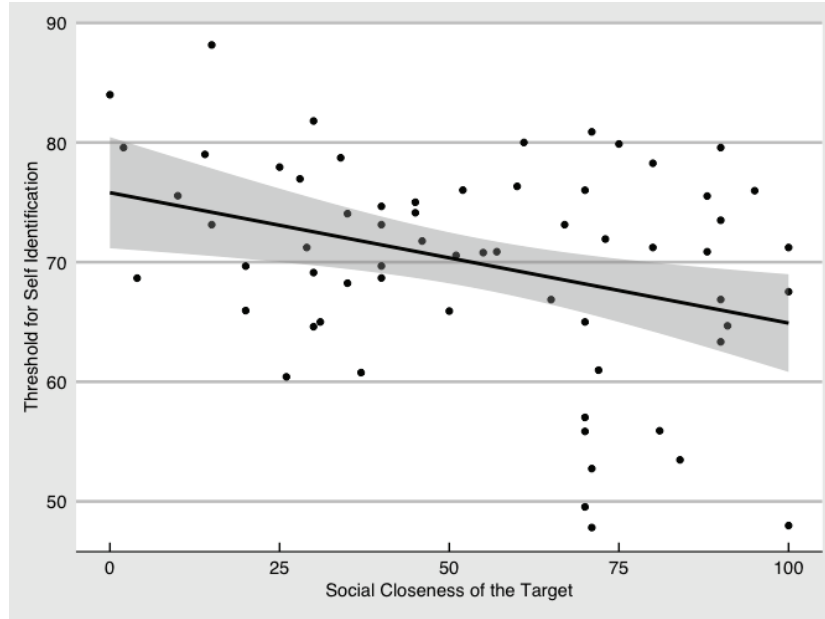
Figure 27. Threshold parameter plotted as a function of the social closeness of the target. Threshold for identifying self decreased as the closeness of the target increased, r(61) = -0.34, p = 0.006.
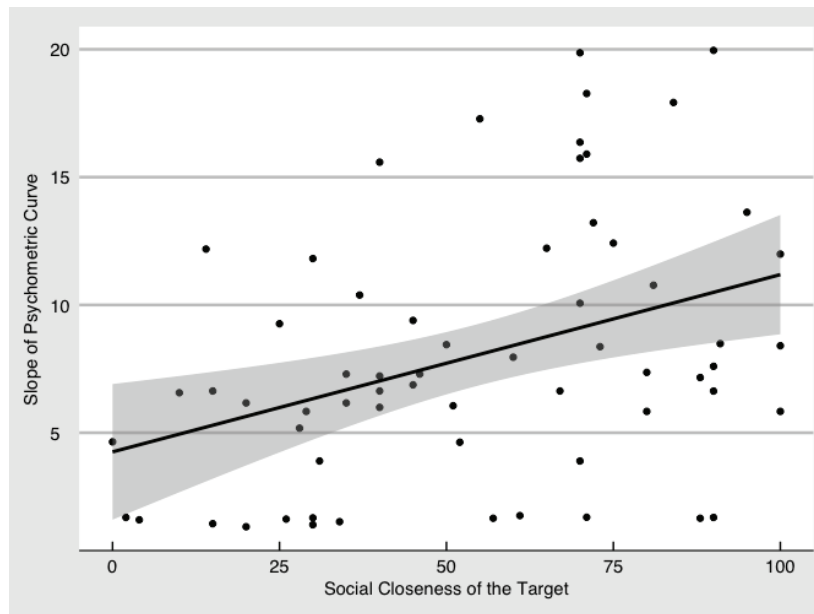
Figure 28. The slope of the psychometric curve plotted as a function of the social closeness of the target. The slope increases as the closeness of the target increased, r(61)= 0.38, p = 0.002.

Discussion

The results from Study 2a suggest that recognition of the self is relatively conserved in perception, with consistent self-recognition occurring significantly closer to the self end of the continuum. Furthermore, these results provide partial support for self-other overlap. The sigmoidal shape of the function suggests that self and other are distinct categories that are readily perceived by participants. Still, the presence of close others biases the detection of the self, suggesting the concepts may be more strongly associated cognitive constructs.

Study 2b: Social Closeness Modulates the Classification of Self and Other from Face

Morphs

Consistent with the notion of overlapping mental representations for self and close others, frequent confusions occur when making judgments between the two (Aron et al., 1992). As an example, participants are slower to judge personality traits that differ between themselves and their spouse than when judging traits that they share, suggesting that partial activation of the self knowledge structure interferes with accurate incongruent judgments about a close other (Aron et al., 1991). If this conceptual overlap exists, we might expect to see confusions in the discrimination of these categories at the level of perception and neural representation. Specifically, the presence of close others may partially activate the concept of self and create category confusion.

Method

Participants

This study was conducted with the same participants from Study 2a.

Stimuli

The same face morph stimuli used in Study 2a were used in this study. For the scanner task, the images were centered and subtended 10° x 10° visual angle at 60cm distance from screen.

Task

Each morph image was presented for 1750 ms with 250 ms of fixation buffering the trials. Participants were instructed to view all of the face morph images and to complete an incidental task to ensure that they were alert and paying attention. For 10% of the trials the fixation cross in the center of the screen changed colors (from black to red), and the participant was instructed to press a button-box button when they detected the change. There were 10 functional runs with 71 trials each for a total of 710 trials.

FMRI image acquisition

An anatomical (T1) image was acquired using a high-resolution 3-D magnetization-prepared rapid gradient-echo (MPRAGE) sequence (TR=9.9ms; TE=4.6 ms; flip angle=8°; $1x1x1mm^3$ voxels). Functional images were collected using a T2*-weighted echo planar imaging (EPI) sequence (TR = 1000 ms, TE = 30ms, flip angle = 59°, bandwidth = 2742, echo spacing = 0.49, 2.5x2.5x2.5 mm resolution) with a simultaneous multi-slice (SMS) of 4 and GeneRalized Autocalibrating Partial Parallel Acquisition (GRAPPA) of 1. Ten functional runs of 228 axial images (52 slices, 130mm coverage) were acquired for each participant. Sequence optimization was obtained using optseq2 (Dale, 1999) and included 30% jittered trials of fixation for obtaining a baseline estimation of neural activity.

Multivariate Classification Analysis

Using PyMPVA, we conducted a multivariate classification analysis on the MPFC cluster identified in the parametric modulation analysis from Study 1 (MNI: -3,

33, -9) to discriminate between self and other conditions in the face morphs. This activation cluster was saved as a binarized ROI mask, and multivariate classification was conducted on this region for each target. Classification was also conducted in the *a priori* MPFC/"self" and DMPFC/"social" ROIs and in the left and right fusiform cortices, ROIs defined from Automated Anatomical Labeling (AAL) . The condition "self" was defined as any morph containing 60% or more of the participant and "other" was defined as any morph containing 60% or more of the target. The resulting classification values reflect the averaged cross-validated classification values across the 10 functional runs for each participant by target. These values were then submitted to a linear mixed-effects model where they were related to the social closeness of the target for each participant.

Results

Multivariate Classification Accuracy

To determine if self and others could be accurately discriminated from activation patterns in the MPFC while viewing face morphs, a linear mixed-effects model was run on the multivariate classification accuracies. Classification was tested in the peak region of the MPFC that showed linear modulation by social closeness in Study 1. Controlling for self-reported similarity and visual similarity between the self and the target with a random-intercept for subject, social closeness was negatively related to classification accuracy in this peak region of the MFPC, B= -0.002, 95% CI [-0.004, -0.0003], t = -2.28, p = 0.026 (Satterthwaite approximated df= 59), suggesting that when one's own face is morphed with a close other it is less discriminable in the MPFC (Figure 29). The same model in the MPFC/"self", B= 0.0005, 95% CI [-0.0009, 0.002], t = 0.63, p = 0.52

(Satterthwaite approximated df= 59), and DMPFC/ "social", B= 0.00008, 95% CI [-0.001, 0.002], t = 0.10, p = 0.92 (Satterthwaite approximated df= 33.9), ROIs revealed no such relationship. To test whether this effect was unique to the MPFC, the same model was tested in known face processing regions, the left and right fusiform cortices. Interestingly, classification accuracy of self and other in the left fusiform cortex was marginally related to social closeness, B= 0.002, 95% CI [-0.0002, 0.004], t = 1.72, p = 0.09 (Satterthwaite approximated df= 41.9), but positively so, suggesting that closeness might facilitate classification in this region (Figure 30). This was not true for the right fusiform cortex, B= 0.001, 95% CI [-0.0006, 0.003], t = 1.37, p = 0.18 (Satterthwaite approximated df= 58.4).
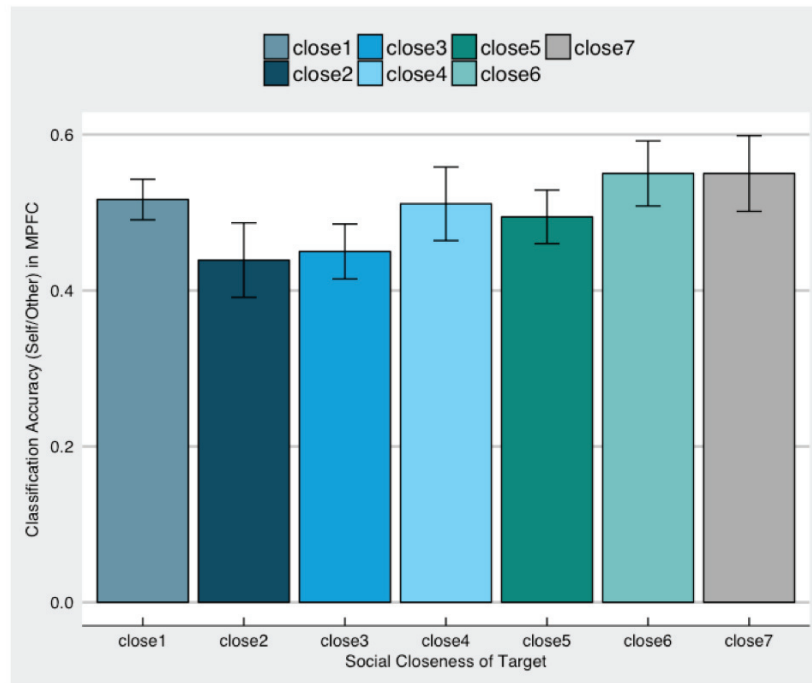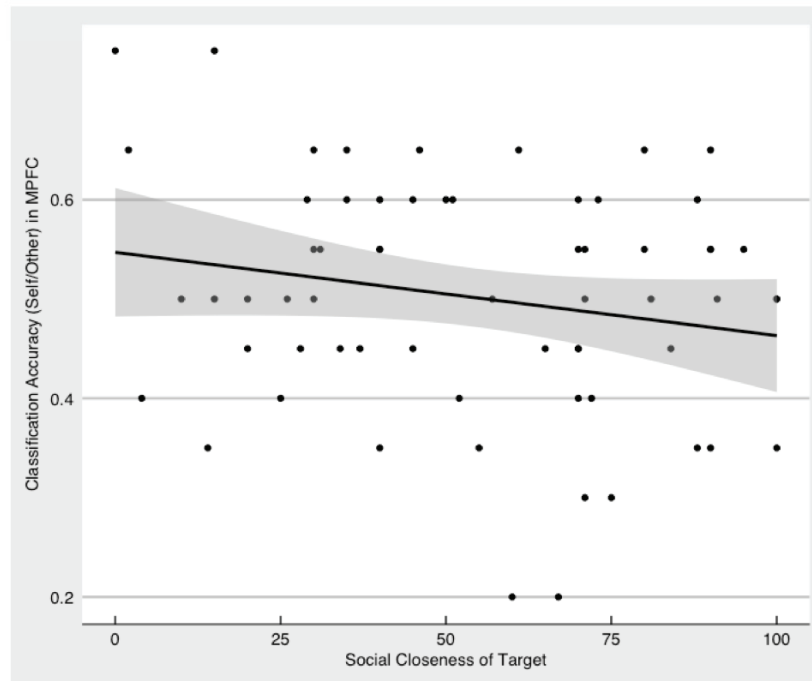
Figure 29. Classification accuracy of self/other face morphs in the MPFC (region selected for linearly increasing with social closeness in Study 1) by target (A) and by social closeness of the target to the self (B). Classification accuracy decreased with social closeness, *B*= -0.002, 95% CI [-0.004, -0.0003], *t* = -2.28, *p* = 0.026 (Satterthwaite approximated df= 59).
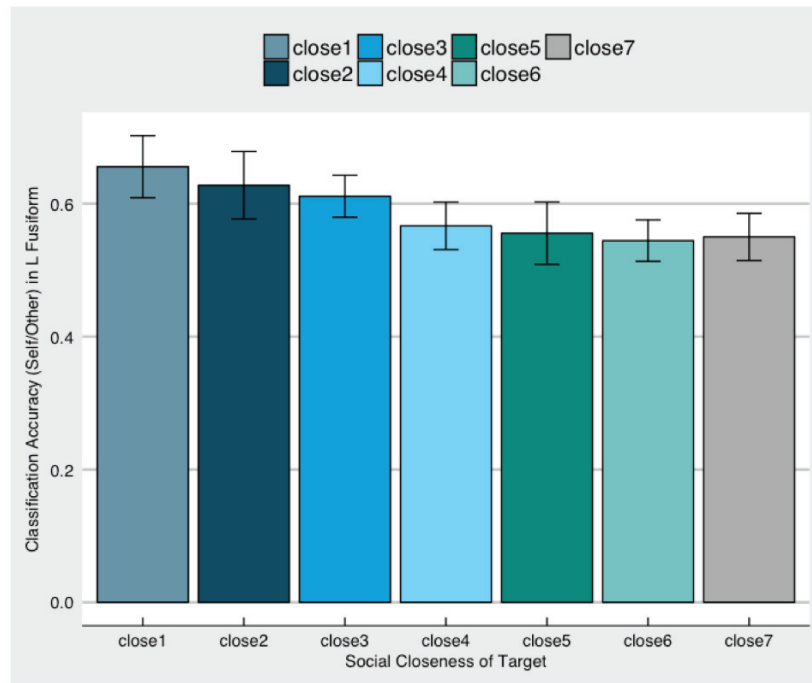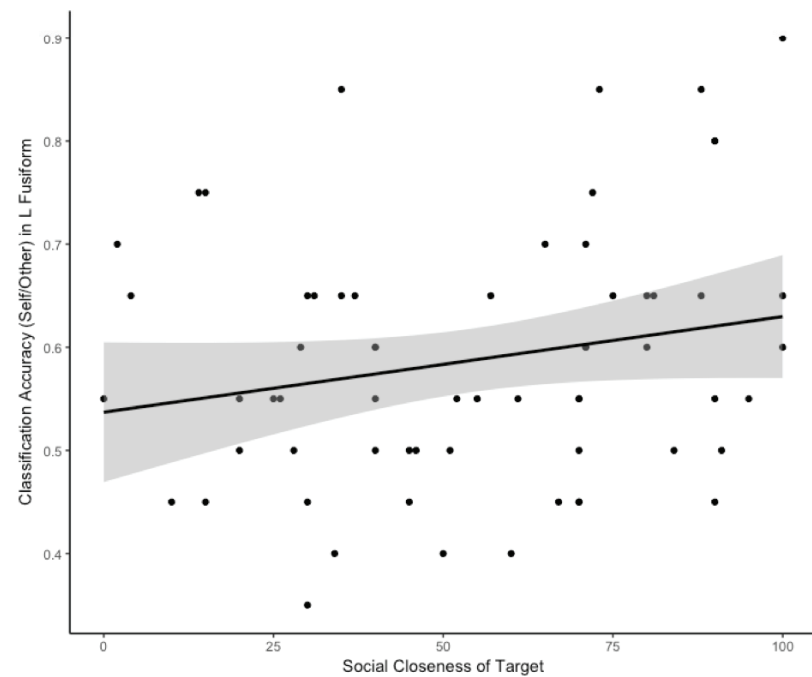
Figure 30. Classification accuracy of self/other face morphs in the left fusiform cortex (AAL) by target (A) and by social closeness of the target to the self (B). Classification accuracy increased with social closeness, B= 0.002, 95% CI [-0.0002, 0.004], t = 1.72, p = 0.09 (Satterthwaite approximated df= 41.9).

Discussion

This study demonstrated that successful classification of morphed faces ranging from self to other based on activation patterns in the MPFC depended on the social closeness of the target to the self. High-level, semantic categories can give rise to low-level indications of categorical perception (Beale & Keil, 1995; Goldstone & Hendrickson, 2009; Harnad, 2006). In this case, self and other comprise different conceptual and perceptual categories, but the category membership of particular face morphs grew less distinct in higher-order association cortex as the targets increased in social closeness. This confusion is striking when considering the fact that self-recognition is quite robust, beginning in early infancy (Bahrick & Moss, 1996). Importantly, classification accuracy is based on spontaneous response patterns in MPFC upon viewing the face morphs. This implies that high-level processing of self-relevance and social closeness occurs automatically upon viewing a familiar face, in keeping with previous research suggesting that familiar face recognition relies on a broader network of face processing and emotional and social processing regions (Gobbini et al., 2004).

Interestingly, classification in the left fusiform cortex, a region commonly associated with face processing (Kanwisher, McDermott, & Chun, 1997), was marginally facilitated—rather than crippled— by social closeness. These results might suggest that personal familiarity may assist identity recognition in this region, and in fact previous research demonstrated both familiarity and identity discrimination in the fusiform (di Oleggio Castello, Halchenko, Guntupalli, Gors, & Gobbini, 2017). Overall, these results provide support for the notion that self and close others share mental representations that are evident at the level of neural representation, even in higher-order association cortex

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associated with self-processing, and creates a challenge for decoding identity in this region.

Study 3: Social Disconnectedness Motivates Perceived Social Closeness

Humans have an innate motivational drive to be socially connected (Baumeister & Leary, 1995). Socially disconnected individuals thus exhibit an increased drive to reconnect and experience enhanced perception of social targets (DeWall et al., 2008; Maner et al., 2007; Powers et al., 2014). Conversely, social connection satiates the need to belong and influences future social behavior. For example, socially connected people show less investment in social interactions (DeWall et al., 2008), even to the point of dehumanizing distant others (Waytz & Epley, 2012). To put it more directly, socially connected individuals treasure their social connections, but fail to seek new ones. Waytz and Epley (2012) summarized it as such, "social connection both diminishes the motivation to connect with other humans and increases the difference between close and distant others" (p. 71).

Conversely, in Study 1, trait levels of loneliness were associated with lower levels of social closeness for personally familiar others. In the present study, we attempted to tease apart this relationship a bit more to determine if temporary feelings of social disconnectedness, as elicited by a social feedback manipulation, modulate feelings of social closeness. It is unclear whether the motivation to reconcile feelings of social disconnectedness with the need to belong would drive greater feelings of social closeness, or whether feelings of disconnectedness might cause one to reinterpret existing relationships. In particular, this could play out differently for close others and for acquaintances. Although loneliness is associated with feeling less close to close others, it is also associated with increased reward and motivation toward them (Inagaki et al.,

2016). Still, exclusion has been associated with the drive to form new relationships, and may inordinately affect the perceived distance from acquaintances.

The present study tested this notion by comparing the social closeness ratings of familiar others following social rejection. Here we attempted to manipulate the boundary conditions between representations of self and other to determine if rejected individuals represented social targets as closer or more distant from the self. By using an experimental manipulation of belongingness we aimed to demonstrate whether feelings of social connection were causally related to self-other closeness. These results could support one of two predictions with respect to feelings of social closeness toward personally familiar others following social rejection or induced social disconnectedness. First, socially disconnected participants could feel closer to their relationship partners, resembling an effort to reconnection. Second, socially disconnected participants could feel more distant from relationship partners in order to reconcile the information about their overall connectedness.

Method

Participants

For Study 3, 182 participants (ages 18-22) were recruited from Amazon's Mechanical Turk and provided informed consent in accordance with the guidelines set by the Committee for the Protection of Human Subjects at Dartmouth College. They were paid in cash through Mechanical Turk upon completion. To probe the boundaries of self-other closeness, participants were randomly assigned to one of two groups, alone (N= 92)

or belong (N= 90), and were administered a commonly used social connection manipulation.

Procedure

As in Study 1, participants first provided the names of five close others and five acquaintances ranked in order of their social closeness. They then completed a short personality survey which included questions from the Eysenck Personality Questionnaire (EPQ; Eysenck & Eysenck, 1975) , Janis-Field Feelings of Inadequacy Scale (Janis & Field, 1959), and the Big Five Aspect Scale (BFAS; DeYoung, Quilty, & Peterson, 2007), along with 24 traits selected from the Anderson personality trait adjectives list (Anderson, 1968). Following the completion of these surveys, participants were administered a randomly-assigned social connection manipulation.

The future-alone-versus-future-belonging manipulation, which has been successfully used to induce feelings of disconnection in previous studies, was used to elicit feelings of social disconnection in one group (alone) and social connection in another group (belong) (Powers, Wagner, Norris, & Heatherton, 2013; Powers et al., 2014; Twenge, Baumeister, Tice, & Stucke, 2001). This manipulation was delivered under the guise of revealing the participant's fit with a personality profile according to their survey responses. The alone group was given the personality profile "Loner" and told that their personality revealed an isolated future with unsuccessful relationships. The belong group was given the personality profiles "Connected" and was assured that they would have a future with deep, meaningful social connection. To maintain the believability of the manipulation, the feedback included personalized statements from

their own EPQ and Janis-Field responses and generic personality feedback typically believed by the average person (the 'Barnum Effect'; Snyder, Shenkel, & Lowery, 1977) along with the manipulation.

Finally, they rated each of the nominated ten targets on the same 24 trait adjectives (0= "not at all", 100= "very much") and provided closeness ratings ("How close do you feel to {target}?", 0= "not at all", 100= "very much"). They were then probed on how believable they found the feedback they received (0= "not at all", 100= "very much") and on how socially (dis)connected it made them feel (0-100 scale transformed so that: -50 = "socially excluded/lonely", 0 = "neither/no change", 50 = "socially connected").

Results

Manipulation check

Participants reported finding the feedback moderately believable (M = 68.87, SD = 27.34; 0 = "not at all", 100 = "very much"). Moreover, the alone group reported feeling more disconnected (M = -24.10, SD = 24.86) than the belong group (M = 22.07, SD = 21.17), $t(176.67) = -13.50$, $p < 0.001$, suggesting that the manipulation was successful in changing perceived social connectedness.

Closeness ratings

Close others (M = 78.31, SD = 20.30) were rated as significantly closer than acquaintances (M = 37.81, SD = 23.15), $t(909) = 48.70$, $p < 0.001$, but there was no overall group difference in self-reported closeness ratings, $M_{Alone} = 57.19$, $SD_{Alone} =$

30.57; M_{Belong} = 68.94, SD_{Belong} = 28.84; t(1815.6) = -1.26, p= 0.21. However, in a linear mixed-effects model with a random intercept for subjects, there was a significant condition (alone vs belong) by category (close other vs acquaintances) interaction, B = 3.84, 95% CI [0.57, 7.10], $t(1636)$ = 2.30, p = 0.02. The difference in the perceived closeness of close others and acquaintances was larger for social disconnected participants than socially connected participants (Figure 31). Distant others were rated as less close by the alone group (M = 35.99, SD = 23.32) than by the belong group (M = 39.66, SD = 22.85), $t(908)$= -2.40, p = 0.02, but there was no difference in the closeness ratings of close others (M_{Alone} = 78.39, SD_{Alone} = 20.66; M_{Belong} = 78.22, SD_{Belong} = 19.95; $t(907)$ = 0.13, p = 0.90. These results suggest that social disconnection may induce feelings of social distance from acquaintances, while exerting no effect on close relationship partners.
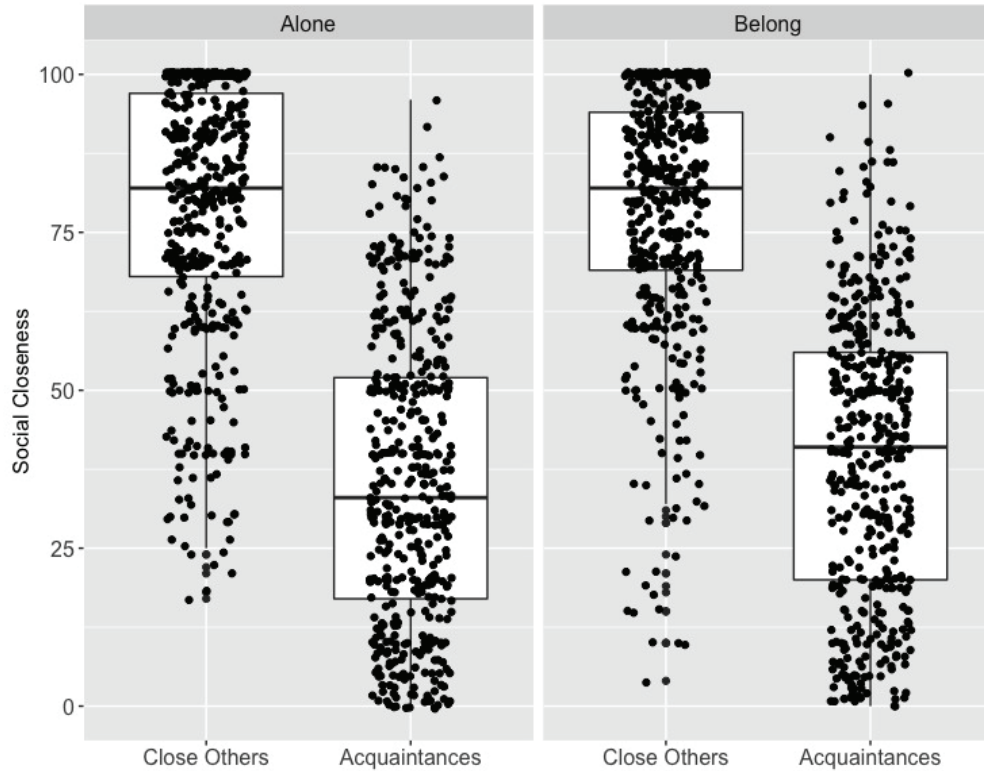
Figure 31. Participants who underwent a social disconnection manipulation subsequently reported less social closeness to previously nominated acquaintances than those who underwent a social connection manipulation (future-alone-versus-future-belonging paradigm; Twenge et al., 2001), but showed no difference in social closeness to close others.

Trait ratings

Close others (M = 0.41, SD = 0.35) were rated as significantly more similar to the participant than acquaintances (M = 0.28, SD = 0.38), t(909) = 9.55, p < 0.001. There was no overall group difference in trait similarity (Fisher z-transformed Pearson correlation coefficients across all 24 traits) between the participant and the targets, M_{Alone} = 0.36, SD_{Alone} = 0.38; M_{Belong} = 0.33, SD_{Belong} = 0.37; t(1817) = 1.36, p= 0.17. (Note: Means and standard deviations are reported as Pearson r values, but statistics were conducted with Fisher z-transformed r values.) In a linear mixed-effects model with a random intercept for subjects, there was no significant condition (alone vs belong) by

category (close other vs acquaintances) interaction, $B = 0.02$, 95% CI [-0.05, 0.09], $t(1636) = 0.46$, $p = 0.64$. Close others were rated as more similar to the self than acquaintances, but this difference did not differ across groups, suggesting that social connectedness has no influence on the perceived similarity of targets.

Discussion

This study demonstrated that inducing temporary feelings of social rejection led participants to report feeling less close to acquaintances than their connected counterparts felt. Together with Study 1, these results support the notion that general disconnectedness, as elicited by loneliness or social rejection, relates to feeling less close to particular relationship partners. In Study 1, loneliness was associated with feeling less close to close others and acquaintances and with showing more dissimilar representations for acquaintances and the self. Here experimentally manipulated disconnectedness was associated with feeling less close to acquaintances only, and might suggest that the power of general disconnectedness to weaken feelings of closeness toward relationship partners is stronger for those that we are familiar with but less close to.

Moreover, this effect may have occurred in an effort to reconcile the feedback about future belongingness with the participant's true feelings of closeness toward relationship partners. One could imagine a compensatory response in which socially disconnected participants report feeling closer to their personally familiar others, or in contrast, an accommodating response in which they update the perceptions of their current relationships to better match their new belief about their connectedness. These results are in line with the accommodating account, and specifically target perceptions of

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more loosely held relationships. It might be the case that close relationships are more robust to this type of manipulation because the participant has access to abounding evidence to the contrary. In response, they may adjust their feelings toward the targets to whom they are less securely attached. Because close relationships may be viewed as more stable than casual relationships, feelings of closeness toward acquaintances may be more susceptible to general feelings of social disconnectedness.

However, we lack evidence to speak to motivational influences on social approach behavior toward non-specific targets. Previous research suggests that social exclusion focuses attention on a broader set of social cues and motivates the pursuit of new social targets. In light of this work, one adaptive response to receiving feedback on social disconnectedness may be to cut weaker social ties and find substitutes that are better able to meet belongingness needs. An interesting follow-up to this study would be to determine how specific social rejection from a single target influences feelings of social closeness to that target, as well as to all other social targets. In that case, it is clear which social tie should be cut—the offending target—and which should be cherished. The general social feedback provided by the future-alone-versus-future belonging paradigm is harder to resolve, and in fact may give rise to temporary feelings of loneliness rather than social rejection, per se. Other forms of social rejection may increase affiliative behavior, whereas our results suggest that participants accommodate their perceptions of weaker ties in order to reconcile their relationships with new information about their belongingness status.

Feeling disconnected from our social world may manifest as reconsidering how close we feel to weak ties. If we receive feedback that we're alone despite having these

connections, maybe we begin to view them more dubiously. Moreover, because this study employed an experimental manipulation, we take these results to imply that inducing a motivational change is sufficient to alter the introspective narrative surrounding one's own relationships and may speak to the development of trait-level relational distortions. Heightened sensitivity to and rumination on personal examples of social rejection may contribute to more global feelings of disconnectedness, or loneliness.

General Discussion

Our personal relationships are the greatest predictor of meaning and happiness in life (Klinger, 1977). As a social species, we are not well equipped to experience life alone; and doing so dramatically decreases our health and happiness. In fact, some have begun questioning whether these relationships are incorporated into our self. William James suggested that close others comprise a core aspect of our material self, stating:

> *Next, our immediate family is a part of ourselves. Our father and mother, our wife and babes, are bone of our bone and flesh of our flesh. When they die, a part of our very selves is gone. If they do anything wrong, it is our shame. If they are insulted, our anger flashes forth as readily as if we stood in their place.*
> (James, 1890, pp. 292-293)

That is, our lives are interconnected: the needs, desires, accomplishments and failures of our close others are experienced as our own. Still others have suggested that these identities merge at the level of mental representation, giving rise to self-other category confusion. In the context of marriage, this could manifest as misremembering the personality traits and experiences that belong to us and those that belong to our partner.

This deep interconnectedness and emotional investment in our close others helps explain the limited size of our support clique (Hill & Dunbar, 2003).

The present studies were designed to reconcile the notion of an interconnected self that is activated by close relationship partners with the notion of the self as special. Specifically, these studies looked for evidence that the representation and perception of self and others varied with social closeness. Study 1 found evidence for more similar patterns of activation in the MPFC with social closeness of the self and other, suggesting that the self and close others may belong to closely associated mental constructs.

While Study 1 tested for this relationship during explicit attributions of the self and other, Study 2 took a more indirect approach aimed at uncovering non-conscious cognitive representations through perceptual confusions. Because we do not have direct access to the semantic architecture organizing these concepts, we cannot directly probe for overlapping mental representations. Instead, we exploited the fact that perceptual choices are sensitive to high-level categorization by introducing perceptual confusion during a self-recognition task. Doing so uncovered the categorical boundaries of the self and others and the malleability of those boundaries to social closeness. Both Study 2a and 2b suggest that close others activate the concept of the self: in Study 2a this made self-recognition easier and in Study 2b it made discrimination harder.

Finally, Study 3 provided evidence that social disconnectedness shifts perceptions of social closeness, making acquaintances feel less close. Similarly, trait loneliness was associated with feeling less close to close others and acquaintances and showing less representational similarity to acquaintances in Study 1. Taken together, we found evidence to suggest that general perceptions of disconnectedness trickle down to

influence perceptions of social closeness at the relationship-level. These results support both a "self as special" model and an interconnected self-other overlap model. First and foremost, self is distinct from others in representation and is well-conserved in perception. But secondly, relationships with others dictate how similarly they are represented to the self, as well as how they influence self-perception.

What Does the MPFC Represent?

Though previous research has identified neural foci for the abstract coding of social distance (Parkinson, Liu, & Wheatley, 2014), the present set of studies explored this concept within the context of self-representation by interrogating self-other representation in the MPFC. To begin understanding what self-other similarity in MPFC means in this context, we should first consider the role of the MPFC in self-referential processing. Moran and colleagues (2013) provided three interpretations on the involvement of the MPFC (and other cortical midline structures) during self-processing: 1) that it supports general social knowledge, of which the self is an especially powerful case, 2) that it is a workspace for integrating input from internal and external sensory processing regions, and 3) that it directs conscious thought.

Because the MPFC is multimodal association cortex that is functionally connected to other social cognitive and memory sub-systems (Andrews-Hanna, Smallwood, & Spreng, 2014; Spreng & Andrews-Hanna, 2015), it likely organizes information along abstract, semantic dimensions, some of which are applicable to person knowledge (Tamir, Thornton, Contreras, & Mitchell, 2016; Thornton & Mitchell, 2017a). However, person-specific knowledge appears to be conserved in MPFC signal, as well, with

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previous research demonstrating successful decoding of person identity in the MPFC (Hassabis et al., 2014; Thornton & Mitchell, 2017a). Its functional connectivity profile suggests that the MPFC belongs to a "core" default subsystem that interacts closely with dorsal medial/social cognitive and medial temporal/memory subsystems (Andrews-Hanna et al., 2014; Spreng & Andrews-Hanna, 2015). Doing so may enable richer reconstruction of self and person knowledge by integrating associative and meta-cognitive information. The MPFC appears to organizing and accessing social knowledge by interacting with and integrating information from other social cognitive and autobiographical subsystems, supporting a combination of the functions described by Moran and colleagues (2013).

Finally, though it was not the primary focus of this set of studies, the present results may contribute to the interpretation of MPFC and DMPFC function. Specifically, that social closeness consistently modulated representation in the MPFC further supports its role in coding self-relevance and value—though these two processes are inherently collinear and difficult to parse (Chavez, Heatherton, & Wagner, 2017). In particular, the cluster identified from the univariate parametric modulation analysis was localized to a more ventral portion of the MPFC, which has classically been associated with representing subjective value (Bartra, McGuire, & Kable, 2013; Clithero & Rangel, 2013). From this perspective, the ventral MPFC may support domain-general value processing, of which the self and close others are powerfully valued stimuli.

Moreover, the DMPFC may represent the abstract person knowledge used in developing and maintaining mental models of other people. In Study 1, the representation of social targets in the MPFC and DMPFC was similarly structured, but it was less

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distinct in the DMPFC. The noisier structure of DMFPC representation could reflect the fact that DMPFC reflects additional trait or person knowledge that was not explicitly plotted but that obscured the organization of social targets by social closeness. That is, these social targets might be more meaningfully organized along other social-cognitive dimensions in the DMPFC. Recent research has begun to better understand the organization of person knowledge in these regions by reducing representation to multiple, highly explanatory dimensions (Thornton & Mitchell, 2017b). The respective functions of the MPFC and DMPFC could be better parsed by allowing social targets to vary across multiple dimensions and estimating their contributions to the organization of of these targets.

Implications for Self and Close Other Representation

One unique theory defines the self as an interpersonal construct composed of many relational elements—one for every significant relationship (Andersen & Chen, 2002). From this perspective, a latent version of the self (the relational self) exists for all relationships, bundling the aspects of the self that are relevant for that relationship. When a particular relational self is activated all of the aspects required for interacting in that relationship are brought online to ensure their accessibility during the interaction. From this view, the self is defined in the context of relationships. Accordingly, the neural similarity observed across conditions could be taken to reflect the aspects of the self that are unique to a relationship with each target rather than the representation of the target itself.

An alternative model suggests that the MPFC attaches self-relevance to the present experience, in collaboration with social cognitive and memory sub-systems, by integrating autobiographical memory and meta-cognitive thought (Andrews-Hanna et al., 2014). By this account, close others may be processed more similarly to the self in the MPFC because they have more associational tags and more extensive autobiographical overlap with the self, in addition to richer social cognitive model for elaborative reconstruction.

Finally, MPFC might be functionally divided into an affective (VMPFC-limbic) pathway for quickly assessing self-relevant value and salience and a cognitive (DMPFC-cortical-hippocampal) pathway for more elaborative introspective processing (Schmitz & Johnson, 2007). A variety of features (e.g., similarity, closeness, familiarity, affective salience, warmth, competence, and emotive and epistemic investment), including closeness, may contribute to self-relevance, ultimately signaling reinforcement value (Murray et al., 2012; Schmitz & Johnson, 2007). In fact, viewing self-relevance as a value signal is supported by recent research demonstrating that the self and positive affect are indeed intrinsically related (Chavez, Heatherton, & Wagner, 2017). By this account, close others need not be a distinct part of the self but may represent one end of a spectrum of self-relevance.

Conclusions

Together these studies provided partial support for both a "self is special" and "inclusion of other in the self" model of self-other representation in MPFC. Overall, the self was represented as distinct in the MPFC, with the overarching representational

structure in the MPFC clustering targets into personally familiar others, strangers, and the self. Additionally, we found both univariate and multivariate neuroimaging evidence to support the notion of a graded representation within the class of personally familiar others such that close others were represented more similarly to the self in the MPFC. In fact, social closeness increased both the activation of the MPFC and representational similarity to the self in the MPFC. Moreover, the presence of close others appeared to facilitate the detection of the self even at the level of visual perception, suggesting that close others bias self-perception and give rise to less distinguishable neural activation patterns in the MPFC. Additional studies found support for the notion that general social disconnectedness—loneliness and expectations of future disconnection—influence perceptions of social closeness toward existing relationship partners.

Overall these results suggest that social closeness may increase the self-relevance of social targets and endow them with a self-related processing advantage in the brain. The mental constructs underlying our concepts of the self and others and their categorical boundaries may be sensitive to the emotional attachment we feel toward our specific relationship partners and how connected we feel to our social world more generally.

Table 1. Mean and standard deviations of ratings (1-100) for each target.

	Closeness	**Familiarity**	**Similarity**
Close others	82.70 (15.28)	83.76 (17.16)	69.07 (20.40)
Acquaintances	46.28 (22.22)	48.64 (24.17)	43.69 (23.59)
Celebrities	7.59 (12.61)	33.56 (26.61)	14.22 (16.90)

Table 2. Correlation coefficients for comparison of MPFC/"self" and DMPFC/"social" representational similarity matrices with theoretically-driven model similarity matrices.

Model	Correlation coefficient (r)	Degrees of freedom (df)	Significance (p)
MPFC/"self"			
all conditions distinct	0.24	49	< 0.001
self vs. other	0.23	49	< 0.001
3 cluster	0.32	49	< 0.001
self and familiar	0.22	49	< 0.001
self and close	0.07	49	< 0.001
self and close vs. acquaintance vs. celebrity	0.19	49	< 0.001
combined 3 cluster-social closeness	0.29	49	< 0.001

DMPFC/"social"			
all conditions distinct	0.13	49	< 0.001
self vs. other	0.14	49	< 0.001
3 cluster	0.17	49	< 0.001
self and familiar	0.11	49	< 0.001
self and close	0.04	49	0.03
self and close vs. acquaintance vs. celebrity	0.11	49	< 0.001
combined 3 cluster-social closeness	0.15	49	< 0.001

Table 3. Brain regions whose activation patterns most closely reflected social closeness (allowing other pairwise relationships) as revealed by searchlight representational similarity analysis (voxelwise p< 0.001, cluster-corrected p<0.001).

Region	Coordinates (MNI)			Volume (mm^3)	Peak T
	X	Y	Z		
Left Occipital Cortex	-6	-90	-3	3029	12.85
Middle Cingulate Gyrus	-6	-24	39	690	6.35
Right Medial Prefrontal Cortex	9	51	33	483	6.71
Left Superior Frontal Gyrus	-24	36	45	293	6.40

Cluster peaks are listed and identified by their region names (adapted from Automated Anatomical Labeling in SPM). Volumes refer to entire supra-threshold clusters.

Table 4. Brain regions whose activation patterns most closely reflected self-close other similarity as revealed by searchlight representational similarity analysis (voxelwise p< 0.001, cluster-corrected p<0.001).

Region	Coordinates (MNI)			Volume (mm^3)	Peak T
	X	Y	Z		
Left Occipital Cortex	3	-90	-6	2561	8.37
Medial Prefrontal/ Orbitofrontal Cortex	-3	36	-12	1733	6.60
Left Inferior Temporal Gyrus	-57	-9	-24	756	7.57

Cluster peaks are listed and identified by their region names (adapted from Automated Anatomical Labeling in SPM). Volumes refer to entire supra-threshold clusters.

Table 5. Brain regions whose activation patterns most closely reflected self-personally familiar other similarity as revealed by searchlight representational similarity analysis (voxelwise p< 0.001, cluster-corrected p<0.001).

Region	Coordinates (MNI)			Volume (mm^3)	Peak T
	X	Y	Z		
Precuneus	-6	-54	30	21276	14.29
Right Inferior Temporal/Fusiform Gyrus	57	-9	-27	757	8.07
Cerebellum	36	-75	-39	316	5.50

Cluster peaks are listed and identified by their region names (adapted from Automated Anatomical Labeling in SPM). Volumes refer to entire supra-threshold clusters.

Table 6. Brain regions whose activation patterns most closely demonstrated a combination of clustered activation patterns differentiating self, personally familiar others, and celebrities and a graded similarity for personally familiar others reflecting social closeness to the self, as revealed by searchlight representational similarity analysis (voxelwise p< 0.001, cluster-corrected p<0.001).

Region	Coordinates (MNI)			Volume (mm^3)	Peak T
	X	Y	Z		
Precuneus	-6	-54	30	30921	15.84
Cerebellum	36	-72	-39	341	6.31

Cluster peaks are listed and identified by their region names (adapted from Automated Anatomical Labeling in SPM). Volumes refer to entire supra-threshold clusters.

Table 7. Brain regions in which trait loneliness modulated the similarity of activation patterns to the self-close other target similarity model, as revealed by a whole-brain regression performed on the searchlight RSA results targeting the self-close other model (voxelwise p< 0.05, cluster-corrected to 200 voxels).

Region	Coordinates (MNI)			Volume (mm^3)	Peak T
	X	Y	Z		
Medial Prefrontal/Dorsal Anterior Cingulate Cortex (MPFC/dACC)	0	39	27	727	3.59
Posterior Cingulate Cortex (PCC)	-12	-42	33	381	3.85
Cerebellum	-33	-93	-36	287	3.33
Right Temporal Pole	66	18	-27	1675	-4.34
Left Inferior Frontal Gyrus	-42	39	-33	1381	-3.62

Cluster peaks are listed and identified by their region names (adapted from Automated Anatomical Labeling in SPM). Volumes refer to entire supra-threshold clusters.

References

Adolphs, R. (2009). The social brain: neural basis of social knowledge. *Annual Review of Psychology*, *60*, 693–716.

Andersen, S. M., & Chen, S. (2002). The relational self: An interpersonal social-cognitive theory. *Psychological Review*, *109*(4), 619–645.

Anderson, N. H. (1968). Likableness ratings of 555 personality-trait words. *Journal of Personality and Social Psychology*, *9*(3), 272–279.

Andrews-Hanna, J. R., Smallwood, J., & Spreng, R. N. (2014). The default network and self-generated thought: component processes, dynamic control, and clinical relevance. *Annals of the New York Academy of Sciences*, *1316*, 29–52.

Aron, A., Aron, E. N., & Smollan, D. (1992). Inclusion of Other in the Self Scale and the structure of interpersonal closeness. *Journal of Personality and Social Psychology*, *63*(4), 596–612.

Aron, A., Aron, E. N., Tudor, M., & Nelson, G. (1991). Close relationships as including other in the self. *Journal of Personality and Social Psychology*, *60*(2), 241–253.

Bahrick, L. E., & Moss, L. (1996). Development of Visual Self-Recognition in Infancy. *Ecological Psychology: A Publication of the International Society for Ecological Psychology*, *8*(3), 189–208.

Balcetis, E., & Dunning, D. (2006). See what you want to see: motivational influences on visual perception. *Journal of Personality and Social Psychology*, *91*(4), 612–625.

Bates, D., Maechler, M., Bolker, B., Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, *67*(1), 1-48.

Baumeister, R. F., & Leary, M. R. (1995). The need to belong: desire for interpersonal

attachments as a fundamental human motivation. *Psychological Bulletin*, *117*(3), 497–529.

Baumeister, R. F., & Tice, D. M. (1990). Point-Counterpoints: Anxiety and Social Exclusion. *Journal of Social and Clinical Psychology*, *9*(2), 165–195.

Beale, J. M., & Keil, F. C. (1995). Categorical effects in the perception of faces. *Cognition*, *57*(3), 217–239.

Berscheid E, Reis HT. Attraction and close relationships. In: T GD, T FS, Lindzey G, editors. The Handbook of Social Psychology. 4 ed. Vol. 2. New York: McGraw Hill; 1998. pp. 193–281.

Brummett, B. H., Barefoot, J. C., Siegler, I. C., Clapp-Channing, N. E., Lytle, B. L., Bosworth, H. B., … Mark, D. B. (2001). Characteristics of socially isolated patients with coronary artery disease who are at elevated risk for mortality. *Psychosomatic Medicine*, *63*(2), 267–272.

Cacioppo, J. T., Hughes, M. E., Waite, L. J., Hawkley, L. C., & Thisted, R. A. (2006). Loneliness as a specific risk factor for depressive symptoms: cross-sectional and longitudinal analyses. *Psychology and Aging*, *21*(1), 140–151.

Chavez, R. S., Heatherton, T. F., & Wagner, D. D. (2017). Neural Population Decoding Reveals the Intrinsic Positivity of the Self. *Cerebral Cortex* , *27*(11), 5222–5229.

Chen, P.-H. A., Wagner, D. D., Kelley, W. M., Powers, K. E., & Heatherton, T. F. (2013). Medial prefrontal cortex differentiates self from mother in Chinese: evidence from self-motivated immigrants. *Culture and Brain*, *1*(1), 3–15.

Clithero, J. A., & Rangel, A. (2013). Informatic parcellation of the network involved in the computation of subjective value. *Social cognitive and affective neuroscience*,

9(9), 1289-1302.

Coan, J. A., Schaefer, H. S., & Davidson, R. J. (2006). Lending a hand: social regulation
of the neural response to threat. *Psychological Science*, *17*(12), 1032–1039.

Cornwell, E. Y., & Waite, L. J. (2009). Social disconnectedness, perceived isolation, and
health among older adults. *Journal of Health and Social Behavior*, *50*(1), 31–48.

Courtois, M. R., & Mueller, J. H. (1979). Processing multiple physical features in facial
recognition. *Bulletin of the Psychonomic Society*, *14*(1), 74–76.

Cox, R. W., Chen, G., Glen, D. R., Reynolds, R. C., & Taylor, P. A. (2017). FMRI
Clustering in AFNI: False-Positive Rates Redux. *Brain Connectivity*, *7*(3), 152–171.

Cunningham, W. A., Van Bavel, J. J., Arbuckle, N. L., Packer, D. J., & Waggoner, A. S.
(2012). Rapid social perception is flexible: approach and avoidance motivational
states shape P100 responses to other-race faces. *Frontiers in Human Neuroscience*,
6. https://doi.org/10.3389/fnhum.2012.00140

Dale, A. M. (1999). Optimal experimental design for event-related fMRI. *Human Brain
Mapping*, *8*(23), 109–114.

D'Argembeau, A., Collette, F., Van der Linden, M., Laureys, S., Del Fiore, G.,
Degueldre, C., … Salmon, E. (2005). Self-referential reflective activity and its
relationship with rest: a PET study. *NeuroImage*, *25*(2), 616–624.

D'Argembeau, A., Ruby, P., Collette, F., Degueldre, C., Balteau, E., Luxen, A., …
Salmon, E. (2007). Distinct Regions of the Medial Prefrontal Cortex Are Associated
with Self-referential Processing and Perspective Taking. *Journal of Cognitive
Neuroscience*, *19*(6), 935–944.

Dehart, T., Pelham, B., Fiedorowicz, L., Carvallo, M., & Gabriel, S. (2011). Including

Others in the Implicit Self: Implicit Evaluation of Significant Others. *Self and Identity: The Journal of the International Society for Self and Identity*, *10*(1), 127–135.

Denny, B. T., Kober, H., Wager, T. D., & Ochsner, K. N. (2012). A meta-analysis of functional neuroimaging studies of self- and other judgments reveals a spatial gradient for mentalizing in medial prefrontal cortex. *Journal of Cognitive Neuroscience*, *24*(8), 1742–1752.

DeWall, C. N., Baumeister, R. F., & Vohs, K. D. (2008). Satiated with belongingness? Effects of acceptance, rejection, and task framing on self-regulatory performance. *Journal of Personality and Social Psychology*, *95*(6), 1367–1382.

DeYoung, C. G., Quilty, L. C., & Peterson, J. B. (2007). Between facets and domains: 10 aspects of the Big Five. *Journal of Personality and Social Psychology*, *93*(5), 880–896.

di Oleggio Castello, M. V., Halchenko, Y. O., Guntupalli, J. S., Gors, J. D., & Gobbini, M. I. (2017). The neural representation of personally familiar and unfamiliar faces in the distributed system for face perception. *Scientific Reports*, *7*(1), 12237.

Diener, E., & Seligman, M. E. P. (2002). Very happy people. *Psychological Science*, *13*(1), 81–84.

Dunbar, R. I. M. (1998). The social brain hypothesis. *Evolutionary Anthropology: Issues, News, and Reviews*, *6*(5), 178–190.

Dunbar, R. I. M., & Shultz, S. (2007). Evolution in the social brain. *Science*, *317*(5843), 1344–1347.

Eisenberger, N. I. (2013). Social ties and health: a social neuroscience perspective.

Current Opinion in Neurobiology, *23*(3), 407–413.

Eklund, A., Nichols, T. E., & Knutsson, H. (2016). Cluster failure: Why fMRI inferences for spatial extent have inflated false-positive rates. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(28), 7900–7905.

Epley, N., & Whitchurch, E. (2008). Mirror, mirror on the wall: enhancement in self-recognition. *Personality & Social Psychology Bulletin*, *34*(9), 1159–1170.

Eysenck, H. J., & Eysenck, S. B. (1975). *Manual of the Eysenck Personality Questionnaire.* San Diego, CA.

Freiwald, W., Duchaine, B., & Yovel, G. (2016). Face Processing Systems: From Neurons to Real-World Social Perception. *Annual Review of Neuroscience*, *39*, 325–346.

Frith, C. D. (2007). The social brain? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *362*(1480), 671–678.

Gardner, W. L., Pickett, C. L., & Brewer, M. B. (2000). Social Exclusion and Selective Memory: How the Need to belong Influences Memory for Social Events. *Personality & Social Psychology Bulletin*, *26*(4), 486–496.

Gobbini, M. I., Gors, J. D., Halchenko, Y. O., Rogers, C., Guntupalli, J. S., Hughes, H., & Cipolli, C. (2013). Prioritized Detection of Personally Familiar Faces. *PloS One*, *8*(6), e66620.

Gobbini, M. I., & Haxby, J. V. (2007). Neural systems for recognition of familiar faces. *Neuropsychologia*, *45*(1), 32–41.

Gobbini, M. I., Leibenluft, E., Santiago, N., & Haxby, J. V. (2004). Social and emotional attachment in the neural representation of faces. *NeuroImage*, *22*(4), 1628–1635.

Goldstone, R. L., & Hendrickson, A. T. (2009). Categorical perception. *Wiley Interdisciplinary Reviews. Cognitive Science*, *1*(1), 69–78.

Gusnard, D., Akbudak, E., Shulman, G., & Raichle, M. E. (2001). Role of medial prefrontal cortex in a default mode of brain function. *NeuroImage*, *13*(6), 414.

Harnad, S. (2006). Categorical Perception. In *Encyclopedia of Cognitive Science*.

Hassabis, D., Spreng, R. N., Rusu, A. A., Robbins, C. A., Mar, R. A., & Schacter, D. L. (2014). Imagine all the people: how the brain creates and uses personality models to predict behavior. *Cerebral Cortex* , *24*(8), 1979–1987.

Hawkley, L. C., Thisted, R. A., Masi, C. M., & Cacioppo, J. T. (2010). Loneliness predicts increases blood pressure: 5-year cross-lagged analyses in middle-aged and older adults. *Psychology and aging, 25*(1), 132.

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences*, *4*(6), 223–233.

Heatherton, T. F., Wyland, C. L., Macrae, C. N., Demos, K. E., Denny, B. T., & Kelley, W. M. (2006). Medial prefrontal activity differentiates self from close others. *Social Cognitive and Affective Neuroscience*, *1*(1), 18–25.

Hill, R. A., & Dunbar, R. I. M. (2003). Social network size in humans. *Human Nature* , *14*(1), 53–72.

Holt-Lunstad, J. (2017). The Potential Public Health Relevance of Social Isolation and Loneliness: Prevalence, Epidemiology, and Risk Factors. *Public Policy & Aging Report*, *27*(4), 127–130.

Holt-Lunstad, J., Smith, T. B., Baker, M., Harris, T., & Stephenson, D. (2015). Loneliness and social isolation as risk factors for mortality: a meta-analytic review.

Perspectives on Psychological Science: A Journal of the Association for Psychological Science, *10*(2), 227–237.

Holt-Lunstad, J., Smith, T. B., & Layton, J. B. (2010). Social relationships and mortality risk: a meta-analytic review. *PLoS Medicine*, *7*(7), e1000316.

Inagaki, T. K., Muscatell, K. A., Moieni, M., Dutcher, J. M., Jevtic, I., Irwin, M. R., & Eisenberger, N. I. (2016). Yearning for connection? Loneliness is associated with increased ventral striatum activity to close others. *Social Cognitive and Affective Neuroscience*, *11*(7), 1096–1101.

Janis, I. L., & Field, P. B. (1959). Sex differences and personality factors related to persuasibility. In C. I. Hovland & I. L. Janis (Eds.), *Personality and persuasibility* (pp. 55-68). Oxford, England: Yale Univer. Press.

James, William. The Principles of Psychology. New York: Henry Holt, 1890, Vol. I, pp. 292-293

Jenkins, A. C., Macrae, C. N., & Mitchell, J. P. (2008). Repetition suppression of ventromedial prefrontal activity during judgments of self and others. *Proceedings of the National Academy of Sciences*, *105*(11), 4507–4512.

Jenkins, R., & Burton, A. M. (2011). Stable face representations. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *366*(1571), 1671–1683.

Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *Journal of neuroscience*, *17*(11), 4302-4311.

Kelley, W. M., Macrae, C. N., Wyland, C. L., Caglar, S., Inati, S., & Heatherton, T. F.

(2002). Finding the self? An event-related fMRI study. *Journal of Cognitive Neuroscience*, *14*(5), 785–794.

Keyes, H., & Zalicks, C. (2016). Socially Important Faces Are Processed Preferentially to Other Familiar and Unfamiliar Faces in a Priming Task across a Range of Viewpoints. *PloS One*, *11*(5), e0156350.

Klinger, E. (1977). *Meaning & Void: Inner Experience and the Incentives in People's Lives*. Minneapolis : University of Minnesota Press.

Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational similarity analysis - connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience*, *2*, 4.

Krienen, F. M., Tu, P.-C., & Buckner, R. L. (2010). Clan mentality: evidence that the medial prefrontal cortex responds to close others. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *30*(41), 13906–13915.

Kuznetsova A, Brockhoff PB and Christensen RHB (2017). "lmerTest Package: Tests in Linear Mixed Effects Models." Journal of Statistical Software, *82*(13), pp. 1-26.

Leibenluft, E., Gobbini, M. I., Harrison, T., & Haxby, J. V. (2004). Mothers' neural activation in response to pictures of their children and other children. *Biological Psychiatry*, *56*(4), 225–232.

Linares, D, & López-Moliner, J. (2016). quickpsy: An R package to fit psychometric functions for multiple groups. *The R Journal*, *8*(1), 122–131.

Maner, J. K., DeWall, C. N., Baumeister, R. F., & Schaller, M. (2007). Does social exclusion motivate interpersonal reconnection? Resolving the "porcupine problem." *Journal of Personality and Social Psychology*, *92*(1), 42–55.

Mashek, D. J., & Aron, A. (2004). *Handbook of Closeness and Intimacy*. Psychology
Press.

McPherson, M., Smith-Lovin, L., & Cook, J. M. (2001). Birds of a Feather: Homophily
in Social Networks. *Annual Review of Sociology*, *27*(1), 415–444.

Meyer, M. L., Davachi, L., Ochsner, K. N., & Lieberman, M. D. (2018). Evidence That
Default Network Connectivity During Rest Consolidates Social Information.
Cerebral Cortex . https://doi.org/10.1093/cercor/bhy071

Meyer, M. L., & Lieberman, M. D. (2018). Why People Are Always Thinking about
Themselves: Medial Prefrontal Cortex Activity during Rest Primes Self-referential
Processing. *Journal of Cognitive Neuroscience*, *30*(5), 714–721.

Meyer, M. L., Spunt, R. P., Berkman, E. T., Taylor, S. E., & Lieberman, M. D. (2012).
Evidence for social working memory from a parametric functional MRI study.
Proceedings of the National Academy of Sciences of the United States of America,
109(6), 1883–1888.

Mitchell, J. P., Neil Macrae, C., & Banaji, M. R. (2006). Dissociable Medial Prefrontal
Contributions to Judgments of Similar and Dissimilar Others. *Neuron*, *50*(4), 655–
663.

Moran, J. M., Heatherton, T. F., & Kelley, W. M. (2009). Modulation of cortical midline
structures by implicit and explicit self-relevance evaluation. *Social Neuroscience*,
4(3), 197–211.

Moran, J. M., Lee, S. M., & Gabrieli, J. D. E. (2011). Dissociable neural systems
supporting knowledge about human character and appearance in ourselves and
others. *Journal of Cognitive Neuroscience*, *23*(9), 2222–2230.

Murray, R. J., Schaer, M., & Debbané, M. (2012). Degrees of separation: a quantitative neuroimaging meta-analysis investigating self-specificity and shared neural activation between self- and other-reflection. *Neuroscience and Biobehavioral Reviews*, *36*(3), 1043–1059.

Norman, K. A., Polyn, S. M., Detre, G. J., & Haxby, J. V. (2006). Beyond mind-reading: multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Sciences*, *10*(9), 424–430.

Northoff, G., & Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Sciences*, *8*(3), 102–107.

Bartra, O., McGuire, J. T., & Kable, J. W. (2013). The valuation system: a coordinate-based meta-analysis of BOLD fMRI experiments examining neural correlates of subjective value. *Neuroimage*, *76*, 412-427.

Parkinson, C., Kleinbaum, A. M., & Wheatley, T. (2017). Spontaneous Neural Encoding of Social Network Position. https://doi.org/10.1101/098988

Parkinson, C., Liu, S., & Wheatley, T. (2014). A common cortical metric for spatial, temporal, and social distance. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *34*(5), 1979–1987.

Parkinson, C., & Wheatley, T. (2015). The repurposed social brain. *Trends in Cognitive Sciences*, *19*(3), 133–141.

Peirce, J. W. (2008). Generating Stimuli for Neuroscience Using PsychoPy. *Frontiers in Neuroinformatics*, *2*, 10.

Pickett, C. L., Gardner, W. L., & Knowles, M. (2004). Getting a Cue: The Need to Belong and Enhanced Sensitivity to Social Cues. *Personality & Social Psychology*

Bulletin, *30*(9), 1095–1107.

Powers, K. E., Chavez, R. S., & Heatherton, T. F. (2015). Individual differences in
response of dorsomedial prefrontal cortex predict daily social behavior. *Social
Cognitive and Affective Neuroscience*, *11*(1), 121–126.

Powers, K. E., Wagner, D. D., Norris, C. J., & Heatherton, T. F. (2013). Socially
excluded individuals fail to recruit medial prefrontal cortex for negative social
scenes. *Social Cognitive and Affective Neuroscience*, *8*(2), 151–157.

Powers, K. E., Worsham, A. L., Freeman, J. B., Wheatley, T., & Heatherton, T. F.
(2014). Social connection modulates perceptions of animacy. *Psychological Science*,
25(10), 1943–1948.

Qin, P., & Northoff, G. (2011). How is our self related to midline regions and the default-
mode network?. *Neuroimage*, *57*(3), 1221-1233.

R Core Team (2017). R: A language and environment for statistical computing. R
Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-
project.org/.

Ramon, M., & Gobbini, M. I. (2017). Familiarity matters: A review on prioritized
processing of personally familiar faces. *Visual Cognition*, *26*(3), 179–195.

Russell, D., Peplau, L. A., & Cutrona, C. E. (1980). Revised UCLA Loneliness Scale.
PsycTESTS Dataset. https://doi.org/10.1037/t01011-000

Saxe, R. (2006). Uniquely human social cognition. *Current Opinion in Neurobiology*,
16(2), 235–239.

Schilbach, L., Eickhoff, S. B., Rotarska-Jagiela, A., Fink, G. R., & Vogeley, K. (2008).
Minds at rest? Social cognition as the default mode of cognizing and its putative

relationship to the "default system" of the brain. *Consciousness and Cognition*, *17*(2), 457–467.

Schmitz, T. W., & Johnson, S. C. (2007). Relevance to self: A brief review and framework of neural systems underlying appraisal. *Neuroscience and Biobehavioral Reviews*, *31*(4), 585–596.

Seger, C. A., Stone, M., & Keenan, J. P. (2004). Cortical Activations during judgments about the self and an other person. *Neuropsychologia*, *42*(9), 1168–1177.

Snyder, C. R., Shenkel, R. J., & Lowery, C. R. (1977). Acceptance of personality interpretations: the "Barnum Effect" and beyond. *Journal of Consulting and Clinical Psychology*, *45*(1), 104–114.

Spreng, R. N., & Andrews-Hanna, J. R. (2015). The Default Network and Social Cognition. In *Brain Mapping* (pp. 165–169).

Spunt, R. P., Meyer, M. L., & Lieberman, M. D. (2015). The default mode of human brain function primes the intentional stance. *Journal of Cognitive Neuroscience*, *27*(6), 1116–1124.

Sui, J., & Han, S. (2007). Self-Construal Priming Modulates Neural Substrates of Self-Awareness. *Psychological Science*, *18*(10), 861–866.

Tamir, D. I., & Thornton, M. A. (2018). Modeling the Predictive Social Mind. *Trends in Cognitive Sciences*, *22*(3), 201–212.

Tamir, D. I., Thornton, M. A., Contreras, J. M., & Mitchell, J. P. (2016). Neural evidence that three dimensions organize mental state representation: Rationality, social impact, and valence. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(1), 194–199.

Thornton, M. A., & Mitchell, J. P. (2017a). Consistent Neural Activity Patterns Represent

    Personally Familiar People. *Journal of Cognitive Neuroscience*, *29*(9), 1583–1594.

Thornton, M. A., & Mitchell, J. P. (2017b). Theories of person perception predict

    patterns of neural activity during mentalizing. *Cerebral cortex*, 1-16.

Turk, D. J., Heatherton, T. F., Kelley, W. M., Funnell, M. G., Gazzaniga, M. S., & Neil

    Macrae, C. (2002). Mike or me? Self-recognition in a split-brain patient. *Nature*

    Neuroscience, *5*(9), 841–842.

Twenge, J. M., Baumeister, R. F., Tice, D. M., & Stucke, T. S. (2001). If you can't join

    them, beat them: Effects of social exclusion on aggressive behavior. *Journal of*

    Personality and Social Psychology, *81*(6), 1058–1069.

van der Meer, L., Costafreda, S., Aleman, A., & David, A. S. (2010). Self-reflection and

    the brain: a theoretical review and meta-analysis of neuroimaging studies with

    implications for schizophrenia. *Neuroscience and Biobehavioral Reviews*, *34*(6),

    935–946.

Van Overwalle, F. (2009). Social cognition and the brain: a meta-analysis. *Human Brain*

    Mapping, *30*(3), 829–858.

Wagner, D. D., Haxby, J. V., & Heatherton, T. F. (2012). The representation of self and

    person knowledge in the medial prefrontal cortex. *Wiley Interdisciplinary Reviews.*

    Cognitive Science, *3*(4), 451–470.

Wagner, D. D., Kelley, W. M., & Heatherton, T. F. (2011). Individual differences in the

    spontaneous recruitment of brain regions supporting mental state understanding

    when viewing natural social scenes. *Cerebral Cortex* , *21*(12), 2788–2796.

Waytz, A., & Epley, N. (2012). Social connection enables dehumanization. *Journal of*

Experimental Social Psychology, *48*(1), 70–76.

Whitfield-Gabrieli, S., Moran, J. M., Nieto-Castañón, A., Triantafyllou, C., Saxe, R., & Gabrieli, J. D. E. (2011). Associations and dissociations between default and self-reference networks in the human brain. *NeuroImage*, *55*(1), 225–232.

Willenbockel, V., Sadr, J., Fiset, D., Horne, G. O., Gosselin, F., & Tanaka, J. W. (2010). Controlling low-level image properties: the SHINE toolbox. *Behavior Research Methods*, *42*(3), 671–684.

Yarkoni, T., Poldrack, R. A., Nichols, T. E., Van Essen, D. C., & Wager, T. D. (2011). Large-scale automated synthesis of human functional neuroimaging data. *Nature Methods*, *8*(8), 665–670.