

Yearning for connection? Loneliness is associated with increased ventral striatum activity to close others

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Abstract

Loneliness is a distressing state indicating that one's basic need for social connection is not being met. In an effort to satisfy the need for social connection, loneliness may increase the processing of social cues and desire to connect with others. Yet the neural substrates that contribute to the drive for increased connection in response to loneliness are not known. The ventral striatum (VS), previously shown to increase in response to craving food and other rewarding stimuli, may contribute to "social craving" when one is lonely. That is, the VS may track one's 'hunger' for reconnection much as it tracks hunger for food. To examine this, participants reported on their feelings of loneliness before undergoing an fMRI scan where they viewed cues of potential social reconnection (images of a close other). Consistent with the hypothesis that loneliness stems from an unmet need for connection, loneliness was associated with reduced feelings of connection with the close other. Furthermore, greater reported loneliness was associated with increased VS activity to viewing a close other (*vs* stranger). Results extend the current literature by showing that lonely individuals show increased activity in reward-related regions to their closest loved ones, possibly reflecting an increased desire for social connection.

Key words: social connection; belongingness; satiation; fMRI

Introduction

Since the seminal writings of Robert Weiss on the pervasive, distressing experience of loneliness (Weiss, 1973), social psychologists have been interested in understanding the causes of loneliness and its consequences for socioemotional well-being and physical health. Described as 'a chronic distress without redeeming qualities' (Weiss, 1973), research has linked loneliness with a host of negative health, emotional and cognitive outcomes, including increased mortality risk (Holt-Lunstad *et al.*, 2010), heightened depressive symptoms (Seeman, 2000; Luo *et al.*, 2012), and reduced self-regulation capacities (Baumeister

et al., 2005; DeWall *et al.*, 2008). Moreover, recent estimates suggest that 20% of the U.S. population feels lonely, and that this percentage has been increasing over time (Cacioppo and Patrick, 2008). While the negative impact of loneliness on well-being has been widely documented (Seeman, 1996; Cacioppo *et al.*, 2011), little is known about the neural underpinnings of this toxic state. Thus, the goal of this study was to investigate how loneliness affects neural responses to social information.

Loneliness has been conceptualized as a state indicating that one's basic human need for social connection is not being met (Peplau *et al.*, 1978). As a consequence, loneliness may lead to an enhanced desire for social reconnection and an increased

Received: 18 August 2014; Revised: 13 February 2015; Accepted: 12 June 2015

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attention to social cues (Gardner et al., 2000; Pickett and Gardner, 2005). Hence, greater loneliness has previously been associated with greater recall of social information (Gardner et al., 2005). In addition, participants who underwent social exclusion (*vs* inclusion), which temporarily thwarts social connection needs, reported more interest in making new friends, a greater desire to work with others (Maner et al., 2007), and increased attention to smiling faces over other expressions (DeWall et al., 2009). To the extent that lonely individuals have unmet social connection needs, loneliness may be associated with a yearning for opportunities to affiliate and reconnect with others.

One analogy commonly used to describe loneliness compares the need for social connection to the need for food (Gardner et al., 2000). In the same way that an individual shows enhanced sensitivity to food cues and a greater desire to eat when hungry, individuals may also show enhanced sensitivity to social cues and a greater desire to affiliate when lonely. This analogy may provide useful clues for understanding the brain bases of loneliness.

Borrowing from research on sensitivity to basic rewards, such as food cues, studies have shown that certain basic rewards consistently activate the ventral striatum (VS), a key region within the dopaminergic reward circuit (O'Doherty, 2004; O'Doherty et al., 2000; O'Doherty, et al., 2002). Thus, the VS is sensitive to the anticipation of rewarding outcomes, such as sweet tastes (Knutson and Cooper, 2005; Berridge et al., 2009). In addition, studies have also shown that the magnitude of the VS activity to pleasurable tastes is altered based on whether one is hungry or full. Hence, the VS shows increased activity in response to consuming a pleasurable drink (chocolate milk) for the first time and then a subsequent decrease in activity after participants drink to being full (Kringelbach et al., 2003). A similar PET study found decreases in rCBF in the VS in participants who ate chocolate to satiety (Small et al., 2001). Collectively, these data suggest that hunger or thirst for a rewarding taste increases VS activity and that satiety decreases this same response. To the extent that loneliness indicates that one's social connection needs have not been met and that one is 'hungry' for social connection, loneliness may be associated with increased VS activity to social cues that may signal an opportunity for social reconnection, such as reminders of close others.

Indeed, though not lonely *per se*, individuals who suffer from complicated grief, who continue to yearn or 'hunger' for their lost loved ones for a protracted period of time, show increased activity in the VS (compared with a bereaved sample without complicated grief) to reminders of the deceased (O'Connor et al., 2008). Moreover, self-reported yearning for the loved one correlates positively with VS activity to reminders of the lost loved one. Although individuals with complicated grief are not necessarily lonely, these data suggest that VS activity may track the desire to reconnect when one's belonging needs have not been met.

To date, there has only been one study investigating the neural underpinnings of loneliness. In this study, lonely and non-lonely female participants viewed images from the International Affective Picture System (Lang et al., 1999) of both pleasant and unpleasant social and non-social scenes (Cacioppo et al., 2009). Here, lonely (*vs* non-lonely) participants displayed less, rather than more, VS activity, to the positive social (*vs* positive non-social) images. However, these stimuli were of strangers, leaving the question of how loneliness relates to neural sensitivity to close others unknown. This question may be particularly important because previous behavioral findings suggest that lonely individuals respond differently depending on the possibility of social connection. Thus, although lonely individuals are generally hesitant to socially engage with

others, being primed with the possibility of social acceptance leads to increased affiliative behavior and efforts at social affiliation (mimicking a confederate) among those who are lonely *vs* not lonely (Lucas et al., 2010). Furthermore, recent findings suggest that the VS response to potential rewarding outcomes is modulated by motivational relevance (Fitzgerald et al., 2009). Hence, to the extent that a close other is a sign of possible connection and to the extent that the VS is more sensitive to cues of social connection as a function of a greater motivation for connection, loneliness may be associated with increased, rather than decreased, VS activity to close others.

To address this possibility, this study examined the association between loneliness and reward-related activity to images of close others (*vs* strangers). Based on its role in reward anticipation, sensory-specific satiety, and close social relationships (Aron et al., 2005; Strathearn et al., 2008; Acevedo et al., 2011; Inagaki and Eisenberger, 2013), analyses focused on the VS. Following the premise that loneliness stems from a felt lack of social connection and intimacy with one's closest friends (Williams and Solano, 1983), it was hypothesized that greater loneliness would be associated with reduced feelings of connection with the close other. Second, greater loneliness was hypothesized to be associated with greater activity in the VS in response to viewing images of close others (*vs* strangers).

Materials and methods

Participants

Thirty-one participants (15 females, *M* age = 24.26, *s.d.* = 7.57) completed this study as part of a larger study examining the effect of inflammation on social processes (Moiens et al., 2015). All participants reported on here were taken from the placebo group (and included only those who completed the picture viewing task used here) so that the effects reported here were not influenced by changes in inflammatory activity. During an initial screening interview, participants were evaluated for MRI contraindications (metal in their bodies, claustrophobia), willingness to provide digital photographs for the scanner task (see details below) and right-handedness. The self-reported ethnicity of the final sample was 35.5% Asian/Pacific Islander, 41.9% Caucasian, 16.1% Latino and 6.5% other. Procedures were run in accordance with IRB guidelines.

Close other stimuli

Before coming in for their scheduled experimental session, participants were asked to send two digital photographs of a person they felt close to. Participants were instructed to send pictures of 'a person they could go to for help or for comfort such as a family member, a close friend or significant other'. Images provided by participants were converted to grayscale, and then resized to fit the same standard space for presentation through the scanner's MRI-compatible goggles.

Loneliness

Trait loneliness was measured before the scan using the Revised UCLA Loneliness Scale (Russell, 1996), a well-validated measure of general feelings of loneliness (*M* = 44.23, *s.d.* = 8.68, range = 33–69). Ratings were made for the 20 individual questions on a 1–4 scale anchored by 'never' and 'always.' Example questions include 'How often do you feel that you are "in tune" with the people around you?', 'How often do you feel alone?' and 'How often do you feel that no one really knows you well?'

Feelings of social connection

Participants rated how connected they felt with their close other using the following questions: ‘How much of a comfort do you find this person to be?’; ‘How much do they really care about you?’; ‘How much do they understand the way you feel about things?’; ‘How much can you rely on them for help if you have a serious problem?’; ‘How much do you open up to them if you need to talk about your worries?’ (Saphire-Bernstein and Taylor, 2013). In addition, participants responded to ‘How close to this person are you?’ The six items were combined into a single measure to assess feelings of connection with the close other ($\alpha = 0.93$). Ratings were made on a 1–7 scale anchored by ‘not at all’ and ‘a lot.’ As expected, feelings of connection with the close other were high ($M = 6.52$, $s.d. = 0.42$). Two data points were removed so that no data points were more than three standard deviations below the average ratings for this sample. In addition, ratings were mistakenly not taken for one participant and so the final sample used to evaluate feelings of connection with the close other was based on data from 28 participants.

fMRI paradigm

To assess VS activity to the close other, a standard imaging task modified from previously published studies on close social relationships was used (Aron et al., 2005; Acevedo et al., 2011). During the task, participants viewed images of their close other during some blocks and images of a gender, race and age-matched stranger during other blocks. In between these blocks, participants performed blocks of serial subtraction (e.g. count back by 7’s from 1753), in which they were asked to simply ‘count backwards silently in your head.’ This control condition was taken from prior work using a similar experimental paradigm (Aron et al., 2005) in order to reduce carryover effects from viewing a close other (i.e. reduce continued thoughts about the close other or feelings that might arise from viewing an image of them). A total of eight 12-s blocks separated by a 1-s fixation crosshair were presented with four blocks each for the close other and the stranger and eight blocks of serial subtraction.

fMRI data acquisition and data analyses

Imaging data were acquired at UCLA’s Staglin IMHRO Center for Cognitive Neuroscience on a Siemens 3 Tesla ‘Tim Trio’ MRI scanner. To reduce head movement, foam padding was placed around participants’ heads. A high-resolution T2*-weighted echo-planar imaging volume (spin-echo, $TR = 5000$ ms; $TE = 33$ ms; matrix size 128×128 ; 36 axial slices; $FOV = 20$ cm; 3-mm thick, skip 1 mm) and T2-weighted, matched-bandwidth anatomical scan (slice thickness = 3 mm, gap = 1 mm, 36 slices, $TR = 5000$ ms, $TE = 34$ ms, flip angle = 90° , matrix = 128×128 , $FOV = 20$ cm) were acquired for each participant followed by a single functional scan, lasting 3 min, 42 s (echo planar T2* weighted gradient-echo, $TR = 2000$ ms, $TE = 25$ ms, flip angle = 90° , matrix size 64×64 , 36 axial slices, $FOV = 20$ cm; 3 mm thick, skip 1 mm).

Data were preprocessed using the DARTEL procedure in SPM8 (Wellcome Department of Cognitive Neurology, Institute of Neurology, London, UK). Next, first-level effects were estimated using the general linear model to investigate neural activity to each of the image types (close other and stranger) compared with blocks of serial subtraction. Random effects analyses of the group were then computed using the first-level contrast images for each participant.

Statistical analyses

To examine whether greater loneliness was associated with reduced feelings of connection with the close other presented during the scanning session, we ran a correlation in SPSS (SPSS 16.0, Chicago, IL) between scores on the UCLA Loneliness Scale and our measure of feelings of connection with the close other.

To examine how loneliness was related to neural activity to viewing images of close others and strangers, region of interest (ROI) analyses were conducted using the *a priori* hypothesized region, the VS. The VS ROI was structurally defined by combining the left and right caudate and putamen from the Automated Anatomical Labeling Atlas (Tzourio-Mazoyer et al., 2002) and then constraining the regions at $-10 < x < 10$, $4 < y < 18$, $-12 < z < 0$. Parameter estimates from the VS ROI were entered into SPSS. To evaluate the relationship between loneliness and VS activity to friends vs strangers, a repeated-measures ANOVA was conducted with target (close other, stranger) entered as the within-subjects factors and loneliness entered as the between-subjects covariate. This allowed us to examine the main effects of target and loneliness as well as the interaction between loneliness and target on VS activity ($P < 0.05$, two-tailed). The interaction between loneliness and target was further interrogated to examine the direction of the effects. A single outlier (more than three standard deviations above the mean) was removed from the ROI data leaving a final imaging sample of 30 participants.

Results

Behavioral results

To assess whether loneliness was associated with self-reported feelings of connection with the close other, a correlation between loneliness and feelings of connection was run. In support of the hypothesis that lonely individuals feel less connected to their close others, those who reported feeling more lonely also reported lower feelings of connection with the close other ($r = -.48$, $P < 0.05$, Figure 1).

Neuroimaging results

We first examined whether neural activity from the anatomical VS ROI was greater in response to viewing the close other vs the

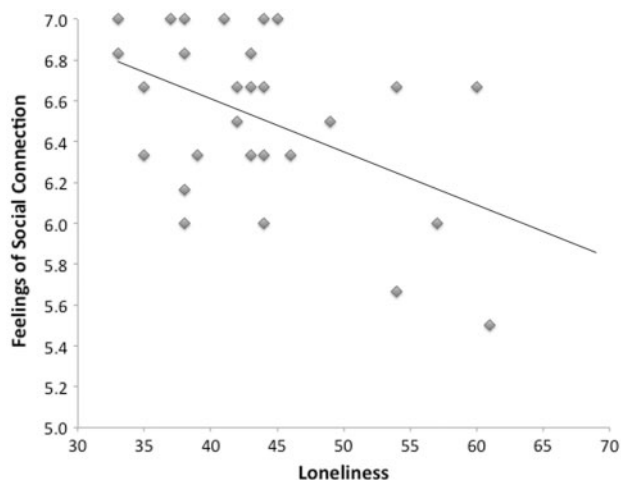


Fig. 1. Association between loneliness and feelings of connection with the close other. More self-reported loneliness, as measured by the UCLA Loneliness scale, was associated with lower feelings of connection.

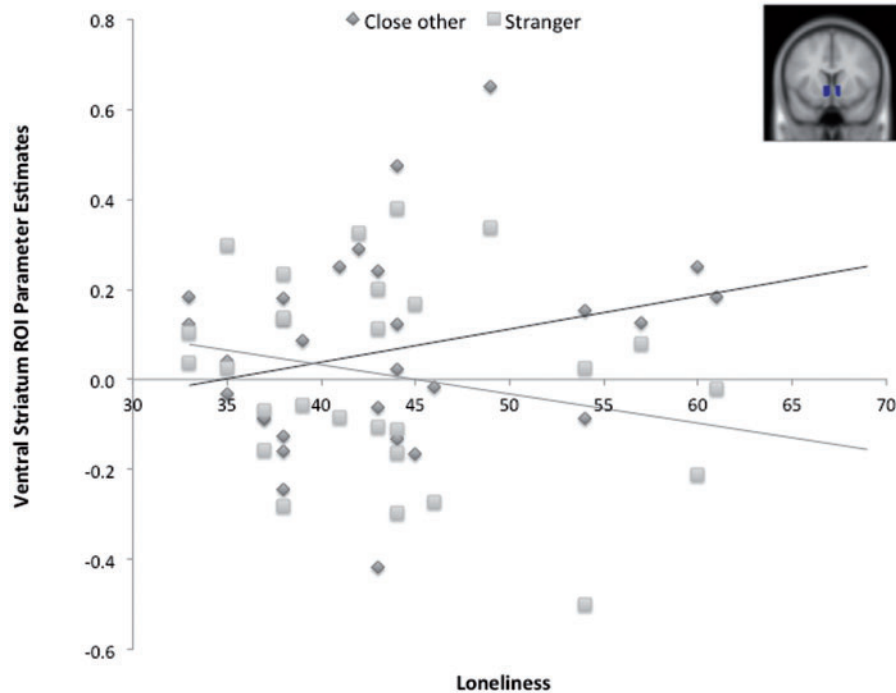


Fig. 2. There was a significant interaction between loneliness and target (close other, stranger) on VS activity. At +1 s.d. above the mean of loneliness, individuals showed greater VS activity to images of close others vs. strangers; at -1 s.d. below the mean of loneliness, there were no differences in VS activity to close others vs strangers.

stranger (irrespective of levels of loneliness). Consistent with prior work (Acevedo et al., 2011), there was a main effect of target with participants displaying greater VS activity to viewing the close other (*vs* serial subtraction; $M = 0.06$, $s.d. = 0.22$) compared with viewing the stranger (*vs* serial subtraction; $M = 0.01$, $s.d. = 0.22$, $F(1, 26) = 5.04$, $P = 0.03$). There was no main effect of loneliness on VS activity ($F(1, 26) = 0.01$, $P = 0.94$). Importantly, and as predicted, there was a significant interaction between target and loneliness ($F(1, 26) = 6.43$, $P = 0.02$).

To further examine this significant interaction, we examined mean differences in VS response to the targets (close others and strangers) at 1 s.d. above and below the mean of loneliness. At higher levels of loneliness (+1 s.d. from the mean), there was greater VS activity to close others compared to strangers ($F(1, 26) = 7.35$, $P = 0.01$). However, at lower levels of loneliness (-1 s.d. from the mean), there was no significant difference between VS activity to the close others compared to strangers ($F(1, 26) = .85$, $P = 0.37$).

As an additional way to understand the simple effects, we also examined correlations between loneliness scores and VS activity to close others and strangers separately. These analyses (though not statistically significant) showed a consistent pattern as that reported above: loneliness was positively associated with VS activity to viewing close others (*vs* serial subtraction, $r = 0.26$, $P = 0.12$, Figure 2), while loneliness was negatively associated with VS activity to viewing strangers (*vs* serial subtraction, $r = -0.23$, $P = 0.24$; consistent with Cacioppo et al., 2009).¹

1 Feelings of connection were not related to VS activity to viewing images of a close other (*vs* serial subtraction, $r = 0.07$, ns).

Discussion

To our knowledge, this is the first study to examine the associations between loneliness, feelings of connection with a specific close other and neural activity in response to images of a close other and a stranger. Greater feelings of loneliness were associated with lower feelings of connection with the close other and greater neural activity in the VS, a key region within the reward circuit, when individuals viewed images of a close other. Together, these results are in line with previous research suggesting that threats to social belonging, such as rejection or feeling lonely, result in increased sensitivity to social cues and an increased desire to reconnect with others (Gardner et al., 2000, 2005; Pickett and Gardner, 2005; Maner et al., 2007). Data from this study extend this prior work to suggest that reminders of close others (compared with strangers) may be particularly salient to lonely individuals, perhaps because they are lacking in support from or intimacy with their close others.

Data from this study are consistent with theories hypothesizing that social connection is a basic need that operates in much the same way as other fundamental drives, like hunger and thirst (Baumeister and Leary, 1995). For example, prior research has shown that while there is initially substantial VS activity to palatable foods such as chocolate (Small et al., 2001; Kringelbach et al., 2003), as individuals consume the food beyond satiety, VS activity diminishes, as presumably the food that was once enjoyable is no longer as rewarding because the person is no longer hungry. Data from this study suggest that social relationships may operate in much the same way: Lonely individuals may be 'starving' or 'thirsting' for social connection, and this state may be associated with enhanced reward-related neural activity to cues of potential connection, while non-lonely people may be 'socially satiated' which may not be associated with the same level of VS activity to reminders of connection.

However, the interpretation that VS activity reflects a heightened desire to reconnect with others should be interpreted with caution until future research can more directly examine this possibility. For instance, future research could deprive individuals of social contact for a period of time and examine their reward-related neural activity to cues of possible social connection. To the extent that being 'socially starved' is a major component of feeling lonely, depriving individuals of social contact may lead to increased reward activity to cues of social connection compared with individuals who have recently had the opportunity to interact with others.

The current results complement and extend the prior neuroimaging study on loneliness (Cacioppo et al., 2009). Hence, while our main finding was that lonely individuals showed greater VS activity to images of close others vs strangers, this effect seemed to be partly due to loneliness being associated with less VS activity to images of strangers, as found previously (Cacioppo et al., 2009), as well as loneliness being associated with greater VS activity to close others, a new finding demonstrated here. One explanation for this differential pattern to close others vs strangers is that lonely individuals may not interpret strangers as possible targets for social connection, but rather as targets that may invite additional feelings of alienation or rejection (Lucas et al., 2010). Close others, on the other hand, may be viewed as more likely to be accepting and thus a target for social connection. Thus, the current results suggest that loneliness may be associated with differential patterns of neural activity depending upon if the individual is exposed to general cues of pleasant social interaction, or reminders of close others within their existing social network with whom they feel close and can potentially interact with at a later time, as studied here.

It is also interesting to note that in this study, overall feelings of connection were high (as indicated by near ceiling levels on this measure, $M = 6.52$ on a scale of 1–7). Nonetheless, variability in loneliness was negatively correlated with feelings of connection. Data such as these represent one of the hallmarks of loneliness; namely, that rather than lonely individuals lacking close relationships, they instead feel less connected and satisfied in these relationships (Williams and Solano, 1983; Russell et al., 1984; Hawkey et al., 2003). It may be that when it comes to close others, loneliness may be even more heightened by one's inability to feel socially connected to those with whom one frequently interacts. However, due to the correlational nature of the current findings, it is unclear whether low feelings of connection are a risk factor for loneliness or a consequence of feeling lonely.

In conclusion, this study found an association between feelings of loneliness and VS activity to close others providing evidence for the possibility that lonely individuals may show a greater yearning for their close others, perhaps because their need for social connection is not being fulfilled. These results contribute to an existing understanding of the neural correlates of loneliness to suggest that loneliness is associated with a 'hunger' for satisfactory social connection particularly with one's closest loved ones.

Acknowledgements

With appreciation, the authors thank the Staglin IMHRO Center for Cognitive Neuroscience, the UCLA Clinical and Translational Science Institute (CTSI: UL1TR000124), and the participants and close others who contributed to making this work possible. We also thank two anonymous reviewers for their helpful comments on the article.

Funding

National Institutes of Health R01-MH091352 awarded to N.I.E. [R01-AG034588; R01-AG026364, R01 CA160245-01, R01-CA119159; R01 HL095799, R01 DA032922-01, P30-AG028748] awarded to M.R.I.; and the Cousins Center for Psychoneuroimmunology.

Conflict of interest. None declared.

References

- Acevedo, B.P., Aron, A., Fisher, H.E., Brown, L.L. (2011). Neural correlates of long-term intense romantic love. *Social Cognitive and Affective Neuroscience*, 7, 145–59.
- Aron, A., Fisher, H., Mashek, D., et al. (2005). Reward, motivation and emotion systems associated with early-stage intense romantic love. *Journal of Neurophysiology*, 93, 327–37.
- Baumeister, R.F., Leary, M.R. (1995). The need to belong: desire for interpersonal attachments as a fundamental human motive. *Psychological Bulletin*, 117, 497–29.
- Baumeister, R.F., DeWall, C.N., Ciarocco, N.J., et al. (2005). Social exclusion impairs self-regulation. *Journal of Personality and Social Psychology*, 88, 589–604.
- Berridge, K.C., Robinson, T.E., Aldridge, J.W. (2009). Dissecting components of reward: 'liking', 'wanting', and learning. *Current Opinion in Pharmacology*, 9, 65–73.
- Cacioppo, J.T., Patrick, B. (2008). *Loneliness: Human Nature and the Need for Social Connection*. New York: W. W. Norton & Company.
- Cacioppo, J.T., Hawkey, L.C., Norman, G.J., et al. (2011). Social isolation. *Annals of the New York Academy of Sciences*, 1231, 17–22.
- Cacioppo, J.T., Norris, C.J., Decety, J., et al. (2009). In the eye of the beholder: individual differences in perceived social isolation predict regional brain activation to social stimuli. *Journal of Cognitive Neuroscience*, 21, 83–92.
- 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, 1367–82.
- DeWall, C.N., Maner, J.K., Rouby, D.A. (2009). Social exclusion and early-stage interpersonal perception: selective attention to signs of acceptance following social exclusion. *Journal of Personality and Social Psychology*, 96, 729–41.
- Fitzgerald, T.H.B., Seymour, B., Dolan, R.J. (2009). The role of the human orbitofrontal cortex in value comparison for incommensurable objects. *The Journal of Neuroscience*, 29, 8388–95.
- 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 and Social Psychology Bulletin*, 26, 486–96.
- Gardner, W.L., Pickett, C.L., Jefferis, V., et al. (2005). On the outside looking in: loneliness and social monitoring. *Personality and Social Psychology Bulletin*, 31, 1549–60.
- Hawkey, L.C., Burleson, M.H., Berntson, G.G., et al. (2003). Loneliness in everyday life: cardiovascular activity, psychosocial context, and health behaviors. *Journal of Personality and Social Psychology*, 85, 105–20.
- Holt-Lundstad, J., Smith, T.B., Layton, J.B. (2010). Social relationships and mortality risk: a meta-analytic review. *PLoS Medicine*, 7, e1000316.
- Inagaki, T.K., Eisenberger, N.I. (2013). Shared neural mechanisms underlying "social warmth" and physical warmth. *Psychological Science*, 24, 2272–80.

- Knutson, B., Cooper, J.C. (2005). Functional magnetic resonance imaging of reward prediction. *Current Opinion in Neurology*, **18**, 411–7.
- Kringelbach, M.L., O'Doherty, J., Rolls, E.T., & Andrews, C. (2003). Activation of the human orbitofrontal cortex to a liquid food stimulus is correlated with its subjective pleasantness. *Cerebral Cortex*, **13**, 1064–71.
- Lang, P.J., Bradley, M.M., Cuthbert, B.N. (1999). *International Affective Picture System (IAPS): Instruction Manual and Affective Ratings*. Gainesville: University of Florida, The Center for Research in Psychophysiology.
- Lucas, G.M., Knowles, M.L., Gardner, W.L., et al. (2010). Increasing social engagement among lonely individuals: the role of acceptance cues and promotion motivations. *Personality and Social Psychology Bulletin*, **36**, 1346–59.
- Luo, Y., Hawkey, L.C., Waite, L.J., et al. (2012). Loneliness, health, and mortality in old age: a national longitudinal study. *Social Science Medicine*, **74**, 907–14.
- Maner, J.K., DeWall, C.N., Baumeister, R.F., et al. (2007). Does social exclusion motivate withdrawal or reconnection? Resolving the 'porcupine problem.'. *Journal of Personality and Social Psychology*, **92**, 42–55.
- Moieni, M., Irwin, M.R., Jevtic, I., et al. (2015). Sex differences in depressive and socioemotional responses to an inflammatory challenge: implications for sex differences in depression. *Neuropsychopharmacology*, **40**(7), 1709–16.
- O'Connor, M.F., Wellisch, D.K., Stanton, A.L., et al. (2008). Craving love? Enduring grief activates brain's reward center. *NeuroImage*, **42**, 969–72.
- O'Doherty, J.P. (2004). Reward representations and reward-related learning in the human brain: insights from neuroimaging. *Current Opinion in Neurobiology*, **14**, 769–76.
- O'Doherty, J.P., Deichman, R., Critchley, H.D., et al. (2002). Neural responses during anticipation of primary taste reward. *Neuron*, **33**, 815–26.
- O'Doherty, J.P., Rolls, E.T., Francis, S., et al. (2000). Sensory-specific satiety-related olfactory activation of the human orbitofrontal cortex. *Neuroreport*, **11**, 893–7.
- Peplau, L.A., Russell, D., Heim, M. (1978). Loneliness: a bibliography of research and theory. *JSAS Catalog of Selected Documents in Psychology*, **8**, 38.
- Pickett, C.L., Gardner, W.L. (2005). The social monitoring system: enhanced sensitivity to social cues as an adaptive response to social exclusion. In: Williams, K., Forgas, J., von Hippel, W., editors, *The Social Outcast: Ostracism, Social Exclusion, Rejection, and Bullying*. New York: Psychology Press.
- Russell, D.W. (1996). UCLA loneliness scale (version 3): reliability, validity, and factor structure. *Journal of Personality Assessment*, **66**, 20–40.
- Russell, D., Cutrona, C.E., Rose, J., et al. (1984). Social and emotional loneliness: an examination of Weiss's typology of loneliness. *Journal of Personality & Social Psychology*, **46**, 1313–21.
- Saphire-Bernstein, S., Taylor, S.E. (2013). Relationships and well-being. In: Boniwell, I., David, S., editors, *Oxford Handbook of Happiness*. London: Oxford University Press, 821–33.
- Seeman, T.E. (1996). Social ties and health: the benefits of social integration. *Annals of Epidemiology*, **6**, 442–51.
- Seeman, T.E. (2000). Health promoting effects of friends and family on health outcomes in older adults. *American Journal of Health Promotion*, **14**, 362–70.
- Small, D.M., Zatorre, R.J., Dagher, A., et al. (2001). Changes in brain activity related to eating chocolate: from pleasure to aversion. *Brain*, **124**, 1720–33.
- Strathearn, L., Li, J., Fonagy, P., et al. (2008). What's in a smile? Maternal brain responses to infant facial cues. *Pediatrics*, **122**, 40–51.
- Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., et al. (2002). Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. *Neuroimage*, **15**, 273–89.
- Weiss, R.S. (1973). *Loneliness: The Experience of Emotional and Social Isolation*. Cambridge: The MIT Press.
- Williams, J.G., Solano, C.H. (1983). The social reality of feeling lonely: friendship and reciprocation. *Personality and Social Psychology Bulletin*, **9**, 237–42.