

Review

Characterizing the mechanisms of social connection

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SUMMARY

Understanding how individuals form and maintain strong social networks has emerged as a significant public health priority as a result of the increased focus on the epidemic of loneliness and the myriad protective benefits conferred by social connection. In this review, we highlight the psychological and neural mechanisms that enable us to connect with others, which in turn help buffer against the consequences of stress and isolation. Central to this process is the experience of rewards derived from positive social interactions, which encourage the sharing of perspectives and preferences that unite individuals. Sharing affective states with others helps us to align our understanding of the world with another's, thereby continuing to reinforce bonds and strengthen relationships. These psychological processes depend on neural systems supporting reward and social cognitive function. Lastly, we also consider limitations associated with pursuing healthy social connections and outline potential avenues of future research.

INTRODUCTION

In the early part of 2020, the world was permanently changed by the COVID-19 pandemic. Amid the initial uncertainty of how to handle treatment for the disease, the focus turned to efforts to decrease transmission. Such approaches included promoting social distancing measures ranging from ensuring a certain physical distance from others in public to full-on isolation and quarantine. Although aimed at preventing the spread of disease and death, one of the unfortunate consequences of these health safety measures was a prolonged increase in social isolation, which had several negative impacts on mental health, including fostering maladaptive behaviors. For example, anxiety-related disorders and substance use (e.g., drugs, alcohol) were exacerbated during the pandemic, the long-term effects of which remain unknown.^{1–3} Importantly, *perceived social connection* can alleviate stress and negative affect,⁴ and recent reports suggest that stronger perceived social connections may have contributed to some resilience against pandemic-induced social isolation.⁵ Thus, there is a growing sentiment emphasizing social connection as a public health priority, given multi-disciplinary efforts highlighting the importance of strong social bonds in mitigating the adverse consequences of social isolation and stress.^{4,6} However, outstanding questions remain regarding the psychological and neural mechanisms through which we form and maintain connections and how these mechanisms may promote resilience or, in some cases, maladaptive behavior in the face of adversity.

As humans, we spend an extraordinary amount of time navigating a complex social world in which we need to learn about others, establish and strengthen relationships, and reduce uncertainty about future interactions. The outcomes of these efforts can be *socially rewarding*, aid in satisfying needs of belonging-

ness, and ultimately promote positive physical, mental, and emotional well-being. This is a particularly important topic given that (1) the advent of social media offers the opportunity to be instantaneously connected with (and isolated from) others in novel ways and that (2) the COVID-19 pandemic placed significant strains on our abilities to spend time with others, with consequences to well-being that are still emerging. Although extensive work across social psychology, health psychology, and neuroscience has underscored the importance of social connection, a unifying perspective regarding the neurobehavioral mechanisms has only more recently begun to come into focus. Here, we highlight the idea that the rewards afforded by positive social interactions foster the ability to share perspectives and preferences, which in turn encourages connection with others and promotes well-being.

We focus on three neural and psychological processes that are commonly involved in social connection (Figure 1): (1) stress-related responses, (2) reward and motivational systems, and (3) social cognitive processes. We first consider the detrimental impacts of social isolation on brain function and behavior, where a significant lack of social contact can impact stress-related mechanisms and reward-seeking behaviors. Through the lens of isolation, we highlight the potency of the desire to connect with others and how feeling connected can benefit well-being. Specifically, we underscore the role of the brain's reward system in processing the motivational aspect of social rewards and helping to build resilience in the face of stress.

We then examine the psychological and neural mechanisms that foster the formation and maintenance of social connections. We expand on the motivational need to pursue social goals and examine how the brain's reward system and regions supporting higher social cognitive processes, such as effectively using theory of mind, interact to help build healthy social relationships. We



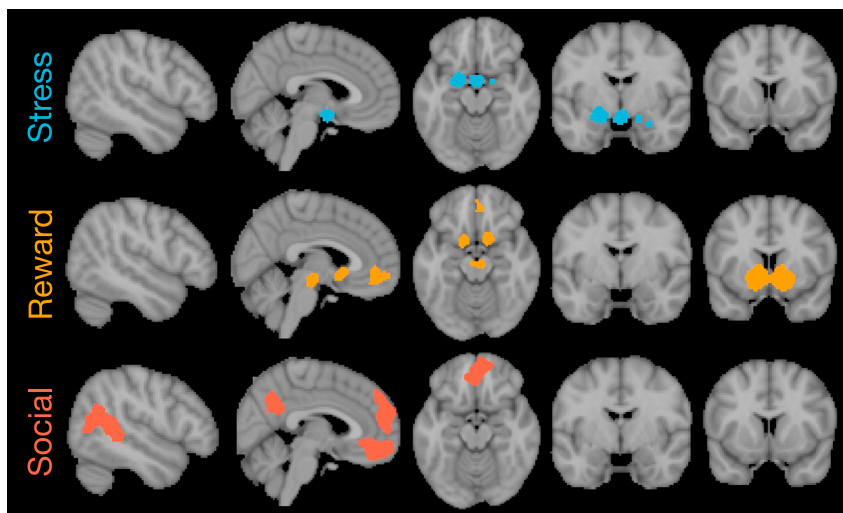


Figure 1. Neural circuitry implicated in social connection

In this figure, we depict three brain networks that are commonly observed in studies of loneliness, isolation, and social connection. These meta-analytic reverse-inference maps created by Neurosynth⁷ reflect regions that are implied by papers that frequently mention stress (e.g., amygdala, hypothalamus), reward (e.g., striatum, ventromedial prefrontal cortex), and social (e.g., medial prefrontal cortex, temporoparietal junction) keywords across 14,371 studies. These maps are thresholded reverse-inference association tests corrected for multiple comparisons using false discovery rate (FDR) $q < 0.01$ and smoothed using a 4 mm full width at half maximum (FWHM) Gaussian kernel.

focus on the hypothesis that individuals compare interpretations of the same experienced events and experience reinforcing signals as a function of the degree of alignment in those interpretations, which in turn allows for the strengthening of a social connection.

Finally, we conclude by acknowledging some of the various complexities associated with connecting with others—for instance, how certain shared interpretations can lead to problematic social connections that promote maladaptive behaviors (i.e., risk-seeking)—and outline noteworthy areas for future research.

THE SOCIAL BRAIN UNDER ISOLATION

Social isolation and loneliness pose significant risk factors for health, including early mortality.^{8–10} This vital research on the negative effects of being socially isolated led the World Health Organization to declare loneliness a major health concern in 2019¹¹ and the U.S. Surgeon General to release an advisory denouncing the “epidemic of loneliness” in the United States of America in 2023.¹² Social engagement tracked over the last 20 years in the United States shows a downward trend, with time spent in person with others significantly decreasing for young people in particular.¹³ This effect was exacerbated by COVID-19, where a 16% decrease in network size and an accompanying increase in loneliness was observed when compared with a similar time period pre-COVID (June 2020 and June 2019, respectively¹⁴). Further, perceived social isolation can lead to a vicious cycle of poor decisions, from avoiding future social contact to increasing substance use¹⁵ that can damage one’s health and social relationships, ultimately promoting further isolation and higher rates of early mortality.⁹

Across species, insufficient social contact for prolonged time periods has been associated with the development of cognitive deficits and diminished resilience to stress,¹¹ with alterations in structural and functional brain processes observed during chronic isolation that are highly detrimental to one’s health.⁸ This is exemplified by studies in rodents on the effects of isola-

tion on stress-related mechanisms. For instance, acute periods of social isolation (i.e., under a week) elicit stress responses similar to exposure to an acute physiological stressor, engaging activation of the hypothalamic-pituitary-adrenal (HPA) axis and increasing cortisol levels.¹⁶ Notably, longer or more chronic isolation fosters a dysregulated HPA axis response that precedes maladaptive long-term changes.¹⁷ This process parallels deficits that emerge as a consequence of early life adversity in humans, including altered social and emotional regulation¹⁸ and reward processing,¹⁹ marked by excessive HPA-related chronic stress responses early in development leading to diminished reward sensitivity and neural responses in brain regions such as the striatum.²⁰

Research on acute social isolation collectively highlights a homeostatic need for social contact that may be modulated by reward-related processes and dopamine more specifically.¹⁶ Indeed, isolation can lead to effects akin to other forms of reward deprivation, promoting reward-seeking behaviors. For instance, mice seek novel social interactions following a period of 24-h isolation, a phenomenon associated with increased activity in dopaminergic neurons in the dorsal raphe nucleus.²¹ Optogenetic activation of GABAergic neurons in the amygdala of mice has also been found to drive dopaminergic release in the ventral striatum and promote more affiliative behaviors such as increasing volitional decisions to seek interaction with novel conspecifics in mice.²² Finally, a novel investigation in humans demonstrated that a period of 10-h social isolation led to increases in social “craving” following presentation of socially conditioned cues, much like food craving after fasting.²³ Interestingly, participants’ self-reports of craving for food and social contact correlated with activation of dopaminergic midbrain regions, consistent with reports in mice.^{21,22}

Taken together, these findings raise the intriguing idea that negative affect experienced by acute deprivation of social stimulation leads to a behavioral coping response of increased affiliative behaviors and motivation to connect.^{24,25} Importantly, the effects of social isolation on subsequent social behavior are more complex and differ based on length of isolation. Exposure to more *acute* forms of social isolation tends to *promote* prosocial behaviors that foster social interactions, while longer, *chronic* social isolation is associated with more *anti-social*

behaviors.¹⁶ Chronic isolation in rodents, for example, is marked by an increase in behaviors such as aggression²⁶ and social avoidance, as expressed by diminished time spent in the presence of a conspecific.²⁷ Similar findings are observed in humans, marked by a tendency to engage in social withdrawal when experiencing loneliness.²⁸ Further, individuals who self-report increased levels of loneliness can show a diminished motivation to engage in prosocial behaviors.²⁹

Loneliness has also been shown to be associated with alterations in structural and functional neural connectivity. In particular, associations have been observed between self-reported loneliness and regions involved in stress-related responding (e.g., prefrontal cortex, amygdala, and hippocampus)³⁰ and within networks including the default mode network (DMN).^{31,32} Although the DMN has traditionally been viewed as a task-negative network (i.e., showing robust connectivity at rest and deactivating during task³³), a large body of evidence implicates this network in directing attention, monitoring environmental change, and priming individuals for self-referential processing and social thought.^{34–37} As such, recent investigations using notably large cohorts (e.g., over 3,000 individuals) have highlighted associations between decreased white matter volume and higher loneliness scores,³⁸ increased connectivity within the DMN and trait loneliness scores, and larger gray matter volume in structures comprising the DMN network.³² Given the prominent role of the DMN in social cognition,^{35,37} a speculative idea raised by Spreng and colleagues³² posited that DMN involvement in lonely individuals may be due to episodic simulation of social interactions. Interestingly, a high level of subjective loneliness is also associated with lower pattern similarity within the DMN among individuals when watching the same videos.³⁹ This is noteworthy as non-lonely individuals typically show similar neural responses when watching videos,⁴⁰ and the dissimilarity in lonely individuals may suggest a diminished sense of being understood by others or experiencing a sense of mutual understanding essential for social connection.

THE INHERENT REWARD OF SOCIAL CONNECTION

The behavioral and physiological issues associated with social isolation underscore the importance of connecting with others and maintaining healthy social bonds. Indeed, the importance of positive social experiences across the lifespan is well established.^{4,41–43} Simply seeing a smile from a parent or peer,^{44,45} or receiving a verbal sign of approval^{46,47} can provide feelings of safety and acceptance,⁴⁸ thereby fulfilling basic homeostatic needs of belongingness and affiliation.⁴⁹ Such positive social signals are the building blocks of relationships and carry social reward value.^{50–52}

Social rewards are reliably processed by corticostriatal circuits similar to primary and secondary rewards such as food or money.^{53–55} For example, overlapping and distinct subregions of the human striatum process monetary and social rewards (e.g., approval from others^{56–58}), and posterior regions of the ventromedial prefrontal cortex (vmPFC) represent a common neural currency for monetary and social rewards.^{58,59} In animals, similar engagement of reward-related circuitry is observed for social reward processing. Increases in dopaminergic release in

the ventral striatum are observed during approach behavior toward both non-social (e.g., food) and social (e.g., conspecific) rewards.^{60–63} Orbitofrontal neurons in non-human primates also respond to social images and rewards that are modulated by social context during social interactions.^{64,65}

The inherent value of social rewards, and in particular social interaction with others, motivates an organism toward social reward-seeking. One potential mechanism that facilitates this is the activation of dopamine neurons during social interactions, which has been found to be increased in the ventral tegmental area (VTA)⁶⁶ and released in the nucleus accumbens⁶⁷ during interactions with rodent conspecifics. Accordingly, human fMRI studies have repeatedly shown activation of the striatum in paradigms where a rewarding social interaction occurs, such as cooperative games,^{68,69} especially if the interaction involves an existing social bond as it represents an opportunity to further strengthen such connection.^{50,70} This rewarding value of social interactions is also captured in our memory. When comparing positive, non-social experiences (e.g., receiving a good grade) with positive social experiences (e.g., celebrating with friends), individuals are (1) more likely to choose to reminisce about positive social interactions with close others, (2) willing to pay more to relive a past positive social memory, and (3) recruiting striatal neural circuits when recalling such memories.⁷¹ Additionally, positive memories of prior social interactions with close others have been shown to impact decisions to pursue further connection with such individuals.⁷²

The reinforcing value of social connection can also have positive influences on decision-making. One example is prosocial decisions or actions that have benefits to others (e.g., donations), which can increase positive feelings in the actor and foster connection more broadly.⁷³ Greater tendency to engage in prosocial behaviors during the pandemic, for example, correlated with decreased subjective measures of loneliness.⁷⁴ Interestingly, the neuropeptide hormone oxytocin, which is well known for its role in social behaviors and social bonding^{75,76} plays a critical role in the reinforcement of social interactions that stimulate prosocial behaviors, particularly given its projections to reward-related regions.^{77,78} Oxytocin neurons in the paraventricular nucleus of the hypothalamus are activated during social interactions in mice, increasing dopaminergic activity in the VTA, and, in turn, increasing prosocial behaviors.⁷⁹ In humans, oxytocin administration has been associated with increasing tendencies to pursue social outcomes (e.g., showing trust in novel partners)⁸⁰ and altruistic behaviors,⁸¹ although the role of oxytocin in human prosocial actions is far more complex given individual differences and environmental context.^{76,82} Taken together, these studies highlight the rewarding mechanisms that underlie social connection and influence behavior.

SOCIAL CONNECTION BUFFERS STRESS AND PROMOTES WELL-BEING

The reinforcing value of social connection has significant implications for an organism's well-being, conferring protective factors that boost survival odds by 50%.⁸³ A prominent benefit of strong social connections is that they foster resilience in individuals across the lifespan,⁸⁴ particularly by buffering against the

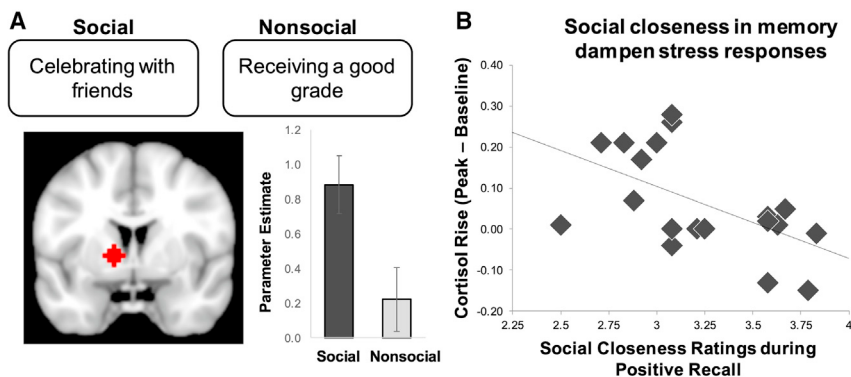


Figure 2. Social memories and reward-related neural circuitry

(A) Recalling positive memories that elicit the same subjective positive feeling yet differ in terms of level of social context inherent in the memory recruits reward-related neural activity. Responses in the striatum as measured by fMRI during memory recall are greater for more social memories (e.g., celebrating with friends) compared with non-social memories (e.g., receiving a good grade). (B) Increased social closeness during positive memory recall correlates with dampening of salivary cortisol following acute stress exposure. Figure adapted from Speer and Delgado.⁷¹

deleterious effects of stress.⁴ Indeed, physiological responses to an acute stressor can be diminished by the perceived presence of social support, depicted by holding one's hand,⁸⁵ an image of a social support figure,⁸⁶ or even a supportive note from a peer.⁸⁷ This is also observed in naturalistic settings across species where affiliative behaviors between wild female baboons helps alleviate stress and are linked with decreased cortisol responses⁸⁸ and life longevity.⁸⁹

Although immediate social support can buffer feelings of acute stress in the moment,^{90–92} social connections can also foster resilience and well-being more broadly through other cognitive processes. Representations of positive experiences with members of our social networks can be evoked by recalling positive memories shared with close others, which in turn elicits positive emotional feelings and recruits activation in reward-related areas such as the striatum (Figure 2A).⁷¹ Reminiscing about the positive past can dampen physiological responses (e.g., cortisol levels) to acute stressors,⁹³ an effect that is amplified when those memories involve close others (Figure 2B).⁷¹ Such results, combined with the observation that nostalgia is a mechanism that can help foster social connection,^{94,95} highlight how social memories create a powerful method for sustaining the benefits of social connection.

The protective benefits of social connection are observed across the lifespan. Early in development, parental presence and actions serve as a key emotion-regulatory mechanism to alleviate stress and diminish threat, a phenomenon referred to as social buffering.^{96,97} For instance, HPA activity is suppressed in rodent pups by the presence of the mother or parental cues.⁹⁸ Research with preschool-aged children parallels these findings, with children more likely to engage with aversively conditioned stimuli when conditioned in the presence of their mother, an effect modulated by children's cortisol levels.⁹⁹ During adolescence, social buffering in humans starts to be co-opted from caregivers to also include close peers,^{97,100} which is particularly significant given that adolescence is a period marked by diminished cortical regulation of reward and stress systems, increased social learning, and approach behavior.¹⁰¹ As a result, adolescence may also be a susceptible period to the detrimental effects of loneliness, which can precipitate the development of anxiety,¹⁰² underscoring the importance of close social relationships during this time. Interestingly, during late adolescence, well-being and empathy are tightly linked with the degree to

which people are “central” to social networks characterized by fun and trust, respectively.¹⁰³ Such in-network centrality is also linked with more similar neural responses in regions supporting social cognition to peers during viewing of dynamic stimuli.¹⁰⁴ Later in life, social connection remains an important tool to combat isolation-related issues that contribute to neurocognitive declines during aging and even the development of dementia,¹⁰⁵ as cognitive abilities have been found to decline as much as 20% faster in lonely adults.¹⁰⁶ Notably, enhanced social cognitive skills in older adults have been associated with closer social networks and the maintenance of social connection.^{107,108} Even the maintenance of weaker social ties has been associated with lower levels of depression.¹⁰⁹ Thus, the benefits conferred by social connection can be protective across the lifespan, with several longitudinal studies highlighting how social connections can protect against mental health issues.¹¹⁰

Social connection can also have a positive influence on decision-making in the context of well-being. In a striking example of the positive influence of social connection on decision-making, rodents are willing to forgo self-administration of addictive substances for the opportunity to seek social interaction with a conspecific.¹¹¹ This further highlights the potential positive benefits of social connection and has implications for therapeutic treatment options that involve substituting substance use with non-drug social rewards such as family and/or friends support groups (e.g., community-reinforcement approach; Stitzer et al.¹¹² and Venniro et al.¹¹³).

PSYCHOLOGICAL AND NEURAL MECHANISMS THAT ENABLE SOCIAL CONNECTION

Social connection thus has wide-ranging short- and long-term positive effects on physical and mental health and our decision-making. Yet, a unifying conception of the psychological and neural mechanisms that help forge connection with others is only beginning to emerge. Here, we suggest that social interactions afford the opportunity to experience a variety of socially rewarding signals that nurture our pursuit of shared affective experiences. Such shared, positive experiences can help us develop shared preferences and goals with others, leading to mutual understanding of the world. We posit that bonding over these shared preferences may then feed back onto this chain, serving to reinforce already established connections.

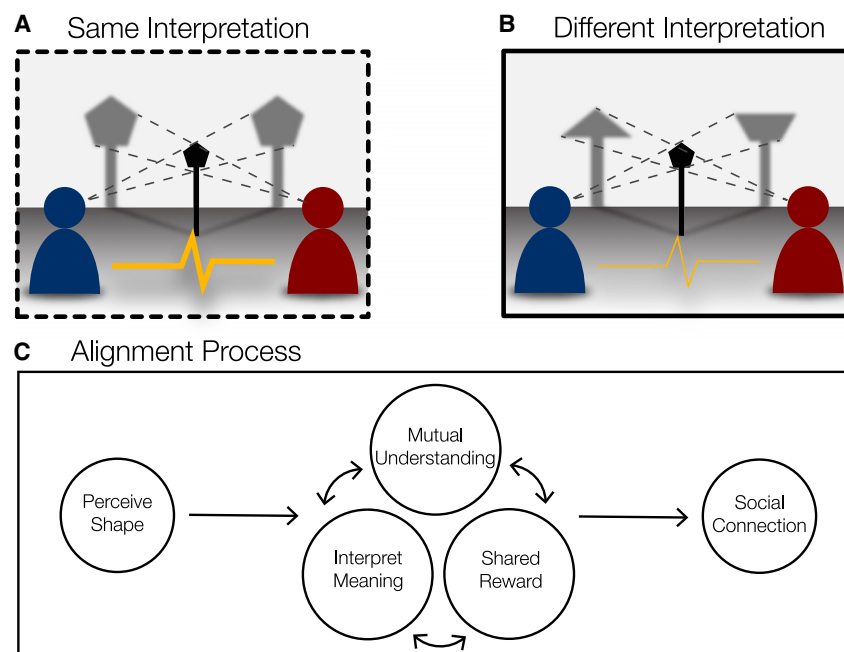


Figure 3. Mechanisms of social connection

(A) Two individuals viewing the same sculpture may have a similar interpretation or experience (represented as shadows on the wall), which might simultaneously increase their confidence in their shared interpretation and also strengthen their social bond (depicted by the thickness of the yellow line).

(B) By contrast, two individuals may have different interpretations to the same stimuli, which may hinder their ability to connect.

(C) Proposed mechanism of alignment. An individual perceives an event and generates an interpretation. The individual then verifies and compares their interpretation of the event with that of another individual via mentalizing or communication. The individual experiences a social reward proportional to the degree of alignment of interpretations, which leads to a feeling of social connection.

A critical function of our social world is to provide a forum through which we can disclose positive affective experiences with others (i.e., going to the movies with a friend, working on a project with a colleague), which in turn can motivate seeking novel interactions based on the value of disclosure and learning about others' preferences.^{114,115} Such shared experiences can elicit emotional responses to the same events providing a vehicle for connection.¹¹⁶ For example, tasting food items and viewing photos with others (relative to alone) enhances the affective impact of those stimuli^{117–119} especially when shared with close friends relative to strangers.¹¹⁸ This phenomenon emerges in reward value signals within the ventral striatum and medial prefrontal cortex when close friends share earned monetary rewards in a gambling game⁷⁰ and within collaborative interactions.⁵⁰ The magnitude of activity within these regions scales with relationship closeness, serving to reinforce established relationships.^{50,70} Related work has observed that there can also be psychological benefits when shared experiences are more negative in nature. For instance, losing with another person seems to feel less bad than losing by oneself, a pattern that is mirrored in ventral striatal activity.¹²⁰ It has been repeatedly demonstrated how beneficial it is to have a source of social support at distressing times,^{4,6} and how disclosing negative experiences to others can provide stress relief¹²¹ and increase feelings of interpersonal closeness.¹²² Thus, close relationships may also serve as a protective factor against shared negative experiences.

The dynamics of shared affective experiences provide an intriguing and important avenue through which we can begin to understand how social connection is established. This can be studied via naturalistic paradigms, which offer a novel and important way in which to probe evolving social dynamics between individuals as they mutually adapt to one another throughout an interaction^{123,124}). For instance, increased tempo-

ral synchrony in brain regions supporting social cognition is observed while participants individually consume naturalistic stimuli (i.e., movies and television shows) while undergoing fMRI.¹²⁵ Increased temporal neural synchrony within dyads when watching the same stimuli is thought to indicate similar interpretations of the events unfolding. Increased neural synchrony has been observed as a function of similarity in personality¹²⁶, one's position within a social network,¹⁰⁴ and social closeness within a social network.¹²⁷ Moreover, non-verbal facial expressions, laughter, and chit-chat between dyads can increase synchronization of shared experiences when watching a movie together compared with watching alone.¹¹⁶ These subtle communicative signals during shared experiences allow people to build a model of others' thoughts, experiences, and preferences, which can ultimately allow social bonds to form and grow over time.

By building models of others' thoughts and preferences based on shared experiences, we can then begin to align with others on key dimensions that hold personal relevance or meaning. According to the social psychological "shared reality theory," aligning with others fosters mutual understanding of the world, simultaneously reducing epistemic uncertainty and facilitating mutual affinity.^{128,129} We further posit that developing such mutual understanding¹³⁰ is born out of the inherent reward in affiliating with another person by identifying common ground, such as shared preferences or life experiences. For example, imagine two people viewing the same art sculpture (Figure 3). Despite sharing similar visual perceptions of the sculpture, they may diverge in their individual appraisals or interpretations of the meaning of the work. These interpretations are likely informed by their past experiences, familiarity with the artist, and also their internal models of the world. How does one know if their particular interpretation is correct? Because there is no ground truth to the subjective meaning of an object or experience, our epistemic uncertainty can be reduced by conferring with another person. Individuals may feel more confident in their interpretation if it is shared by other individuals, which is reinforced by the shared reward arising from mutual understanding,

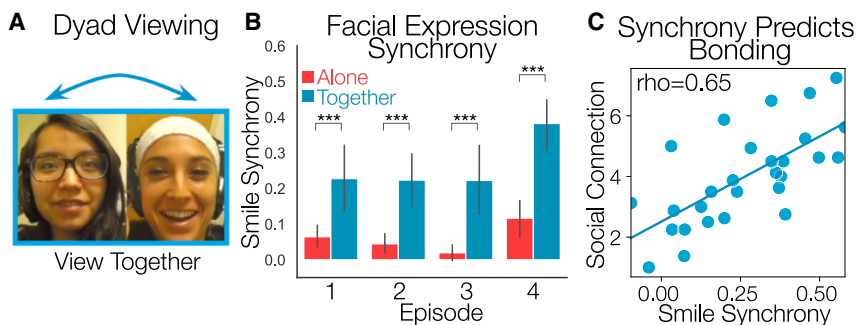


Figure 4. Mutual understanding

(A) Cheong et al.¹¹⁶ had participants watch a television drama by themselves or with another participant.

(B) Facial expressions depicting smiling behavior were automatically labeled for each frame using a neural network computer vision model.¹⁴¹ Temporal synchrony of smiling behavior was computed for each dyad using Pearson correlations. Synchrony in the alone group was computed between all pairwise participants who watched individually, whereas synchrony in the dyad group was computed only between the pairs of participants who watched physically together sitting next to each other. Significance of group differences

was tested with a two-sample permutation test (error bars indicate 95% confidence intervals *** $p < 0.001$).

(C) The magnitude of temporal synchrony of dyadic smiling averaged over four episodes correlated with the dyads' average self-reported feelings of social connection. Figure adapted from Cheong et al.¹¹⁶ with permission from the authors.

and ultimately increases mutual perceptions of social connection (Figure 3C). They are likely to feel closer if they are having a more similar viewing experience, which might arise from sharing a similar interpretation of the meaning of the piece (Figure 3A), compared with when they have different interpretations (Figure 3B). This process of alignment requires sharing a similar appraisal or internal subjective representation of a target (i.e., another person or an event) and presumably recruits regions involved in generating affective meaning, such as the vmPFC.^{131–135}

A growing body of behavioral evidence has found that people can develop a social bond by sharing an emotional experience. For example, participants who watch a television show with another person (Figure 4A) are more likely to synchronize their facial expressions and levels of autonomic arousal compared with watching a television show by themselves (Figure 4B), which predicts how connected they feel to their viewing partner (Figure 4C). The magnitude of this relationship is amplified the longer the dyads interact. This effect is likely mediated by sharing similar cognitive interpretations of the events that unfold and preferences for the characters.¹¹⁶ Engaging in discourse through conversation or exchanging gossip¹³⁶ can facilitate mutual understanding and strengthen feelings of connection, which can be revealed through subtle behaviors such as the length of gaps in between turns^{137,138} or eye contact.¹³⁹ We posit that achieving a mutual understanding of the world carries with it a shared affective signal⁵⁰ that serves as a reinforcer, contributing to both feelings of reward that enhance a connection with others and our collective cognition.¹⁴⁰

How do we know what another person is thinking or feeling? Social interactions provide a forum for using socially rewarding signals to learn about others. For instance, receiving a generous offer from someone or observing others act in prosocial ways can improve our initial impressions,¹⁴² allowing us to learn about their traits and reputations.^{143–147} Certainly, representing another's internal states and motivations go a long way toward establishing and maintaining connections with them,¹⁴⁸ and neural circuits may have evolved to support such phenomena in humans.^{149,150} A requisite for building healthy social relationships is the ability to effectively use social cognitive functions, such as theory of mind and empathy, to reconcile our predictions about others and the social world.^{151,152} Doing so facilitates

alignment and contributes to the connections or ties that we have with others.^{129,153,154} One mechanism through which this occurs is mentalizing, or being able to represent and/or reason about the mental states of another person, which can be used to adapt internal models about others^{155,156}. Mentalizing requires that we are able to use our internal states as an “anchor” or prior for trying to understand what others are thinking, while also accounting for the fact that we are unique individuals that have to account for the external world. Mentalizing processes begin to emerge in early childhood¹⁵⁷ and continue to mature through adolescence with the ongoing development of regions involved in social cognitive processes.^{158,159}

A recent model has posited that the role of the DMN is to integrate both internal and external information to facilitate communication and understanding.¹⁵⁴ This model builds on evidence suggesting that a significant function of the DMN, including regions associated with social processing such as the medial prefrontal cortex (mPFC) and temporal-parietal junction (TPJ), is to prime humans for social cognition.^{35,37,160} A number of studies have implicated components of the DMN, such as the mPFC, in representing the overlap between self and other that scales with similarity¹⁶¹ and social closeness.¹⁶² Interestingly, pattern similarity within the components of the DMN (i.e., mPFC) also appears to cluster according to the social closeness we feel toward others.³¹ In line with models suggesting that the DMN is also critical for prediction,¹⁶³ when prospectively thinking about others' mental states, this network tends to represent predictions about their future states with neural patterns similar to current states.¹⁵² Taken together, these findings suggest potential neural mechanisms through which we are able to establish mutual understanding of the world with others.

We note that here we are highlighting one potentially important aspect of forming social connections. Yet, there may be times in which we may not align with others in terms of our affective interpretation of an experience. This may be associated with skewed neural representations of close and distant others, which in turn may be linked to loneliness. For example, people high in loneliness tend to exhibit increased pattern similarity within components of the DMN (i.e., mPFC and posterior cingulate cortex [PCC]) for categories of individuals that should be distinct, such as close others and celebrities.³¹ However, such “misalignment” does not necessarily imply that meaningful

connections cannot be formed. Rather, such situations may require us to update our models of others and the social world and adjust our own interpretations and behaviors. Continued discourse regarding our differing interpretations may thus provide an alternative means to establishing a meaningful connection.

CONNECTION ISSUES: POTENTIAL CONCERNS IN CONNECTING WITH OTHERS

We have discussed how developing a mutual understanding of the world can create shared experiences and facilitate the formation and maintenance of strong social bonds. However, the context of these shared experiences and social interactions is critical, as it can potentially foster unhealthy connections and shape decision-making in maladaptive ways. Here, we focus on situations where behavior can be negatively influenced by social connection, such as taking up smoking in the presence of specific peers. We also consider how some vehicles aimed at facilitating social connection (e.g., social media) may inadvertently compromise well-being, which underscores how difficult it can be to connect with others and sustain positive social bonds.

A prominent example of how social connection can go awry is the reinforcement of a potentially detrimental behavior due to social influences. For instance, the desire to connect with others may promote a tendency to engage in risky behaviors, which can be particularly problematic early in adolescence when social rewards provide a strong incentive.¹⁶⁴ That is, the social reward value inherent in the interaction with others, particularly peers at this stage of development, can have significant influences on decision-making. An elegant illustration of this phenomenon is the observation that the presence of peers in a driving simulator task increases risk-taking behaviors and is associated with enhanced recruitment of reward-related neural signals in regions such as the striatum.¹⁶⁵ More recent studies have suggested that the effect of peers on risk-seeking during adolescence is moderated by experimental contexts and, in particular, pro-risk attitudes expressed by the peers.¹⁶⁶ Other social contexts, such as the presence of a parental figure, can have the opposite effect, promoting safer decisions (i.e., stopping at a yellow light) supported by increased recruitment of cognitive control regions such as the ventrolateral prefrontal cortex¹⁶⁷ (but see cf. Kwon et al.¹⁶⁸). Finally, peer influence on risk-seeking behaviors is also affected by individual differences in psychological traits such as one's reward drive¹⁶⁹ and neural responses to social rewards as assessed by fMRI signals in the ventral striatum, with individuals that show high responsivity to social rewards also displaying greater risk-seeking behaviors when surrounded by deviant peers.¹⁷⁰ Taken together, this promising line of work highlights the susceptibility of the reward system to the environmental context created by peers in modulating risk-seeking behaviors in adolescence and raises important considerations regarding future experimental designs and applications.^{164,166}

The complicated relationship between social connection and risky decision-making is also noteworthy in addictive behaviors. On the one hand, peer approval can enable risky choices such as exploring substance use, and on the other hand, stable social support networks and close relationships have been associated

with positive health outcomes,^{4,164} such as decreased relapse risk among treatment-seeking drug users.¹⁷¹ However, meta-analyses of long-term social support in close couples have failed to produce reliable evidence of effectiveness in maintaining smoking cessation beyond 6 months.¹⁷² One possibility is that for couples in which both members smoke, the act of smoking creates a *shared experience* that aids in regulating emotional instability within the relationship.¹⁷³ This can be explained by the family systems theory of "symptom-system-fit"^{173,174} in which the symptom or act of smoking serves as an important communication function that facilitates positive mutual social support and maintains a particular interpersonal dynamic. To this end, dual-smoker couples have been shown to increase in affective synchrony during smoking from baseline, whereas single-smoker couples tend to decrease in affective synchrony during smoking.¹⁷⁴ Further, couples who engage in more shared unhealthy negative behaviors, such as smoking or general inactivity, tend to report higher levels of interpersonal closeness.¹⁷⁵ Thus, although social connection can promote healthy behaviors and well-being, there are also situations when shared interpretations in close social relationships foster maladaptive decision-making.

Another example of how shared interpretations can be problematic is the potential consequences of negative social experiences or poor social interactions. Sometimes social relationships are fostered by a unique shared social experience of a negative or even traumatic event, which can be therapeutic for some (e.g., bereavement care; Breen¹⁷⁶). However, shared representations of negative experiences can also have adverse consequences, such as poor recognition of others' emotions,¹⁷⁷ maladaptive shared coping mechanisms (e.g., substance use),¹⁷³ and enhancing the recall of previous stressful memories—an effect mediated by the hippocampus as observed in male rodents.¹⁷⁸ For instance, younger individuals have shown a tendency to seek help via online communities, which can be supportive at times but can also serve to reinforce harmful behaviors (e.g., disordered eating) given potential shared experiences.¹⁷⁹ In general, negative social experiences can diminish the subjective value of social rewards and promote sustained avoidance of potential future social interactions. Following repeated negative interactions in a chronic social defeat stress paradigm for example, mice exhibit social avoidance behavior and altered neuronal activity in lateral septum neurotensin neurons,¹⁸⁰ a region implicated in stress-induced anxiety processes given connectivity with amygdala and hypothalamus.¹⁸¹ In humans, negative social experiences resulting from ostracism, rejection, or stressful social encounters can also affect behavioral and neural systems involved in stress and emotion regulation.^{182–184} Individuals afflicted with depression or social anxiety may also be less likely to pursue potential positive social experiences,¹⁸⁵ reinforcing a difficult cycle of social avoidance that can preclude developing healthy social bonds.

It is important to acknowledge that it can be inherently challenging to make or strengthen connections in the first place. Aberrant social functioning is a hallmark of various neuropsychiatric disorders, including social anxiety disorder, where social avoidance is commonly displayed,¹⁸⁶ and autism, where social "disconnection" occurs given deficits in attention and interpretation of social signals from others.¹⁸⁷ Poor social skills in

general can serve as precursors for anxiety disorders, perpetuating a cycle of elevated stress and social isolation that is detrimental to health.^{188,189}

Beyond clinical issues that complicate social interactions, there are various reasons why individuals may express reluctance to connect with others. First, individuals may have social “set points” of how much connection is necessary, leading some experiences to become overwhelming.¹⁹⁰ Second, the degree of uncertainty regarding the outcome of a potential social interaction may induce a fear of rejection and limit social reward-seeking behaviors. Such unwillingness to take social risks can reflect social cognitive errors such as mis-estimating how others may respond to even small acts like engaging in a brief conversation with a stranger.¹⁹¹ Third, negative prior social experiences such as feeling ostracized may promote more antisocial behaviors and move an individual toward solitude (e.g., Ren et al.¹⁹²).

Notably, the ways in which we can seek out social interactions have changed dramatically in recent years with the advent of widespread social media platforms (e.g., Facebook and Instagram), providing novel opportunities to instantaneously experience positive (and negative) social feedback based on our opinions, preferences, and experiences.¹⁹³ Instances of positive feedback on social media may be perceived as highly rewarding^{194–196} and can increase the likelihood of continuing to share one’s personal experiences.¹¹⁵ This, in turn, can facilitate feelings of trustworthiness and connection toward novel partners.¹⁹⁷ It is possible that this positive feedback loop can facilitate homophily where people seek out others perceived to be similar to themselves.¹⁹⁸ However, this can also have potential negative consequences such as social media echo chambers.¹⁹⁹ Thus, social media has afforded new possibilities of connecting with others but may also inadvertently create feelings of isolation via unrealistic social comparisons,²⁰⁰ fear of missing out,²⁰¹ or poor-quality interactions that are insufficient substitutes for real-life interactions.²⁰²

Given such difficulties in connecting, an important consideration is identifying ways to facilitate connection opportunities that can serve as protective factors. This can occur via seemingly small acts that mutually increase positive affect within a dyad, such as a smile⁴⁴ or positive feedback toward someone,¹⁹⁷ and engaging in minimal social interactions with others during casual everyday interactions and activities.²⁰³ It can also occur via something more meaningful, leveraging mutual alignment that can lead to long-lasting connections. For instance, group activities organized around cultural activities meaningful to a particular community have been found to be good sources for building on shared interests and fostering connection.²⁰⁴ Additionally, prosocial behaviors, such as donating time for a common cause,^{205,206} and collective behaviors, including marching for a common cause, or even just getting together with others for a favorite television show watch party, are all examples of actions that may help build new relationships with roots in shared interests.

CHALLENGES AND FUTURE DIRECTIONS

Our relationships with others can have profound influences on our mental and physical well-being throughout our lifespan

from infancy to the end of life. The world shared a direct experience of being simultaneously isolated during the COVID-19 global pandemic. However, there is still much to know about the specific psychological and neural mechanisms that facilitate the development, maintenance, and dissolution of connection. Gaining greater insight into these dynamic processes is critical for improving our understanding of how these processes can go awry and create physical and mental health issues and also for designing effective interventions. A major challenge facing future work is building models that capture the complexities of how micro-systems of neurons within a single person interact with the macro-systems of people interacting with other individuals. How can we build a cross-species consensus understanding of the neurobiology of social connection?

One key methodological challenge for the study of social connection has been the complexity of studying social processes in real-life interactions.^{124,207,208} Much of the foundational literature that informs our current knowledge on the mechanisms of social connection has relied on elegant but mostly static paradigms in which participants are exposed to conditions where social interaction occurs in a sterile laboratory setting with hypothetical scenarios, fictional partners, or experimental confederates. More recently, a wave of new and ambitious naturalistic experimental designs has emerged, which present the ability to study behavior and phenomena in real-world settings, fostering ecological validity and enhancing the generalizability of results.^{116,136,137,139,209–213} These new approaches allow researchers to observe the complexity and nuance of social interactions that might be missed in controlled laboratory settings. However, these types of experiments come with a host of their own challenges such as (1) difficulty measuring key behaviors or latent thoughts or feelings without disrupting the interactions, (2) difficulty in creating causal experimental manipulations that can obfuscate meaningful interpretations, (3) difficulty in statistical analyses due to complicated dependencies between observations, (4) difficulty in collecting and sharing data due to privacy issues, and (5) difficulty in generalizing effects beyond a specific interaction context. There has been some preliminary success in experimentally manipulating the social context within naturalistic interaction designs by restricting information availability,¹³⁶ or the beliefs of one side of the interaction,²¹⁰ but future work will require continuing to engineer innovative ways to directly manipulate the interaction itself.¹³⁷ Such future efforts may capitalize on sharing positive experiences with others^{116,197,214} to inspire interventions that promote new, healthy social connections, particularly for individuals who may experience difficulty with connection in general.

Naturalistic designs allow for an exciting broadening of experimental questions surrounding social connection.¹²⁴ A fruitful area of investigation that is prone for exploration with such designs is human conversation.²¹⁵ During most instances of conversation, individuals share information, reminisce about shared memories, bond over shared interests, and collaboratively create new ideas and insights.²¹⁶ Links between conversation and the forming/maintenance of social connections may be explored in a variety of ways during naturalistic interactions^{136–139,212} from examining semantic similarities in speech or written shared entries across dyads or groups,^{217–219}

to non-verbal communication (i.e., facial expressions) during live interactions,^{116,210} or even via emojis or memes popularly shared via texts and social media.²²⁰

Another important future avenue surrounds the role of relationships beyond close peers or family members. As humans, we have the unique ability to relate to fictional characters depicted in books or television shows,²²¹ and the advent of artificial intelligence has the potential to add additional opportunities to foster connections with chatbot agents that are not actual humans.²²² These opportunities are complex, with potential positive and negative consequences that require further study. For example, what are the mechanisms by which we develop parasocial connections with television show or book characters, and how might these resemble or differ from connections that dynamically develop with real people?²²³ Is there similarly a protective aspect to connections to fictional characters and artificial intelligence agents? Although one can imagine certain benefits such as helping individuals who struggle or find difficulty with typical human connection, it also raises questions about whether and how well-being is maintained by reliance on artificial connections and whether that discourages seeking out of actual meaningful relationships.

An interesting direction for future research is exploring the neural mechanisms of social isolation and connection via animal models. Although it is not clear to what extent we can directly translate findings from animal work to humans in the domain of social connection, there are exciting approaches and techniques that can provide unique information. This is highlighted by recent excellent examples that have started to aid our understanding of complex social influences on behavior and neural processes involved in social connection (e.g. Heilig et al.,¹⁵ Shi et al.,⁶⁵ Testard et al.,²²⁴ Snyder-Mackler et al.,²²⁵ and Lavenda-Grosber et al.²²⁶). Finally, research on social connection has also gained an enhanced focus in addiction neuroscience research.¹⁵ This involves ways of mitigating stress to avoid maladaptive coping or recalibrating reward valuation systems to incorporate desirable social rewards.^{111,227} For example, efforts can be aimed at fostering social interactions and social support to promote seeking social connection instead of substance use in times of stress. Taken together, the theoretical and methodological advances via multi-methods and naturalistic designs offer a promise of new insight about the mechanisms of social connection and prospective interventions that can help potentiate its benefits.

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AUTHOR CONTRIBUTIONS

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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