An Empirical Review of the Neural Underpinnings of Receiving and Giving Social Support: Implications for Health

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Abstract: Decades of research have demonstrated strong links between social ties and health. Although considerable evidence has shown that social support can attenuate downstream physiological stress responses that are relevant to health, the neurocognitive mechanisms that translate perceptions of social ties into altered physiological responses are still not fully understood. This review integrates research from social and affective neuroscience to illuminate some of the neural mechanisms involved in social support processes, which may further our understanding of the ways in which social support influences health. This review focuses on two types of social support that have been shown to relate to health: receiving and giving social support. As the neural basis of receiving support, this article reviews the hypothesis that receiving support may benefit health through the activation of neural regions that respond to safety and inhibit threat-related neural and physiological responding. This article will then review neuroimaging studies in which participants were primed with or received support during a negative experience as well as studies in which self-reports of perceived support were correlated with neural responses to a negative experience. As the neural basis of giving support, this article reviews the hypothesis that neural regions involved in maternal caregiving behavior may be critical for the health benefits of support-giving through the inhibition of threat-related neural and physiological responding. Neuroimaging studies in which participants provided support to others or engaged in other related forms of prosocial behavior will then be reviewed. Implications of these findings for furthering our understanding of the relationships between social support and health are discussed. **Key words:** social support, health, functional magnetic resonance imaging, social neuroscience, brain, neural, fMRI.

SNS = sympathetic nervous system; HPA = hypothalamus-pituitary-adrenal; dACC = dorsal anterior cingulate cortex; AI = anterior insula; PAG = periaqueductal gray; VMPFC = ventromedial prefrontal cortex; PCC = posterior cingulate cortex; VS = ventral striatum.

INTRODUCTION

One of the most reliable findings in health psychology and social epidemiology is the strong relationship between social ties and both morbidity and mortality. Relative to socially isolated individuals, socially integrated individuals (those with more social ties) live longer (1–3), have better mental health outcomes (4), and show increased resistance to a variety of somatic diseases including cardiovascular disease, cancer, and infectious diseases (5–7). In fact, some studies have shown that simply having at least one confidant (as opposed to none) significantly reduces the likelihood of a negative mental health outcome after a major life stressor (8). On the basis of these findings, it has been noted that a lack of social relationships constitutes a major risk factor for health, on par with other more "standard" risk factors such as high blood pressure, cigarette smoking, and obesity (2,3).

But what is it about social relationships that are critical for health? For the past several decades, scientists have taken a bottom-up approach to understanding the links between social ties and health by focusing their attention on the health-relevant physiological responses (autonomic, neuroendocrine, and immune responses) that are altered by social support. Indeed,

considerable research has linked the perceived presence or absence of social support to altered activity of neural and endocrine systems that affect disease pathophysiology, such as the sympathetic nervous system (SNS) and the hypothalamus-pituitary-adrenal (HPA) axis (9,10). A growing body of research has also followed these dynamics downstream to chart their impact on disease-regulating biological processes such as immune cell gene expression (11–13) and inflammatory dynamics involved in metabolic disease, atherosclerosis, and tumor metastasis (6,14). Still, little is known about the upstream neurocognitive processes that translate the presence or absence of social support into these physiological responses that affect physical health.

This review aims to add to this foundational work by incorporating a top-down approach to understanding the relationship between social ties and health. To do this, this review integrates work from social and affective neuroscience to identify some of the neural mechanisms involved in social support processes, which may shed additional light on the ways in which social ties influence health. Specifically, this review will focus on the neural underpinnings of two types of social support processes that have been linked with health: a) receiving or perceiving support from others and b) giving support to others.

First, the behavioral literature that has highlighted the protective role of social support in the context of stress will be reviewed. This section will then outline a set of neural regions involved in responding to safety and threat and will suggest that receiving or perceiving social support may ultimately benefit health by activating safety-related neural regions and inhibiting threat-related neural regions, which may serve to reduce health-relevant physiological stress responding. Finally, this section will review studies in which participants received or were primed with social support during a negative experience as well as studies in which self-reported assessments of perceived support were correlated with neural responses to a stressful experience.

Next, the literature showing the health benefits of support giving will be reviewed. This section will then outline a set of neural regions involved in maternal caregiving behavior in

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animals and will suggest that these regions may be critical for the health benefits of support giving, in part, because some of these regions act to inhibit threat-related responding. This section will then end by reviewing studies examining the neural substrates associated with giving support to others. These studies will include those in which participants provided support or help to someone (close other, stranger) and studies in which participants engaged in other forms of prosocial behavior.

Finally, this review will conclude by noting that the neural regions involved in processing the receipt and provision of social support are, generally speaking, part of a set of neural regions involved in processing reward. This review will then discuss the implications of this for understanding the neural bases of social support and will suggest that additional research is needed to further understand the reciprocal relationships between the reward-related neural regions involved in processing social support and the threat-related neural regions that seem to be attenuated by social support processes.

RECEIVING OR PERCEIVING SOCIAL SUPPORT
Received/Perceived Social Support and Health
The study of the health consequences of social support was invigorated by a series of studies published in the late 1970s and early to mid-1980s showing that social integration (e.g., having more key social ties) was a prospective predictor of mortality (2). Across multiple studies, those who had more social ties were approximately 2 times less likely to die in a 9- to 13-year follow-up period (depending on the study) (1,15–18). These findings have, in the years since, led to an outpouring of studies aimed at indentifying the mechanisms underlying the health benefits of social support.

Although some work has indicated that social isolation may contribute to negative health outcomes (6,19–21), most of the work in this area has focused on the health benefits of "social support"—having or perceiving to have close others who can provide help or care, particularly during times of stress (10,22,23). The predominant hypothesis has been that receiving social support from others or perceiving that one has social support buffers the negative impact of stressors, thus reducing physiological stress responses that have implications for poor health (23–25). Indeed, this hypothesis has been supported by multiple experimental studies highlighting the protective effect that close others can have during times of stress (25,26).

Experimental animal research has demonstrated that aversive stimuli (e.g., shock) elicit less fear and stress when animals are tested in the presence of a companion than when they are tested alone (27–29), a phenomenon referred to as "social buffering." For example, electric shock punishment was less effective in training rats that were tested in groups versus alone (27), a rat's immobility caused by electric shocks was reduced by the presence of a companion rat (28), and baby goats receiving electric shock displayed fewer emotional reactions when their mothers were present versus absent (29). Similarly, in both monogamous prairie voles and nonhuman primates, stress responses (corticosterone/cortisol) to a novel environment were reduced when accompanied by a con specific (30,31). Linking

the presence of familiar others to health-related outcomes, the efficacy with which unexpected electric shock led to peptic ulcers in rats was shown to be caused, in large part, by whether the rats were shocked in isolation (high ulcer rates) or in the presence of littermates (low ulcer rates) (32). Moreover, social crowding led to hypertension in mice, but only when mice were placed with strangers, not when they were placed with littermates (33).

Similar social buffering effects have been shown in humans, as well. The presence of a friend or supportive companion during a stressor can attenuate cardiovascular reactivity (10,34–38) and cortisol responses (in males (39,40)). Similarly, the presence of a supportive companion (versus stranger) has been shown to reduce self-reported pain unpleasantness in response to painful stimuli (41,42).

In addition, though not experimental, correlational studies have highlighted the benefits of social support on various health-relevant outcomes (25). For example, one study showed that 91% of pregnant women with high life stress and low social support had pregnancy-related complications, whereas only 33% of those with high life stress and high social support showed complications (43). In these correlational studies, a distinction is made between self-reports of received support (a measure of the specific supportive behaviors provided to the recipient) and perceived support (a measure of the perceptions of the general availability of and satisfaction with social support), with perceived support more strongly predicting health and well-being (44,45). However, it can be challenging to map these self-report measures onto experimental manipulations of social support. Although self-reports of perceived and received support correlate only modestly ($r = 0.35$) (44), experiments that manipulate the presence versus absence of a supportive companion may increase this correlation in the moment. Thus, in the experimental neuroimaging studies reviewed here, the term *receiving* or *perceiving* social support will be used to describe features of the manipulation, rather than a self-report assessment of the subjective nature of the experience.

Together, these studies suggest that having social support can be protective during times of stress and that this may occur through the buffering effect of social support on health-relevant physiological stress responses. To gain insight into the possible mechanisms linking perceptions of social support with attenuated stress reactivity, the next section turns to relevant findings from the fields of social and affective neuroscience.

Possible Neural Correlates of Received/Perceived Social Support
On the basis of considerable research showing that social support can attenuate stress- or threat-related responding, it seems likely that received or perceived social support will reduce neural activity in regions that respond to basic survival threats. However, how this threat-related activity might be reduced by social support remains more of a mystery.

One possible mechanism linking social support to attenuated threat-related neural activity is through neural regions that have been shown to be responsive to safety cues. Considerable research has shown that there are certain reward-related neural

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regions that a) are responsive to "safety," the relative absence (versus presence) of threat or the presence of stimuli known to be protective from threat and b) reduce threat-related neural activity in response to detecting safety (46,47). Thus, it is possible that social support reduces threat-related neural and physiological responding through the activation of safety-related neural regions and the subsequent inhibition of threat-related neural regions. Indeed, this account maps nicely onto attachment theory which suggests that the attachment bond—first formed between child and caregiver—provides a sense of safety and a reduced sense of distress for the child who is not yet capable of taking care of himself/herself (48). This sense of safety that comes from knowing that a caregiver is there or from receiving support from a loved one may serve as a kind of safety signal, letting the individual know that he/she is safe and leading to a reduction in threat- or distress-related processing.

On the basis of these proposed neural underpinnings of the stress-reducing effects of social support, the next section will review the neural regions that process threat or danger as well as those that are responsive to safety and reduce threat-related activity. This section will also review how these regions relate to downstream physiological stress responses (e.g., SNS and HPA) that may have health implications.

Threat-Related Neural Regions

In studies of fear-related responding, it has been shown that the regions involved in detecting and responding to impending danger or threat include (but are not limited to) the amygdala, dorsal anterior cingulate cortex (dACC), anterior insula (AI), and periaqueductal gray (PAG) (Fig. 1). The amygdala responds to innately threatening stimuli, such as impending pain or an approaching tarantula (49,50), and is also involved in fear conditioning—learning contingencies that predict aversive outcomes (46,51). The dACC, AI, and PAG, though most well known for their roles in pain processing (52), respond similarly, showing increased activity to impending pain, an approaching threatening stimulus (e.g., spider and snake) (49,50,53,54), or during fear conditioning (51,55,56). Consistent with this, rodent studies demonstrate that the prelimbic cortex, homologous with the dACC and dorsal portion of the medial prefrontal cortex (MPFC; BA 8/9) in humans, is involved in sustaining

fear or threat responses (57), possibly through excitatory projections to the amygdala (56).

In response to detecting threat, most of these regions trigger downstream physiological stress response systems. The central nucleus of the amygdala controls the expression of threat-related changes in autonomic (SNS) and endocrine responses (cortisol) through projections to the hypothalamus and brainstem areas (46). Stimulating the central nucleus of the amygdala increases blood pressure in rats (58), and greater amygdala activity during fear acquisition in humans is associated with greater SNS activity (skin conductance response) to a conditioned stimulus (51). Conversely, lesions to the central nucleus of the amygdala can reduce SNS and HPA responses to conditioned stimuli (59,60). Similarly, stimulation of the dACC induces SNS responses, whereas lesions to the dACC reduce SNS responses (56,61). In fact, the amygdala and dACC may be particularly relevant for physiological stress responses that have negative health implications because lesions to the dACC and amygdala were found to reduce inflammatory-related gastric pathology (62). With regard to the other regions, PAG activity can increase or decrease SNS responding depending on the type of stressor (e.g., escapable and inescapable) and the specific PAG column activated (63). The AI, on the other hand, although often associated with SNS activity, may be more involved in representing autonomic responses in conscious awareness than in directly generating these responses (64).

Safety-Related Neural Regions

In addition to neural regions that respond to impending danger or threat, the brain is also equipped with certain neural regions that are responsive to safety, or the relative absence of threat, and that reduce threat-related neural activity in response. One of these regions, the ventromedial prefrontal cortex (VMPFC), is part of a larger neural circuit implicated in reward processing and seems to be involved more specifically in encoding the subjective value of stimuli (65). In the context of threat or stress, this region responds to the relative absence or reduction of threat or stress (66–68), which is more subjectively rewarding than the presence of threat or stress. However, from an experiential perspective, a reduction in perceived threat or stress seems less akin to "reward" and more akin to
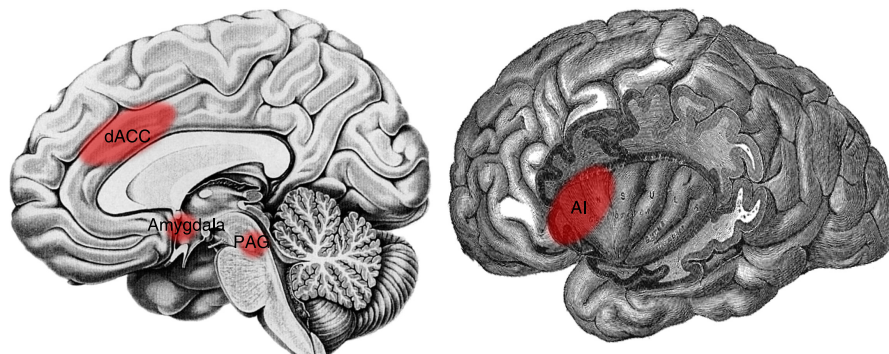

Figure 1. Neural regions involved in detecting and responding to basic survival threats include the following: the dorsal anterior cingulate cortex (dACC), amygdala, periaqueductal gray (PAG) (left), and anterior insula (AI) (right).

the experience of "relief" or safety. Hence, building on work showing that this reward-related region is also involved in responding to safety cues, the discussion of this region will be couched in terms of safety rather than reward per se (although both of these outcomes can be conceptualized as being rooted in greater subjective value).

Along these lines, considerable research has implicated the VMPFC, a reward-related region, as well as the posterior cingulate cortex (PCC), in responding to cues that signal safety (46,47) (Fig. 2). For example, moving a tarantula a safe distance away from a participant's foot is associated with increased VMPFC and PCC activity (50). In addition, fear extinction, a form of "learned safety" in which a cue that previously predicted a negative outcome (e.g., shock) now predicts safety (e.g., no shock) also, activates these regions (46,50). Importantly, the VMPFC, in particular, reduces fear responding through inhibitory connections with the amygdala (69). Thus, stimulating the infralimbic cortex in rats—homologous to the VMPFC (BA 11) and subgenual anterior cingulate cortex (BA 25) in humans—diminishes fear responding to fear cues (69), and greater VMPFC activity is associated with reduced fear responding (skin conductance responses) in humans (46,51). (These same inhibitory connections have not been observed for the PCC.) In addition, the VMPFC and PCC also seem to respond to safety in the context of pain and stress, activating to conditions of low (versus high) pain or stress (66–68).

Critical for the role that these regions may play in the threat-reducing effects of receiving social support, activity in these regions has been shown to correlate with reductions in autonomic and endocrine responding in humans. For example, VMPFC and PCC activity during mental or social stress correlates negatively with cardiovascular, cortisol, and threat-related neural responses (67,68,70–72). In addition, damage to the VMPFC increases feelings of threat and cortisol responses (for females) in response to social stress (73). Interestingly, greater activity in the VMPFC/subgenual anterior cingulate cortex has been shown to be associated with increases in parasympathetic responding, which is associated with reduced cardiovascular arousal (74). Thus, activity in these safety-related regions may

be involved in inhibiting sympathetic and promoting parasympathetic responses (75), which may be health protective. Indeed, highlighting a causal role for these regions in inhibiting threat-related disease outcomes, lesioning the VMPFC or PCC in animals leads to increases in inflammatory-related gastric pathology (62).

Summary

In sum, research from social and affective neuroscience has highlighted a set of neural regions involved in processing threat and facilitating physiological stress responses as well as a separate set of neural regions involved in responding to safety and attenuating physiological stress responses. Given the importance of social support in producing a sense of safety and reducing distress, it is possible that social support attenuates psychological and physiological threat reactivity by activating safety-related neural regions and inhibiting threat-related neural and physiological responding. In the next section, findings from neuroimaging studies will be reviewed to examine the extent to which these regions are implicated in receiving or perceiving social support during stress.

Neuroimaging Studies of Received/Perceived Social Support

Several studies have now examined neural activity while individuals are either primed with or receive social support during stress. For example, two studies have examined neural activity while participants viewed pictures of social support figures (romantic relationship partners) while receiving physical pain (76,77). In one of these studies (76), viewing pictures of social support figures was meant to serve as a low-level form of social support—being reminded of a loved one who typically provides support (to be included, participants had to rate their partners as a significant source of support). Interestingly, in both studies, participants reported feeling significantly less pain when viewing their relationship partners (versus strangers, acquaintances) while receiving pain. In addition, both studies showed increased activity in neural regions previously implicated in responding to safety and decreased activity in regions previously implicated in responding to threat and pain. Thus, Younger et al. (77) showed increased activity in the VMPFC and PCC, regions associated with responding to safety, when participants viewed their partners (versus familiar acquaintances) during pain and decreased activity in the dACC and posterior insula. Moreover, greater pain relief was associated with decreased activity in the dACC and AI. Similarly, Eisenberger et al. (76) showed increased activity in the VMPFC when participants viewed their partners (versus strangers) during pain and decreased activity in the dACC and AI. In this study, greater activity in the VMPFC was associated with greater perceived support from the partner as well as larger reductions in self-reported pain and pain-related dACC activity.

A similar study examined the receipt of social support in the context of awaiting a painful stimulus. In this study, married women were exposed to the threat of shock while holding their husband's hand, the hand of a male experimenter, or no
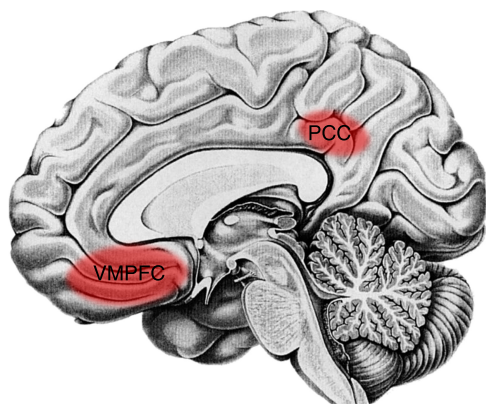
Figure 2. Neural regions that are responsive to safety include the following: the ventromedial prefrontal cortex (VMPFC) and posterior cingulate cortex (PCC).

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hand (78). When participants held their husbands' hands (versus strangers' hands or no hands), they reported lower levels of general unpleasantness. To investigate the types of neural activity altered by social support, the researchers first identified "threat-related" neural regions that were more active when participants awaited physical pain compared with when they knew they would not be receiving pain (during the no-handholding condition). The researchers then showed that several of these regions were less active when participants held their partners' hands. Although this study showed reduced activity in task-defined threat-related regions, this study was not able to examine neural regions that were more active during the social support trials because the analyses were restricted to neural regions that were more active during the threat of pain. However, on the basis of these findings, Beckes and Coan (79) proposed Social Baseline Theory, which posits that social proximity is the "baseline" human state and that deviations from this state lead to an increased need for cognitive resources and threat-related neural activity.

Two other studies examined the effect of social support during the stress of social exclusion. In one study, neural activity was assessed as participants received emotional support (e.g., "Sorry, I know it was unpleasant for you to be excluded") during a social exclusion episode (80). Results demonstrated that participants showed increased activity in the VMPFC and PCC/precuneus and decreased activity in the insula during the emotional support (versus exclusion) condition. Another study examined how neural responses to social exclusion were affected by the imagined presence of an attachment figure (81). Consistent with the stress-buffering effects of social support, participants reported less distress during exclusion when an attachment figure was imagined to be present. This effect was instantiated neurally by the hypothalamus; there was significantly less activity in the hypothalamus, a region implicated in stress-related responding, when participants imagined that their attachment figures were present during social exclusion compared with when they imagined that nonattachment figures were present during social exclusion.

Although the previously mentioned studies are the only ones that have used functional magnetic resonance imaging to assess neural activity while being primed with or actively receiving social support, a few other studies have examined how self-report measures of social support correlate with neural responding during threatening tasks (e.g., social exclusion). In one study, participants who interacted more frequently with supportive individuals on a daily basis (which may relate to greater perceived support), showed reduced activity in the dACC and PAG during an episode of social exclusion (72). In another study, participants who spent more time with friends during adolescence showed reduced activity in the dACC and AI during social exclusion (82). Finally, although not a direct measure of social support, participants low in attachment anxiety, who tend to feel more comfortable and secure in their closest relationships (which may relate to greater perceived support), showed reduced activity in the dACC and AI in response to social exclusion (83). Thus, in each of these studies, measures

likely related to perceived social support correlated negatively with threat-related neural activity.

Finally, studies examining the neural underpinnings of thinking about close others have yielded activations similar to those observed in studies examining received social support. Participants asked to think about close others versus strangers showed greater activity in the VMPFC and PCC (84). Likewise, participants who were asked to make judgments about friends versus strangers showed increased activity in the VMPFC and PCC (85). Although neither of these studies examined the stress-reducing aspects of thinking of close others, it is interesting that the pattern of activations was similar to those studies that have examined the benefits of being primed with or receiving social support during stress.

In sum, although there are relatively few studies examining the neural correlates of receiving or perceiving social support, some consistent findings have emerged. In most studies of social support, there is attenuated activity in threat-related neural regions. In addition, more than half of the studies that have examined neural responses to primed or received social support have shown increased activity in regions responsive to safety. These regions also show activity in studies that simply require participants to think about close others. However, these regions are not typically observed in studies that examine correlations between self-reports of social support and neural responses to threat. It is possible that these safety-related regions are only recruited in response to the direct presentation of social support stimuli or that they are only observed when neural activity to the presence of social support is directly compared with its absence. It is also possible that there are other neurobiological mechanisms involved in the threat-reducing consequences of social support (79). Further work will be needed to better understand the mechanisms that lead to reduced threat-related activity among those who report higher levels of social support.

GIVING SOCIAL SUPPORT
Giving Social Support and Health

Although it is commonly assumed that the benefits of social support come from the support that individuals receive or perceive from others, new research has begun to highlight the possible health benefits of giving support to others. Several studies have shown that support giving is a strong predictor of reduced depressive symptoms and better mental health (86–89). In fact, one study demonstrated that those who provided more support, after the loss of a spouse, exhibited an accelerated decline in depressive symptoms (89). Support giving also has implications for physiological responding and mortality. The tendency to give social support predicted lower ambulatory blood pressure and heart rate during a 24-hour period (87). Moreover, individuals who provided more support to others (90) or who engaged in more volunteer service (91,92) evidenced a reduced risk of mortality.

Although these findings are suggestive of a link between support giving and health, they are limited by several factors. First, given the correlational nature of these studies, the relationship between support giving and health may be driven, not

by support giving leading to better health but by those who are in better health being better able to provide support. Additional experimental evidence is needed to further investigate whether support giving can causally influence mental or physical health outcomes.

A second limitation of these findings is that, on the surface, they seem to contradict a separate literature highlighting the detrimental consequences of being a "caregiver" in the context of chronic illness (e.g., individuals who provide support to a spouse with Alzheimer's disease) (93). Numerous studies have shown that caregivers show an increased risk of physical health problems and mortality relative to noncaregivers (93,94). Although these findings have typically been interpreted as indicating that the act of providing care to others has negative health consequences, these studies have typically not disentangled the effects of providing care to others from those of watching the decline of an ailing loved one. Indeed, some data suggest that some of the negative effects of caregiving may stem from witnessing the decline and impending death of a loved one (95). In fact, a recent study demonstrated that individuals who provided more hours of care to a spouse had lower rates of mortality, whereas those whose spouses had poorer health had higher rates of mortality (96). Hence, although caregiving for an ailing loved one clearly has negative health implications, it is possible that this is not caused specifically by the act of providing support or care to others, and thus, it is important to examine the role of support giving in the link between social relationships and health.

Possible Neural Correlates of Giving Social Support

To identify the neural substrates of support giving, this review borrows from animal research on maternal caregiving behavior (which involves providing support and care to offspring) because certain forms of prosocial behavior, such as support giving, have been hypothesized to rely on the neural and neuropeptide substrates of a mammalian caregiving system (97–99). Interestingly, work in this area has shown that neural regions involved in maternal caregiving behavior play a role in a) increasing activity in reward-related neural regions that promote maternal approach behaviors and b) decreasing activity in threat-related regions to reduce avoidance responses

to offspring and facilitate adaptive caregiving responses during times of stress (100). The following section reviews the neural regions implicated in maternal caregiving behavior and expands on the inhibitory relationship that these regions may have with threat-related neural and physiological responses.

It is important to note that most of the work on caring for offspring comes from animal studies of female maternal behavior (as females are typically more involved in caring for offspring than males); humans who typically engage in biparental care may show fewer sex differences in the neural substrates and possible health benefits of support giving. Indeed, many of the studies highlighting health benefits of support giving show effects that remain significant after controlling for sex. Thus, although the research here will focus on maternal behavior in female animals, it is possible that the neural substrates of these behaviors are relevant to both sexes in humans. Future work, however, will be needed to more directly test this hypothesis.

Animal research has shown that many of the regions that have been implicated in maternal caregiving behavior fall within the basal forebrain. These include the medial preoptic area (MPOA) in the rostral hypothalamus and the adjoining ventral bed nucleus of the stria terminals (vBST) as well as certain reward-related regions such as the septal area (SA), the nucleus accumbens within the ventral striatum (VS), and the ventral tegmental area (VTA) (Fig. 3; MPOA/vBST not shown).

In the rat, the MPOA/vBST plays a central role in maternal behavior (100), such that lesioning these regions disrupts maternal behavior (e.g., retrieving pups) (101,102), whereas hormonal stimulation of the MPOA/VBNST increases maternal responsiveness (100,103). According to animal models, the MPOA/vBST has inhibitory projections to threat-related regions, such as the anterior hypothalamic nucleus and the PAG, involved in withdrawal responses. Inhibiting activity in these regions is hypothesized to reduce a rat's natural avoidance response to pups to facilitate maternal approach behaviors (100).

The MPOA/vBST also has excitatory projections to reward-reward neural regions, such as the nucleus accumbens within the VS, the VTA, and the SA (100,104), which act to increase maternal responsiveness. The VS and VTA are part of a dopaminergic reward circuit and have been shown to activate to
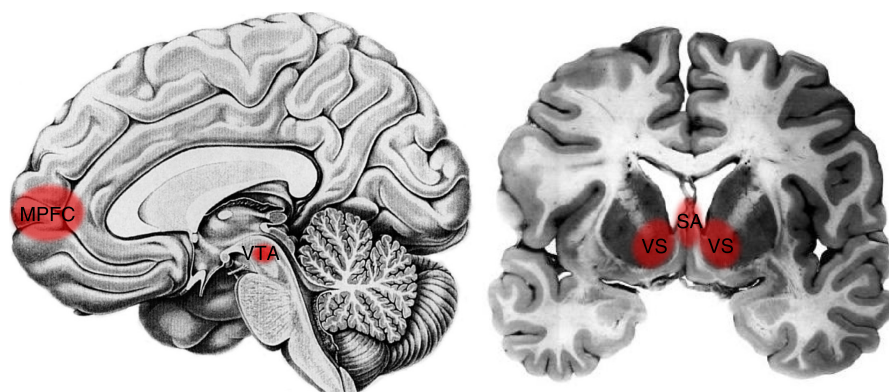

Figure 3. Neural regions involved in maternal caregiving behavior include the following: the medial prefrontal cortex (MPFC), ventral tegmental area (VTA) (left), the ventral striatum (VS), and septal area (SA) (right).

the anticipation of basic rewards such as food or money (105,106). The SA, though not part of this dopaminergic circuit, has been identified as a "pleasure center," on the basis of studies showing that both animals and humans will work to maintain electrical stimulation to this region (107,108). Consistent with the role of these regions in reward-seeking and reinforcement, these regions also underlie approach-related maternal behavior. Lesions to the VS, VTA, or SA dramatically disrupt maternal behavior, reducing approach and interaction with pups (109–112).

Interestingly, one of these regions, the SA, has also been shown to reduce threat-related responding, in part, through inhibitory connections with the amygdala (113,114). Hence, stimulating the SA decreases SNS activity, leading to cardiac decelerations and reductions in blood pressure (114–116), whereas lesioning the SA increases startle reactions, indicative of SNS activity (117). Indeed, it has been suggested that the SA may contribute to maternal behavior by reducing threat-related responding to facilitate responsive caregiving during times of stress (97,104). Although more research has focused on the role of reward-related regions in reinforcing maternal behavior (118), the threat-reducing effects of maternal caregiving may be a critical avenue to explore in elucidating the links between support giving and health (90,97,119).

In addition to the regions described previously, the MPFC, which has extensive connections to the MPOA, VS, and VTA, also seems to play a role in maternal behavior (120). The MPFC seems to facilitate maternal behavior in more complex environments in which multiple stimuli compete for attention (120).

Although no studies to date have specifically examined the neural regions associated with maternal caregiving behavior in humans, some studies have examined neural activity while participants view infant pictures or hear infant cries, which may elicit caregiving motivations. These studies (although not reviewed systematically here because of the difficulty associated with identifying the specific experiential state evoked by these stimuli) generally show widespread activation that includes activity in the SA (121), VS (121–123), VTA (123), and MPFC (121,123–126), as well as increased or decreased activity in the amygdala (124,126–128). Regions such as the MPOA/vBST are too small to reliably isolate with neuroimaging methods and thus are not typically reported.

Although not fully understood, the neural processes that facilitate the threat-reducing effects of maternal caregiving may be mediated, in part, by neuropeptides involved in social bonding, such as endogenous opioids and oxytocin (99,129). Linking these neuropeptides to caregiving-related neural regions, studies have shown that the VS, SA, and MPFC (as well as the amygdala) have high densities of opioid and/or oxytocin receptors (130–132). Moreover, opioids and oxytocin are known to reduce physiological stress responses. Opioids attenuate SNS and HPA activity, reduce conditioned fear responses, and enhance fear extinction (133). Opioids are also potent immunomodulators, inhibiting the production of proinflammatory cytokines (134). Likewise, oxytocin reduces SNS and HPA responses and may do so, in part, through opioid-related activity (129). Future

work will be needed to examine whether these caregiving-related neuropeptides contribute to the health benefits of support giving.

In sum, animal models of maternal caregiving behavior provide useful information about the neural regions that may be implicated in support giving in humans. Different regions within this network function to motivate approach-related maternal behavior as well as inhibit withdrawal or threat-related responding to facilitate adaptive caregiving during stress. In the next section, neuroimaging studies of support giving will be reviewed to examine whether these neural regions underlie support-giving processes in humans.

Neuroimaging Studies of Giving Social Support

Although no neuroimaging studies have directly focused on the health benefits of support giving, several studies have started to examine the psychological benefits of support giving. In one study that examined the neural underpinnings of providing emotional support to a loved one, female participants were scanned as they provided support to their male partners who were in pain (97). On support-giving trials, each female participant was able to hold her partner's arm as he received painful electric shock (while he stood just outside the scanner bore). Participants showed greater VS and SA activity while providing support to their partners (versus control conditions), suggesting that some of the regions involved in maternal caregiving behavior in animals may underlie support-giving processes in humans. In addition, consistent with the role of the SA in inhibiting amygdala activity (113,114), those who showed greater SA activity during support giving showed reduced bilateral amygdala activity. Although physiological responses were not measured here, reduced amygdala activation could have implications for reduced physiological threat responding (e.g., SNS responses) in the context of support giving.

Another study examined the neural underpinnings of giving financial support to loved ones. White and Latino adolescents were scanned as they made decisions to contribute money to their family and/or themselves (135). Results demonstrated that Latino participants, who tend to value helping the family, showed greater activity in regions implicated in reward and caregiving (dorsal striatum, VTA) when they provided costly donations to their family (gave money to their families while losing money for themselves). Interestingly, for both white and Latino participants, those who derived more fulfillment from helping their family showed greater activity in regions implicated in reward and caregiving (VS, dorsal striatum, VTA; (135)) as well as greater functional coupling between the MPFC and VS (136) when making costly donations to the family. These findings suggest that the altruistic motivation to help family members may rely on some of the reward-related regions that underlie maternal caregiving behavior in animals (VS, VTA) as well as those that help sustain these responses under competing motivations (MPFC).

A few other studies have examined giving monetary support to charities. In one study, participants made a series of decisions regarding how they were willing to spend an endowment (98). For each trial, participants made yes or no

decisions about various payoff types for themselves and a charity, including a) pure monetary reward (YOU: $+2 CHARITY: $0), b) noncostly donations (YOU: $0 CHARITY: $+5), and c) costly donations (YOU: $-2 CHARITY: $+5). Both costly and noncostly decisions to donate (versus pure monetary reward) led to greater activity in the VS and SA. Moreover, greater activity in the VS/SA was associated with greater decisions to donate throughout the experiment. Similar results were demonstrated in a study looking at neural activity during voluntary giving to charity and mandatory giving for taxation (137). Here too, participants showed greater VS/SA activity for both mandatory (taxation) and voluntary (charity) forms of giving behavior, suggesting that regions involved in caregiving behavior may underlie these more abstract forms of giving behavior.

Moving from giving behavior to more general forms of prosocial behavior, several studies have examined neural responses to hypothetical scenarios that elicit prosocial feelings or motivations. Thus, imagining prosocial behavior toward a friend led to increased activity in the MPFC and VTA, and feeling more positively in response to this task was associated with greater SA activation (138). In another study, reading scenarios that elicit prosocial motivation led to increased activity in the VS and VTA (139). Moreover, in a related study of frontotemporal dementia patients, who tend to behave less prosocially, reduced activity in the SA and MPFC was directly related to feeling less prosocial motivation after reading these scenarios (140). Thus, several of the neural regions implicated in caregiving behavior seem to contribute to prosocial motivation.

In a related vein, another study attempted to disentangle affiliative motivation from positive emotional experience. Here, participants read hypothetical scenarios that varied in whether they were about close others (termed *affiliative*) or strangers (termed *nonaffiliative*) as well as whether they were positive or negative (141). For example, participants read statements that were a) affiliative and positive (e.g., "You taught your son to ride a bike and he came to thank you with a hug"), b) nonaffiliative and positive (e.g., "You delivered a beautiful speech and the audience stood up to applaud you"), c) affiliative and negative (e.g., "You were distracted and lost your young child in the park") or nonaffiliative and negative (e.g., "You were blamed for a problem that was not your fault and lost your job"). A direct comparison of affiliative versus nonaffiliative conditions revealed activation in the SA/MPOA/anterior hypothalamus and the MPFC that was not simply caused by the valence of the stimuli. The authors suggested that their findings indicate that the SA/MPOA/anterior hypothalamic area may be uniquely engaged by affiliative experiences.

Finally, several studies have examined the neural underpinnings of empathy-induced prosocial behavior and have reliably shown the involvement of the MPFC in predicting these responses. Greater MPFC activity when viewing ingroup members in painful situations was associated with a greater willingness to donate time or money to these individuals (142). Greater MPFC activity in response to viewing another person experience social rejection was associated with greater prosocial behavior aimed at helping that person (143). Finally, greater

MPFC and VS activity while empathizing with sad pictures was associated with a greater tendency to help friends in daily life (144). It is not yet clear why these studies converge on MPFC activity as a key predictor of prosocial behavior following empathy. Additional data on the neural substrates of prosocial behavior will be needed to further understand the complex role of the MPFC in caregiving-related behaviors.

In sum, although few studies have directly investigated the neural underpinnings of support giving, those that have point to a fairly consistent pattern (in both males and females) of activity in reward-related regions known to contribute to maternal caregiving behavior in animals. In addition, widening the focus to include studies of prosocial behavior highlights similar patterns of neural activity. What remains to be examined is the role that these caregiving-related neural regions play in attenuating health-relevant physiological stress responses. Future work will be needed to examine whether increased activation in caregiving-related regions is associated with subsequent reductions in threat-related neural and physiological responses as well as whether these effects are similar in both males and females. This may be one important pathway whereby support giving influences health.

SUMMARY AND CONCLUSIONS

Although it has long been demonstrated that social ties are strongly linked to health, the neural mechanisms that translate perceptions of social support into downstream health-relevant physiological responses are just beginning to be explored. In this review, two possible pathways that might contribute to the link between social support and health were highlighted: receiving or perceiving social support from others and giving social support to others.

In response to receiving or perceiving social support, studies have consistently shown reductions in threat-related neural activity (e.g., dACC, AI, amygdala, and PAG). In addition, studies that have specifically examined the threat-reducing effects of being primed with or receiving social support have also shown increased activity in regions that process safety (VMPFC, PCC). Given that animal models have shown inhibitory connections between the VMPFC and threat-related neural activity (69), it is possible that receiving or perceiving social support attenuates threat-related neural and physiological responses through the inhibitory action of the VMPFC. This may represent one pathway that links the receipt of social support with health. Other pathways should be explored, as well (79).

Studies examining support giving and more general forms of prosocial behavior have shown neural activity in regions implicated in maternal caregiving behavior, including parts of the basal forebrain (VS, VTA, SA) and the MPFC. On the basis of animal models showing that some of these neural regions have inhibitory connections with threat-related neural regions, it is possible that support giving attenuates threat-related neural and physiological responses through the inhibitory action of caregiving-related neural regions. Indeed, animal work suggests that this serves to inhibit natural withdrawal responses to pups and facilitate responsive caregiving behavior toward offspring

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in the face of stress (100,104). Thus, caregiving-related reductions in threat-related responding may represent another pathway through which social support relates to health.

It is important to note that several of the neural regions that serve to inhibit threat-related responding (VMPFC, SA) also play a critical role in reward processing. Interestingly, this observation fits with early brain stimulation studies showing not only that there are separate neural systems that mediate reward and punishment but that these two systems are mutually inhibitory. Reward-related neural regions reduce sensitivity to pains and punishments, whereas punishment- or threat-related neural regions tend to reduce sensitivity to reward (145). For example, stimulating reward-related regions reduces fear behavior and pain sensitivity, whereas stimulating punishment/threat-related regions reduces the effect of stimulation in reward areas (146–148).

Behavioral studies reveal consistent findings. Rewarding stimuli such as pleasant music or palatable food can reduce pain or threat responding, whereas sustained pain can inhibit the experience of reward from morphine (149,150). Moreover, μ-opioids, which are known to increase the experience of reward also decrease the aversiveness of punishing stimuli (151). Thus, converging lines of evidence highlight a potentially inhibitory relationship between the neural systems that process reward and punishment.

The inhibitory relationship between the neural regions involved in reward versus punishment may have important implications for health-relevant physiological responses. Although more work is needed in this area, it has been suggested that the reward system mediates parasympathetic function and is inhibitory with respect to autonomic and neuroendocrine responses, whereas the punishment/threat system facilitates sympathetic and neuroendocrine responses to stress (145). For example, stimulating the SA in animals seems to have parasympathetic-type effects, leading to reductions in heart rate and blood pressure (114–116). Likewise, the VMPFC has been shown to play a role in parasympathetic responding (74), and stimulating the VMPFC in rats can suppress cardiovascular responses to stress (152).

These findings lead to several new avenues of exploration for health research. For example, to the extent that caregiving-related neural regions contribute to reduced physiological stress responding, could other forms of behavior that use this caregiving system, such as volunteering or prosocial acts, also reduce health-relevant physiological responding? Might an intervention that manipulates prosocial behavior ultimately benefit physical health? Furthermore, to the extent that the VMPFC inhibits stress responding to social support, how might nonsupportive relationships interfere with these inhibitory processes, and does this affect other types of inhibitory processes, such as those involved in emotion regulation (47), which also rely on this neural region? Finally, how do early life experiences, particularly those involving exposure to harsh parenting and unstable attachment, fundamentally alter the functioning of these neural regions? Also, does this exposure to early life stress permanently change how an individual responds to various types of stressful experiences, which has implications for negative health outcomes?

In sum, neuroimaging research has just begun to examine the neural correlates of social support with the hope of uncovering additional clues regarding the mechanisms that link social support with health. On the basis of increasing evidence for the role of reward-related regions in social support processes and suggestive evidence for an inhibitory relationship between reward- and threat/punishment-related neural regions, future research would benefit from a more direct focus on the relationships between these reward-related neurobiological mechanisms and physiological stress responses. Although considerable research has focused on the negative effects of social stressors or a lack of social support on SNS and HPA pathways, much remains to be discovered about the possible reward-related pathways through which social support might independently regulate the physiological underpinnings of health. Focusing on the ways in which reward-related neurobiological processes attenuate health-relevant physiological responses may open up an important new area within health psychology that examines the ways in which various types of positive experience, including social support, can influence health.

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