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REVIEW

Neural mechanisms of the link between giving social support and health

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Giving social support to others has emerged as an additional route by which social ties influence health. Thus, giving support to others not only influences the health of the individual receiving support, but also the health of the individual giving the support. However, the neural mechanisms by which giving support leads to health are only beginning to be explored. In hopes of consolidating and guiding future research on giving support and health, the current review considers why, how, and when giving support is health promoting. Special emphasis is placed on neural regions known to contribute to parental care in animals that both reinforce giving support behavior (ventral striatum and septal area) and reduce stress-related responding (e.g., amygdala) to facilitate care. Hypothesized links between neural regions involved in giving support and peripheral physiology (sympathetic nervous system, hypothalamic–pituitary–adrenal axis, and related inflammatory responding) are considered as well as the conditions under which giving support should be most beneficial for health. Finally, the implications of the current perspective for understanding how social relationships, more broadly, contribute to health and suggestions for future directions are offered.

Keywords: providing social support; prosocial behavior; altruism; caregiving; health neuroscience

Introduction

Social experiences are primary for humans. We rely on satisfying, fulfilling social connections to thrive and survive[1,2] and decades of research confirm these notions to show that social connections have significant effects on long-term health and well-being.[3–7] Hence, social connections have emerged as one of the major contributors to health (also see Refs. 8 and 9). Beyond having social connections, the perceived quality of the interactions, specifically the supportive interactions, that occur within one's connections is proposed to make social ties particularly health promoting.[10,11] Social support, defined as the perception or experience of being loved and cared for by others, esteemed and valued, and part of a social network of mutual assistance and obligations,[12] may thus be one of the "active ingredients" in the health benefits derived from social connections.

To date, most of the research on social support and health has focused on the receiver of support and the health effects of perceiving that support is available from others.[10–13] However, we and others have proposed that giving social support may also have beneficial health effects for the individual giving.[14,15] That is, giving support to others may be an additional health promoter. Until recently, whether and how giving support contributes to health has been underexplored.

The original focus on the receiver of support was certainly warranted. Ongoing debates about the motives behind and existence of altruistic behavior[16–18] coupled with an influential literature on the detrimental health effects of prolonged caregiving for ill family members[19] strongly suggested that giving support was costly. Given this background, perceiving that support is available *from* others might appear to be the central way in which social support affects health. From this perspective, the hypothesis that giving support *to* others influences the health of the giver in positive ways might be counterintuitive. However, more

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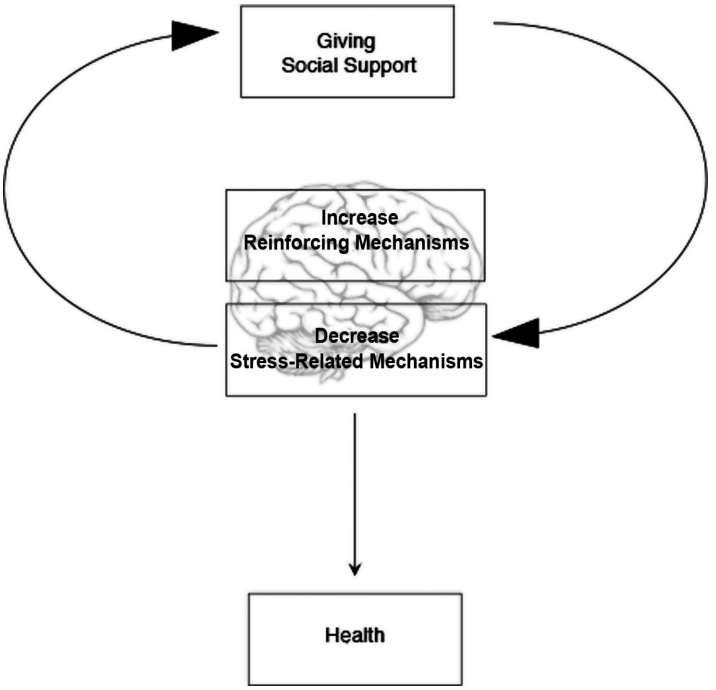

Figure 1. **Mechanisms that support continued giving support behavior. Increases in reinforcing-related neural mechanisms and reductions in stress-related neural mechanisms ensure continued giving support behavior that, over time through an iterative process, can lead to health.**

recently, an accumulating body of findings supports the hypothesis that giving support to others does indeed benefit the health of the individual giving under certain circumstances.

A health neuroscience perspective on giving support

Should giving social support to others positively affect health, the next question is *how* this might be happening. One potentially rich answer to this question can be gleaned from taking a health neuroscience perspective.[20] Health neuroscience emphasizes the integration of theoretical perspectives from social and health psychology with affective neuroscience to understand the biological pathways that lead to health. In particular, there is an emphasis on the brain, the central command center of the body, as a determinant of the peripheral physiological responding that most proximally impacts health. Although we have known since the 1970s that social ties and health are linked, the appreciation of the brain as a key mediator has only emerged in the last 12 years.[21–23] Thus, the questions at the heart of the present manuscript and those at the center of health neuroscience are one and the same, that is, to understand how the brain links giving support to others with downstream physiological responding, and ultimately, resilience against clinical illness.

For this special issue on health neuroscience, I review an underexplored facet of social support, namely giving support, and how giving support to others can be health promoting. I begin by outlining our theoretical perspective for why giving support might be health promoting[15,24] followed by two mechanisms proposed to ensure continued giving support behavior: (1) reinforcing mechanisms and (2) stress-reducing mechanisms (Fig. 1). I take a cross-species approach with particular emphasis on the neural mechanisms implicated in parental care in animals and their relevance to giving support in humans. Next, I review evidence of the role of the two mechanisms in giving support's health effects and consider when giving support might be particularly health promoting. Finally, I end with the implications of the current perspective for psychosocial interventions aimed at harnessing social connections to improve health and suggestions for future research.

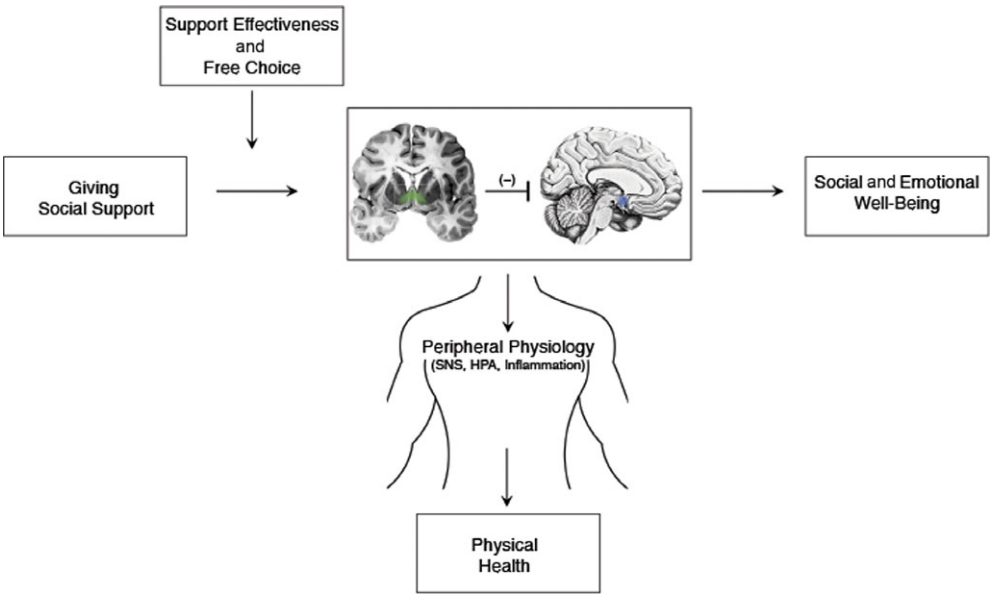

Figure 2. How giving support leads to health: the proposed neural mechanisms by which giving support leads to mental and physical health. Increased activity in regions that reinforce parental care in animals (VS, SA) and decreased activity in stress-related regions that also inhibit parental care (e.g., amygdala) connect to downstream physiological responding (SNS, HPA, immune), which lead to mental (social and emotional well-being) and physical health. In addition, perceptions of support effectiveness and free choice alter the benefits from giving to others.

Why giving support?

Many have theorized that the human capacity to care for others evolved from the parenting behavior given to offspring.[14,17,25–30] Although most species exhibit some parenting behavior, human infants are born especially vulnerable and dependent on others and require a prolonged period of intense caregiving following birth. As a consequence, humans display some of the highest levels of parenting behavior of all species. This is in direct contrast to parenting behavior in species who birth self-sufficient (precocial) offspring who have less parenting needs.[18] As such, giving support behavior and the desire and ability to care for others must not just be present in humans, but is necessary to ensure the survival of their offspring and thus further the species as a whole. Due to the importance of giving support behavior for individual survival, we have proposed that mechanisms may be in place to ensure continued supportive behavior.[15] Over time, the mechanisms that ensure giving support behavior continues may also have consequences for health (Fig. 1). That is, the mechanisms that ensure giving support behavior occurs in the first place, may also contribute to long-term health effects through an iterative process. In particular, a system of parental caregiving mechanisms that help mammals care for their own young may extend to also underlie caring for others in need such as friends, romantic partners, other family members, or even strangers. Although questions about the intentions,[31] skills (e.g., ability to infer mental states of others),[32] individual differences,[33] and characteristics of the target that motivate giving support behavior[34] in the giver are important for understanding what initiates such behavior, the current focus is on *how* giving support, over time, might be health promoting. In other words, once the decision to give support has been made, how does that intention or behavior influence health?

We have focused on two mechanisms that ensure an individual gives support to others: (1) those that reinforce giving behavior and (2) those that reduce stress or withdrawal (Fig. 2).[15] Thus, giving support may be positively reinforced by increases in affective, social, and neural reward-related outcomes that strengthen the likelihood that giving support behavior will continue. In addition, giving support may reduce withdrawal and stress-related responding in

order for the individual to give. That is, effective giving behavior requires an individual to dampen their own distress to witnessing another in need in order to approach and care for them. Over time, a consequence of these reinforcing and stress-reducing mechanisms may be better health.

How giving support leads to health: Overview of neural regions implicated in parental care

Animal models on the neurobiology of parental care provide important clues into the neural mechanisms that may be involved in giving support behavior in humans and ultimately, how giving support leads to health. In particular, experimental brain manipulations in animals provide mechanistic (causal) knowledge about the neural regions that are critical to giving support behavior that is difficult, if not impossible, to obtain from humans. From this literature, a system of subcortical neural regions important to parental care has emerged.[35] These include the ventral striatum (VS), septal area (SA), medial preoptic area (MPOA), ventral bed of the stria terminalis (vBST), ventral tegmental area (VTA), and amygdala. Consistent with our view that reinforcing and stress-reducing mechanisms underlie giving support in humans, parental care regions in animals have been shown to both reinforce parental care behavior (e.g., VS, SA, MPOA) and inhibit nonparental behavior (amygdala), such as avoidance of and aggression toward offspring. In our work on humans, we have largely focused on the VS, SA, and amygdala due to their relevance to mental[36–38] and physical health,[39] though other regions, such as the medial prefrontal cortex (mPFC) are likely also involved in giving support (see "Implications and future directions" section).[40]

Ventral Striatum

Effective parental care in animals is characterized by a set of well-defined behaviors, including pup retrieval (carrying pups to the nest), huddling, licking and grooming, nursing, and nest building, which, taken together, ensure that the litter thrives and survives. The consequences of deviations from normal parental behavior for the litter are, therefore, severe. The NAcc, and surrounding VS, broadly implicated in incentive motivation toward a range of reinforcing stimuli in humans,[41–44] is one neural region that centrally contributes to parental care in animals. Thus, Fos protein expression, a marker of neuronal activity, increases in the NAcc during parental behavior such as retrieval and licking.[45,46] As stronger evidence that the NAcc plays a causal role in parental behavior, lesions to the NAcc, which render the region ineffective, result in severe disruptions to parental behavior. For instance, mothers with NAcc lesions show less licking, retrieving, nest building, and crouching over pups compared to mothers with sham lesions.[47–49] Moreover, lesions to the NAcc in parents result in more than mere reductions in parental behavior, but reduce parental behavior to levels similar to those of nonparents.[50]

Although the NAcc broadly functions to incentivize animals toward a diverse array of reinforcing stimuli, there is some evidence for the region's specificity on parental behavior. Indeed, nonparental behaviors, such as sexual behavior[48] and self-grooming,[49] remain intact in NAcc-lesioned parents. Thus, even though both sexual behavior and self-grooming could be argued to be equally reinforcing as parental behavior, in the context of parenting, the NAcc selectively affects parental behavior. In other words, the NAcc is known to serve a wide variety of functions (e.g., reward, motivation, learning, etc.), but these findings hint at the possibility that the multifaceted behavior of parenting particularly relies on an intact NAcc. Further evidence for the specificity of the NAcc on parental behavior is shown by lesions to other surrounding regions such that lesions to the dorsal striatum,[48,51] hippocampus,[50,51] thalamus, and caudate[50] leave parental behavior unaltered.

Turning to human parents, many of the regions known to be important for parental care in animals, including the VS, show increased activity to infants in human parents. Thus, exposure to cues of one's own infant (e.g., crying), which may motivate parenting behavior, elicit activity in the VS and SA.[52] Furthermore, parents with altered VS activity to other forms of reinforcing stimuli hint at a causal role for the VS in human parenting behavior. As one example, drugs of abuse such as cocaine, opiates, and alcohol activate mesocorticolimbic systems, including the VS, and significantly alter reward-related processing to various kinds of reinforcing stimuli.[53,54] Separately, parents struggling with addiction have been shown to display deficits in parenting behavior relative to non-addicted parents. Cocaine-using mothers show

less emotional engagement with their own children, are more intrusive and hostile, and tend to parent in ways that do not match the child's developmental age (e.g., give commands or inappropriate instruction).[55] In addition, dismissive (versus secure) mothers, as determined by the Adult Attachment Interview, show less VS to images of their own infants smiling.[56] Taken together with the animal literature, these results suggest that the VS contributes to normal parental behavior and is a likely candidate for giving support behavior more broadly.

Septal area

In addition to the VS, the SA, including the septal nuclei through the anterior commissure, anterior to the optic chiasma, has also been shown to be important for parental behavior across a number of different species.[57–62] Lesions to the SA, like lesions to the NAcc, have severe consequences for the litter. SA lesions disrupt nest building,[57] licking,[59] pup retrieval,[60] and general care of and interest for offspring.[58] As further evidence that activity in the SA is important for effective parental behavior, fewer offspring of parents with SA lesions (versus intact animals) survive beyond the first week.[58,62] Interestingly, postmortem analyses of offspring reveal the presence of milk in the stomach suggesting it is the lack of care and not malnutrition per se, that affects survival.[58]

Beyond parenting, the SA is characterized as a "pleasure center" important for reinforcement learning.[63] A seminal finding on this region showed that rats implanted with electrodes to the SA quickly learned to self-stimulate by pressing a bar to deliver stimulations and self-stimulated significantly more during a learning phase than during a period of extinction.[63] In addition to its role in reinforcement, the SA is also involved in relief from stress-related stimuli (e.g., fear and anxiety).[64] That is, increased SA activity is found in the presence of stimuli that signal a break from a stressor. As such, stimulating the SA on its own increases calm[64] and reduces stress-related behavior[65] and physiological responding (blood pressure, heart rate[66–68]). Conversely, lesions to the SA (versus control) increase stress-related behavior such as defense, attack,[69] startle reaction to loud noise, emotional reactivity (squealing, muscular tension[70]), and physiological stress-related responding (epinephrine and norepinephrine levels),[71] effects that may be occurring via inhibitory connections with the amygdala (see "Giving support and health" section). To the extent that giving support in humans involves the SA, activity in this region may explain how giving support is both reinforcing and stress-reducing.

Amygdala

Giving support is not only reinforcing on its own, but may also inhibit stress-related responding in order to facilitate care during times of stress.[30,46] Thus, another route by which giving support may lead to both continued supportive behavior and health is by reducing withdrawal or stress-related responding.[15,24] Animal models of parenting support this notion. Naïve, virgin animals (i.e., nonparents) display avoidant and sometimes aggressive behavior toward pups; behaviors that are mediated, in part, by the amygdala.[35] In other words, the amygdala's role in a parental care system is in inhibiting parental behavior. Consistent with this notion, presenting pups (versus other novel stimuli) to nonparents results in greater Fos-IR in the amygdala.[73] However, repeated exposure to pups, which presumably dampens amygdala activity, can initiate parental behavior in nonparents.[74–76] As direct evidence that the amygdala inhibits parental behavior, lesions to the amygdala result in decreased pup avoidance and greater subsequent parental behavior (pup retrieval and nursing posture[74,76]). Based on the animal literature, dampening amygdala activity to offspring may be critical to the initiation and maintenance of parental behavior.

Findings from human parents align with these animal findings. Infant crying, a signal that the infant is in need of care, elicits greater amygdala activity in both parents and nonparents (versus baseline,[77] versus adult crying[78]). However, intrusive parents who provide less high-quality care (as coded from actual mother–infant interactions) show greater amygdala activity to videos of their own infant (versus a stranger infant).[79] Though correlational, these results align with the animal literature to suggest that higher quality parenting may rely on dampening amygdala activity to infant cues of distress. Outside of the context of parenting behavior, simply viewing images of one's own infant (versus a familiar but unrelated infant who one is less likely to parent) leads to less amygdala activity.[80] Collectively, findings from studies on the human response to infant cues further hint at

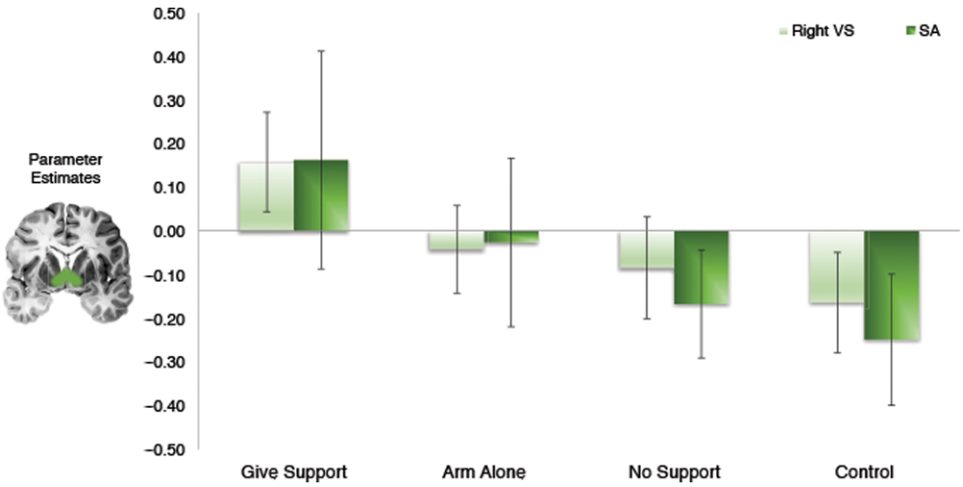

Figure 3. Giving support leads to increased VS and SA activity. The figure comes from a prior study and shows that giving to a romantic partner in need leads to greater activity in the VS and SA compared to not giving support.[90] Further, results show that giving support elicits greater VS and SA activity than a condition where the participant is touching the partner when he is not in need.

the possibility that the amygdala is involved in the inhibition or withdrawal of parenting.

Parental care neural regions and giving support

Data from humans suggest that some of the neural regions implicated in animal parental behavior are also relevant for giving support to others. Specifically, the VS, SA, and amygdala appear to contribute to giving support behavior. For example, giving support to others in need, such as other family members,[81] strangers,[82] or charitable organizations,[83,84] elicit greater VS activity than keeping for the self. Results such as these suggest that giving to others, more than receiving for the self, is particularly reinforcing. The SA has also been shown to contribute to giving support in humans. Self-reported care for others predicts greater SA and VS activity to listening to biographies of others in need and VS activity from this analysis predicts greater charitable giving outside of the scanner.[85] Likewise, SA activity to emotionally evocative social images is associated with greater daily giving support behavior outside of the scanner.[86] Though not specifically about giving support behavior, higher prosocial sentiments (defined as acting in accordance with one's own values toward one's best friend) are associated with increased activity in the SA in response to a social emotions task,[87] whereas neurodegeneration to the SA is associated with lower scores on a prosocial task.[88] Finally, reduced amygdala activity has also been shown to facilitate giving support behavior in humans. Patients with basolateral amygdala damage (versus healthy controls) show significantly more giving behavior (trust decisions during an economic game) but no differences to a nonsocial risk-taking game nor in expectations of receiving payment back.[89] In other words, dampened amygdala activity via damage to the region leads to greater giving support behavior. These last results strongly suggest that the amygdala is causally involved in giving support behavior.

In the first study to examine the contribution of parental care regions to a real-time giving support interaction in the scanner, participants gave support to their romantic partners by holding the partner's arm as he received unpleasant electric shocks. Giving support (versus not giving support) to the romantic partner elicited greater activity in the VS and SA (Fig. 3).[90] Further, VS and SA activity was greater when participants gave support compared to a condition where they simply touched the partner when he was not in need, suggesting that giving support, beyond close physical proximity to a close other, was particularly reinforcing. As evidence for giving support's stress-reducing effects and the inhibitory relationship between the SA and amygdala, SA activity to giving support was negatively

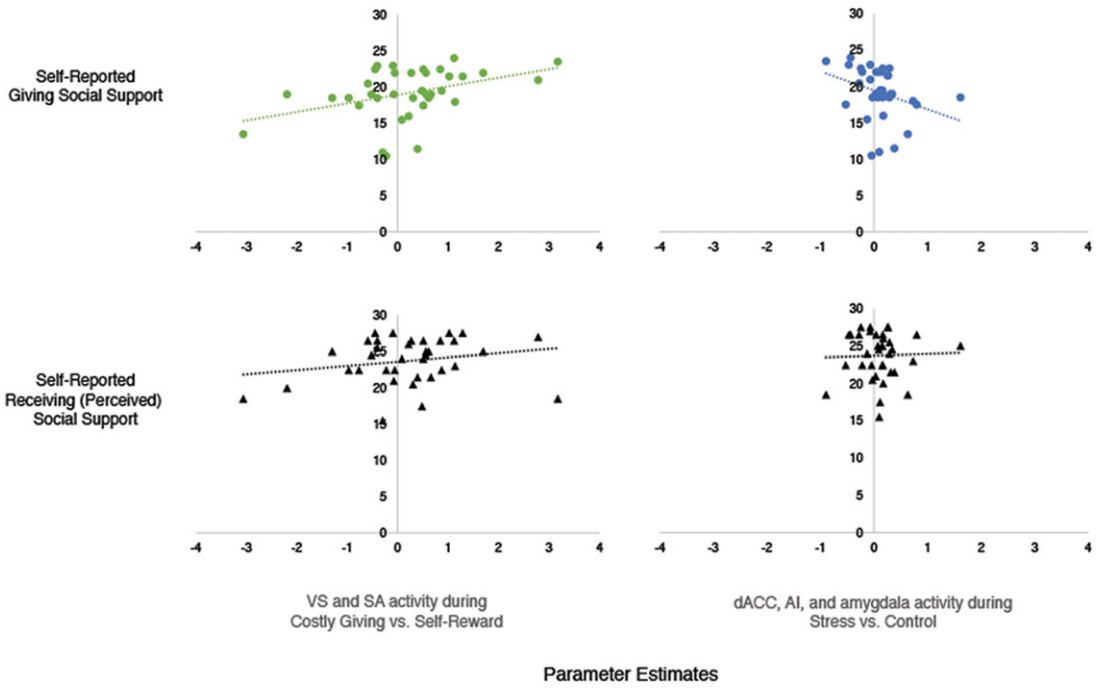

Figure 4. Self-reported giving support and parental care–related neural activity to prosocial and stress tasks. Data come from Ref. 24 to show that greater reports of giving support are associated with greater VS and SA activity to a prosocial task and less dACC, AI, and amygdala activity to a stress task. Perceptions of receiving support were not associated with neural activity.

correlated with amygdala activity. This study provided the first evidence that giving support to those other than one's own offspring involves reinforcing and stress-reducing mechanisms that are also involved in parental care.

In a second test of the reinforcing and stress-reducing neural mechanisms involved in giving support, participants reported on how much they generally gave support to others and then completed three separate tasks in the functional magnetic resonance imaging (fMRI) scanner: a giving support task where participants had the opportunity to give money to a close other in need, an affiliative task where participants viewed images of their own close others, and a stressful task.[24] In this study, endorsing statements such as "I give others a sense of comfort in times of need" was associated with greater VS and SA and less stress-related neural activity, including the amygdala. Thus, greater self-reports of giving support were associated with greater VS and SA activity to the giving support task (Fig. 4) and greater VS to the affiliative task. In addition, giving support was negatively correlated with stress-related neural activity to the stressor such that greater reports of giving support were associated with less amygdala, dorsal anterior cingulate cortex (dACC), and anterior insula (AI) activity. Self-reports of receiving support from others was not associated with neural activity to any of the three tasks further highlighting the potential benefits of giving support to others.

Should the benefits of giving support depend on mechanisms that originally evolved for caring for infants, it is possible that giving *targeted* support to a single, identifiable individual may be more health promoting than giving *untargeted* support (e.g., to societal causes or the world in general). That is, should giving support behavior have evolved from parental care that was originally directed toward a single offspring in need, giving targeted support to others may also be best for health.

To examine whether giving targeted and untargeted support are differentially related to health-related outcomes, participants engaged in a giving support task while in the fMRI scanner. After identifying a close other in need of money (giving targeted support condition) and reading about

charitable organizations (giving untargeted support condition), participants chose whether to give raffle tickets to these other parties at a cost to themselves. The raffle tickets were placed into a lottery drawing where individuals could win larger cash prizes. In preliminary support of hypotheses, SA activity as participants gave targeted support (versus a condition where no support was exchanged) to a close other in need was negatively correlated with amygdala activity to a separate emotion reactivity task such that greater SA activity was associated with less amygdala activity.[91] However, SA to giving untargeted support was not related to amygdala activity suggesting that giving targeted support to someone in need, but not untargeted support, might be particularly stress reducing.

In summary, neural regions involved in parental care in animals also appear to contribute to giving support behavior in humans. Specifically, increased activity in the VS and SA to giving support and decreased activity in the amygdala and other stress-related neural regions (dACC, AI) to stressors may facilitate giving support behavior in humans. Next, I turn to the relevance of these two mechanisms for mental and physical health.

Giving support and health

The current perspective suggests that giving support to others may influence the health of the giver via mechanisms that both reinforce giving support behavior and also reduce stress in order for giving behavior to occur. In particular, neural regions implicated in parental care in animals may contribute to giving support behavior in humans. A consequence of giving to others via activity in regions that support parental care (VS, SA, amygdala) over time may be better mental and physical health (Fig. 2). The known health effects related to giving support to others that stem from each of the proposed mechanisms are reviewed next.

The reinforcing-related neural mechanisms proposed to underlie giving support, namely the VS and SA, may have their strongest effects on mental health, specifically emotional and social well-being. Thus, giving support to others is associated with positive emotional and social outcomes such as increased happiness,[92–94] self-esteem,[95] and self-worth.[96] Though most results have been correlational, experimental evidence suggests that giving support may causally influence mental health. For instance, giving support to others (versus oneself) results in greater reported happiness,[93] psychological flourishing,[97] and subjective well-being.[98] Furthermore, giving support to others increases feelings of social connection compared to control conditions in which one is holding a partners arm when the individual is not in need[90] or giving untargeted support to a charity.[91] Greater feelings of social connection are also associated with greater VS and SA activity to giving support to a romantic partner in need.[90] Few imaging studies have directly explored parental care–related neural activity to giving support and health outcomes, however, one study conducted on adolescents examined relationships between VS activity to giving support and mental health.[99] In this study, participants underwent an fMRI scan as they chose whether to give support to family members by giving them money and, in another condition, whether to keep money for themselves. One year later, depressive symptoms were measured. Consistent with the possibility that giving support-induced increases in the VS affect mental health outcomes, greater VS activity to giving to family members was associated with less depressive symptoms a year later. VS to keeping for the self, on the other hand, was associated with more depressive symptoms. Outside of this one study, the contribution of VS and SA activity when giving support to mental health has not been studied.

Though less commonly examined in humans, the VS and SA may directly affect the activation of downstream physiological pathways implicated in physical health (i.e., the hypothalamic–pituitary–adrenal (HPA) axis, sympathetic nervous system (SNS), and inflammatory processes[39]). The VS projects to the hypothalamus, bed nucleus of the stria terminalis, and brain stem[39] to influence HPA axis and SNS responding. In addition, the SA inhibits HPA and SNS responding such that stimulating the SA reduces SNS responding[64,66–68] and SA lesions enhance SNS responding to an acute stressor (epinephrine and norepinephrine levels).[71] An underexplored possibility is that VS and SA may, on their own, contribute to peripheral physiological responding in ways that promote physical health.[72] However, the direct contribution of the VS and SA when giving support to others and physical health needs further research.

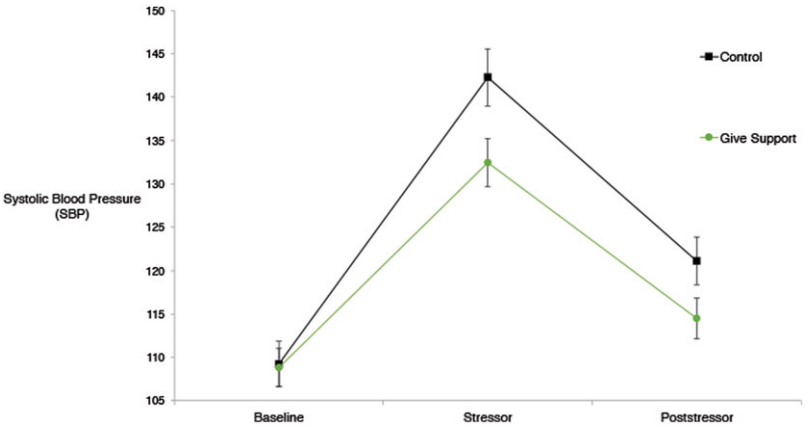

Figure 5. Giving support causes reductions in stress-related responding. Experimental evidence from Ref. 114 that giving support (versus writing about one's route to school or work) leads to reductions in stress-related responding (systolic blood pressure) to a laboratory stressor.

In addition to the possibility that reinforcing mechanisms have direct effects on health, we have proposed that an inhibitory relationship between neural regions that support effective caregiving and those that inhibit such care (i.e., interactions between reinforcing and stress-reducing mechanisms) facilitate the provision of support and over time, lead to better health. Results from animal studies show that activation of the SA, one of the key regions within the parental caregiving system, inhibits stress-related responding through inhibitory connections with the amygdala.[64,100] Thus, SA lesions result in enhanced stress to electric shock.[100] However, the addition of an amygdala lesion eliminates the stress-increasing effects of the SA lesion suggesting a complementary effect of the two regions. Therefore, giving support may dampen stress responding in order for effective care to occur via inhibitory anatomical connections between the SA and amygdala.

In addition to its role in parental inhibition,[35] the amygdala is among other limbic forebrain structures that translate and process stressors to influence downstream physiological responding implicated in physical health.[39] In animals, stimulating the amygdala increases SNS-related responding (blood pressure, heart rate).[102] Conversely, lesioning the amygdala, which renders the region ineffective, reduces stressor-evoked SNS-related responding.[103,104] Similarly, greater amygdala activity to acute stressors is associated with greater increases in blood pressure[105] and greater increases in IL-6, a key proinflammatory cytokine and measure of immune system activity, in humans.[106]

Amygdala-induced changes in peripheral responding likely occur via anatomical connections with the paraventricular nucleus of the hypothalamus and brain stem regions.[107,108] Furthermore, the amygdala is networked with other stress-related neural regions such as the ACC and AI that also have direct connections to peripheral physiological systems[109] and have been shown to negatively relate to giving support to others.[24] Thus, a second route by which giving to others leads to health benefits is reduced stress.

As correlational evidence for giving support's stress-reducing effects, macaques who groomed others more, a form of giving support behavior, showed lower stress levels, as measured by fecal glucocorticoid concentrations.[110] Similarly, macaques showed less anxiety-related behaviors (self-scratching, self-grooming, aggressive actions) after grooming others than after other behaviors.[111] In humans, greater support giving is associated with reduced self-reported stress, blood pressure, and heart rate throughout the day;[95] an accelerated decline in depressive symptoms following the death of a spouse;[112] and a reduction in the association between stress and mortality.[113]

Although these results are correlational, the stress-reducing effects of giving support have also been demonstrated experimentally. Participants were randomly assigned to give support to a close other in need by asking them to write a supportive

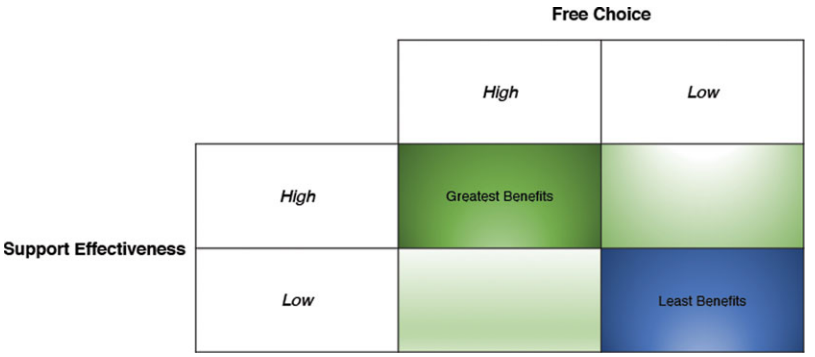

Figure 6. When is giving support beneficial? When perceptions of support effectiveness and free choice are high, giving support should lead to the greatest benefits and when perceptions of both factors are low, giving support should lead to the least benefits. High perceptions of either support effectiveness or free choice may still lead to some benefits.

note or were asked to write about their route to school or work. Following the writing, participants completed a standard laboratory psychosocial stressor while their salivary cortisol, alpha-amylase (sAA), heart rate, and blood pressure responses were collected (i.e., measures of HPA axis and SNS-related responding). Consistent with the hypothesis that giving support is stress reducing, giving support (versus writing about one's route to school or work) caused reductions in sympathetic-related responding (sAA and systolic blood pressure) to the stressor (Fig. 5).[114] However, giving support did not alter cortisol responses to the stressor, a commonly studied output of the HPA axis, suggesting giving support may more directly benefit health through SNS pathways.

Consistent with our experimental laboratory findings, interventions outside of the lab have shown that being randomly assigned to give money to others (versus spend on oneself) leads to lower resting diastolic and systolic blood pressure after the intervention.[115] Furthermore, being randomly assigned to give support to specific others for 4 weeks (versus giving to the world in general, giving to the self, or keeping track of one's daily activities) leads to less proinflammatory gene expression, an inflammatory marker of stress influenced by SNS responding.[116] Similarly, random assignment to a volunteering intervention (versus wait-list control) leads to significantly lower IL-6 and cholesterol levels 4 months later.[117] These results suggest that giving support can reduce SNS and inflammation-related responding in the short term (i.e., minutes, weeks, and months), which may have implications for long-term physical health.

Taken together, the existing literature on giving support and health suggests that giving support affects health by increasing social and emotional well-being and reducing stress-related SNS, HPA, and inflammatory responding, physiological pathways known to contribute to both mental and physical health.[118] However, much more experimental work is needed to clarify the pathways by which giving support leads to health, particularly the role of the reinforcing pathways as proposed here. In addition, more experimental work will clarify causal directions between giving support and health.

When is giving support beneficial for health?

The results reviewed so far suggest that giving support is good for health. However, giving support is not always health promoting. For example, caregiving for an ill spouse, child, or family member has well-known negative consequences for physical health[119,120] and is recognized as a major stressor for some caregivers.[19,121] Understanding *when* giving support to others is beneficial is important for clarifying the conditions that lead giving support to be health-promoting or harming. We have focused on two factors that may affect health outcomes: perceptions that the support given was effective (support effectiveness) and perceptions of choice (free choice; Fig. 6).[15,122]

Support effectiveness

Giving support to others, as conceptualized in the current perspective, is performed in the service of helping a target in need. Therefore, perceptions that the support given was effective toward

the goal to help may influence the benefits that come from giving support. In particular, perceptions that one's support is effective should lead to benefits, whereas perceiving one's support is ineffective should not. Indeed, our previous work on neural regions involved in parental care and giving support showed that greater reports that one's support was effective was associated with greater VS and SA activity to giving support.[90] In the context of caregiving, some results are also consistent with the notion that the effectiveness of one's support can alter the health outcomes from caregiving. For example, caregiving for a recipient who one is less likely to effectively help, such as an individual suffering from dementia, was associated with poor health.[123,124] That is, giving support to an individual whose care needs are difficult to meet may render any giving ineffective. Giving ineffective support may in turn result in poorer, rather than better, health.

If support effectiveness is important to see the benefits of giving to others, how can perceptions of support effectiveness be increased? One factor that increases support effectiveness comes from the support recipient: when the support recipient appreciates or recognizes the support provided.[125] For example, perceiving that one's spouse appreciates the support that they receive moderates the association between giving support and self-reported physical symptoms such that greater perceptions of support effectiveness are associated with less physical symptoms.[126] In a similar vein, being acknowledged for the support one gives, which may increase feelings that one's support was effective, is associated with greater well-being (satisfaction with life).[127] In the other direction, signs that one's support was less effective, as evidenced by the receiver's reactions to the support, do not lead to benefits. For instance, those low in self-esteem are potentially less receptive to social support and less likely to interpret such support as helpful. Giving support to an individual low in self-esteem may thus be less beneficial for the giver. Indeed, giving social support to an individual with low (versus high) self-esteem results in less feelings of happiness and lower perceived relationship quality.[128] In other words, less benefits. These results suggest that the reaction from the receiver of support may influence the giver's health, especially as it relates to the effectiveness of one's support.

Although the role of support effectiveness has not been extended to examine long-term mental or physical health outcomes, results suggest that reactions from the recipient of the support can provide feedback to the giver. Extending current research on giving social support and health to examine interpersonal dynamics between the receiver's reaction and the health of the support giver will be interesting avenues for future research.

Free choice

A second factor that may influence whether giving support is beneficial is whether the giver feels they had the freedom to choose when and how they gave support.[15] In the only neuroimaging study to manipulate whether giving was freely chosen or not, both freely chosen and mandatory giving to others (versus the self) increased activity in the VS.[83] However, VS activity to giving was higher when participants freely gave to others compared to when they did not. Furthermore, satisfaction ratings with the giving were greater when participants freely gave. In another experimental study that manipulated free choice during a giving support scenario outside of the scanner, participants were either given the choice to choose how much money they wanted to give to others or were told how much to give. Those who freely chose to give support experienced greater emotional and social well-being (increased positive affect, vitality, and self-esteem), whereas participants without a choice did not experience benefits.[129] Finally, receiving external rewards for giving support to others can also undermine the perception that one freely gave and as a consequence, the benefits from giving. Although benefits from giving were not directly measured, children given a toy for helping (versus praise) were subsequently less likely to help again suggesting that external rewards can indeed undermine further giving behavior.[130] One reason why external rewards might be particularly damaging to the beneficial effects of giving are that they threaten perceptions that one freely chose to give support to someone else out of their own volition.

The health effects associated with chronic caregiving may also depend on free choice. The decision to become the primary caregiver for a sick loved one involves many considerations (e.g., one's economic situation, social resources available). As a result, there may not be a choice in whether one becomes a caregiver or not and this lack of choice may affect the benefits that come from caregiving. For instance,

those who felt they had a choice in whether they originally took responsibility for their loved one's care reported significantly less stress than those who felt they did not have a choice.[131] Conversely, lack of choice for caregiving among caregivers was associated with higher levels of emotional stress,[131] physical strain, and negative self-reported health from caregiving.[132] Similarly, giving support that is performed out of a sense of obligation, and thus a lack of free choice, has also been shown to relate to worse health-related outcomes such that giving more help in response to more frequent requests for help was associated with a higher inflammatory response (basal IL-6 and C-reactive protein (CRP) and stimulated proinflammatory cytokines to microbial challenge).[133] Should the reasons why one gives support to others undermine the perception of free choice, giving support may not lead to beneficial health outcomes.

These findings provide initial evidence that the two proposed factors, support effectiveness and free choice, help explain when giving support produces benefits for the giver. Although no experimental studies have included both support effectiveness and freedom of choice in the same study to examine its effects on the mechanisms proposed here, future research examining the brain's contribution to the health effects of giving support may benefit from a consideration of these two factors.

Implications and future directions

The current theoretical perspective suggests that an underexplored factor in the social ties–health link is the care given to others. One implication of this perspective is that known associations between socially supportive relationships and longevity (e.g., parenting,[134] marriage,[135] and social integration[5]) may be driven both by the support that is given and the support that is received. Indeed, greater volunteering in older adults is associated with greater longevity[136] and greater self-reported giving support within a close relationship is associated with lower mortality, above and beyond perceptions of receiving support.[137]

Should giving support to others be an additional avenue by which we benefit from being social, psychosocial interventions aimed at improving emotional, social, and physical health may consider ways to increase giving support behavior. Giving support to others may be an ideal behavior to target through intervention methods because giving to others is a controllable, modifiable behavior that can be encouraged and shaped to be effective for the giver. It is difficult to advise individuals to be more social or to receive more support from others as the barriers to being social or receiving support may be outside of the individual's control. Giving support, on the other hand, can be initiated by the giver themself and can be encouraged through both informal routes, such as when a friend writes a supportive note to another friend,[114] or formal routes, such as established volunteering programs. Furthermore, by encouraging giving support behavior, perceptions of receiving support, which is already an established and important contributor to the benefits of supportive social interaction,[11,138] may also increase. Therefore, the effects of socially supportive interactions may compound as more individuals benefit from both the support that is given and received.

A handful of giving support interventions already show promising results. Random assignment to giving support (versus nongiving) conditions leads to beneficial mental and physical health outcomes, suggesting giving support is a feasible social intervention.[116,117] However, it remains important to understand *how* giving support to others contributes to health. Some future directions have already been suggested (i.e., contribution of reinforcing mechanisms on health outcomes, integrating interpersonal dynamics that influence the benefits from giving support, measuring and manipulating support effectiveness and free choice), but I end with three additional future directions based on the proposed model (Fig. 2).

First, giving support appears to have effects on social well-being. Specifically, giving support (versus control conditions where no support is given) leads to increases in feelings of social connection[90,91] and greater feelings of social connection are associated with greater VS and SA activity to giving support.[90] These results suggest that giving support may have additional benefits by reinforcing feelings of social connection, feelings that are critical to the perceived quality of one's relationships and long-term health.[11,139] A largely unexplored part of the current model is whether and how giving to others strengthens existing social bonds or helps to create new bonds. However, the effect of giving support on social connections may be a fruitful avenue of

research for those interested in how social ties ultimately influence health.

Second, there is a potential role for the mPFC in giving support and health that deserves attention. Historically, animal models of parental care have focused on the contribution of subcortical regions, such as the mPOA, NAcc, and amygdala.[35] However, more recent data suggest a role for the mPFC as well.[140] Thus, chemical (tetrodotoxin) lesions (versus artificial cerebrospinal fluid) to the mPFC reduce pup retrieval.[141] In humans, greater NAcc activity to videos of one's own infant in mothers classified as giving synchronous, responsive parental care (versus intrusive care) is functionally correlated with mPFC activity.[79] However, intrusive parenting is characterized by a different pattern. Greater amygdala activity, rather than NAcc activity, in mothers classified as intrusive (versus synchronous) is functionally correlated with mPFC activity, suggesting ineffective inhibition of responses that disrupt responsive parental care. Outside of the context of parental care, greater mPFC to witnessing another person get socially rejected is positively correlated with observer ratings of how supportive participants are toward the victim (i.e., whether observers rate emails addressed to the victim as supportive)[142] suggesting activity in the mPFC to seeing others in need may predict support giving. Separately, the mPFC has emerged as an important mediator in the link between psychological experience and physical health,[109,118,143] in part through anatomical connections with some of the regions highlighted as critical to parental care (i.e., amygdala and VS).[39,144] Whether mPFC activity to giving support to those in need also mediates the link between giving social support and health remains an open, but intriguing, question.

Third, many of the neural regions implicated in parental care in animals, including the VS and amygdala, are densely concentrated with oxytocin, dopamine, and opioid receptors, neurochemicals theorized to play an important role in parental behavior.[145,146] Out of these three, oxytocin and dopamine are known to contribute to parental behavior in animals[147–149] and humans.[150,151] In addition, opioids are implicated in giving support-type behaviors in animals (e.g., allo-grooming[152,153]) and more broadly, to human prosociality, specifically toward one's close others.[154,155] Whether the benefits, including the health benefits, of giving support *relies* on activation of these neurochemicals on the neural regions implicated in parental behavior remains open for study, but future inquiry into the mechanisms linking giving social support and health may benefit from an understanding of neurochemical contributors.

Conclusions

Humans are fundamentally social. They thrive off supportive social relationships and suffer without such relationships.[1] Some of the strongest evidence for the importance of supportive social ties for humans comes from the longstanding finding that perceptions of support are associated with better health.[10,11,13,138] The current review examined an underexplored facet of socially supportive interactions, namely giving social support, and the beneficial health effects that the giver can acquire from providing support to others. In addition, emphasis was placed on the neural mechanisms that underlie giving support behavior and how recursive giving can then contribute to mental and physical health in the long term. Giving support may exert effects on health via neural regions shown in animals to be involved in parental care that both reinforce giving support behavior (VS, SA) and reduce stress and stress-related responding (amygdala). Finally, two conditions that foster positive health outcomes when giving support were highlighted: support effectiveness and free choice. The present approach contributes to the understanding of how social ties contribute to health by considering the support giver. Moving forward, researchers and practitioners should use this knowledge to design new interventions that increase giving behavior under the conditions that have been shown to influence health and well-being.

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Competing interests

The author declares no competing interests.

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