Introduction

Until recently, conceptual and empirical research on psychopathology has tended to focus on symptomatology and on grouping symptoms into syndromes. So, for example, studies of anxiety or depression focus on the neurophysiological, behavioral, or cognitive components of the symptoms of “anxiety and depression.” In the last 20 years, however, evolutionary approaches to psychopathology have emerged that focus on evolved strategies and their complex regulators. This directs attention to the evolved functions of motives and emotions, and, importantly for this paper, how they can suppress and coregulate each other. The evolutionary model starts with the fact that a range of emotional and motivational systems evolved because they helped meet the challenges of survival and gene replication in competitive environments. Brains and minds therefore monitor their social contexts and change their relationship to them with regard to risks, opportunities, and potential supports.

It is now recognized that one of the most important strategic adaptations for primates, and especially humans, is sociality; we are basically wired to seek helpful connections with others. It is our human motivation for connecting, relating, and communicating that has
driven social intelligence, from toolmaking to science, and more recently, the proliferation of communication technologies, social media on a global scale, and emotion regulation. Within this drive for connection and relating, humans play out a complex variety of motivations and interacting styles with each other (e.g., they can be supportive, caring, and desirous, or indifferent, exploitative, or hostile). These multifaceted and multiform motivations may compete for expression across relationships and even within any one relationship. In addition, we have minds with internal relationships with ourselves, so we can feel friendly, indifferent, or hostile to ourselves. What has become clear over the last 20 years is that certain motivational and emotional processes, which are linked to phenotypic and strategic orientations, are more strongly linked to physical and mental health than others. In brief, threat focus and competitive self-focus may be less conducive to well-being than a prosocial focus on self and others.

In fact, prosocial relationships have major impacts on a range of physiological systems, including genetic expression. Fredrickson et al. discovered that eudemonic well-being (positive emotion associated with meaning and helping others), in contrast to self-focused pleasure and hedonic well-being, was linked to motives and emotions that alleviate and help prevent mental health difficulties. Therefore, prosocial behaviors are beneficial to mental health and well-being.

**Evolution and motivation**

Motives can be understood in terms of their evolved function. Obvious nonsocial ones are harm avoidance, food, and shelter-seeking. In the social domain, social motives require specialist systems for processing social signals to engage in interactional sequences. For example, sexual behavior involves a (courting) dance between two partners, and at any point, miscommunication can result in one partner attacking or taking flight from the other. Social motives that require specialist competencies for processing potentially rapidly changing, dynamic, and reciprocal interactional sequences, have been referred to as social mentalities. Cen-
are associated with taking an interest in caring for others, in contrast to self-focused (competitive) motives to get ahead or avoid being inferior, shamed, and rejected, are associated with improved well-being and reduce vulnerabilities to psychopathology.\textsuperscript{8,12,18,22} Derived from social mentality theory, McEwan et al\textsuperscript{26} showed that in students and a depressed population, depression was linked to thwarted competitive motives (feeling inferior, unable to compete in the world, feeling like a loser) but was not related to caring motives (being kind, helpful, and trustworthy); depressed patients do not feel inferior in caring domains. So it is not negative self-evaluation in general, but a sense of self within a particular motivational system that is an issue for depression. In addition, depressed people can be fearful of being open to receiving compassion from others, as well as blocking self-compassion.\textsuperscript{27}

**Types of social affiliation**

In regard to motivational systems underpinning prosocial motivation and emotion, there appear to be two main forms. One relates to kin-based attachment-type relations.\textsuperscript{28} The other relates to alliance-building, cooperation, and friendship-network formations.\textsuperscript{29,30} Bailey\textsuperscript{31} distinguishes these two domains in terms of: (i) genetic kin-like forms of relating focusing on intimacy and closeness; and (ii) psychological kinships based on similarity of values and interests with cooperative potential. These can blend together. The simplest form of relating arises in dyads where two individuals come together for various reasons such as caring, helping, sharing, or sexual engagement. Working together, with a number of others, and feeling part of a group, “from me-ness to we-ness,” expands out into issues of group identity and group belonging.\textsuperscript{3,29}

It is well-known that kin-like, intimate and close, prosocial, loving, and caring early attachment relationships provide a wealth of resources which shape physiological systems and set phenotypes for increased health and well-being, whereas neglect and/or abuse do the opposite.\textsuperscript{13,17} In addition, there is now considerable evidence that alliances and friendships also play vital roles in physical and mental health, while, in contrast, loneliness and a lack of cooperating alliances (friendships) are highly detrimental to well-being.\textsuperscript{5} Indeed, studies of loneliness show it to be associated with a range of physiological problems, including adverse effects on telomere length.\textsuperscript{32} In many forms of psychological difficulty “feeling alone, different, and separate(d) from others,” is a very common experience.\textsuperscript{22} In addition, shame and self-criticism not only constitute negative self-experiences, in contrast to prosocial, liking, and helpful relationships with oneself, they also interfere with people’s abilities and confidence to develop supportive, affiliative relationships with others. People can be fearful of others being compassionate towards them because of what (they fear) might be discovered about them if other get too close, and the risk of rejection.\textsuperscript{33} Such fears disrupt the potential benefits of prosocial relationships and are associated with depression and anxiety.\textsuperscript{27}

**Evolution and emotion**

Researchers have long sought to derive an evolution-based, functional classification of emotions and identify their universal regulators,\textsuperscript{34} and roles in clinical problems.\textsuperscript{4} Panskepp\textsuperscript{35} delineated seven types of evolved functionally specific emotions that can also blend and operate together. These include: (i) emotions for seeking rewards/resources; (ii) emotions linked to lust which are particularly (but not only) focused on sexual stimuli; (iii) emotions linked to caring and affection; (iv) emotions linked to loss and feelings of grief; (v) threat emotions of rage; and (vi) fear; (vii) emotions that are linked to play and give a sense of joyfulness in activities.

A complimentary but different evolutionary functional analysis uses a more macro approach. Derived from the work of Depue and Morrone-Strupinsky,\textsuperscript{10} LeDoux,\textsuperscript{37} Panskepp,\textsuperscript{35} and others, based on clinical observation, and focusing on more general rather than specific functions, Gilbert\textsuperscript{2} highlighted three core evolved functions of emotions, loosely identified as:

1. Emotions that serve the functions of threat detection and generating defensive and safety strategies
2. Emotions that serve the functions of detecting, energizing and seeking/acquiring resources for survival and reproduction
3. Emotions that serve the function of contentment, satisfaction, calming, settling, and allowing “rest and digest.”

These are represented in Figure 1.

Although they are described as “systems,” it is more accurate to see them as rooted in patterns of (neuro) physiological activation that are constantly blending and coregulating. Importantly, affiliative relationships
Translational research can be linked to all three systems. For example, a threat to people we love raises anxiety, or anger to those who are threatening; spending time with friends and loved ones can be activating, enjoyable, and exciting; being in the presence of caring others helps us feel safe and content, and when we are distressed, can be soothing and calming.\textsuperscript{3,20,21,8} The reasons why social relationships that signal either threat or positive support/help, have such powerful psychophysiological regulating impacts, are related to our evolution as socially interacting mammals; indeed there is general agreement that it was our sociality that drove human intelligence.\textsuperscript{7}

The “three-circle” model of emotion is linked with attachment theory. Gilbert\textsuperscript{20} Bowlby,\textsuperscript{38-40} and Mikulincer and Shaver\textsuperscript{28} highlighted the fact that early attachments provide the young with proximity maintenance, a secure base and safe haven that are fundamental for development. A secure base provides the encouragement and confidence to go out and explore the world; a safe haven provides a source to return to for protection, soothing, and calming should the infant become distressed. These functions continue throughout life and we turn to others—friends, partners and lovers—to provide them. Importantly, signals indicating a presence or absence of a secure base and safe haven are linked to all three systems.

The value of this way of thinking can be seen when working with trauma, particularly in veterans. During their training, and while on missions, military personnel will experience elevated threat. They are then subsequently “calmed and soothed” in the context of being with their “buddies.” Indeed, the military deliberately fosters close interconnectedness. In essence, the secure base and safe haven become (re)wired from family and home to signals of the presence of buddies. When they return home with these rewired systems, a sense of connectedness and soothing may (for some) no longer be stimulated by wife and children, or even old friends. The removal of a sense of buddy-connectedness and safeness signals can activate the threat-vigilance systems; typical of major loss/separation. So veterans can experience high levels of threat from the sudden removal of important safeness signals, with a yearning to return to be with their (safe haven) buddies. However, they are so expecting (hoping) to feel safe and well when they come hope that they can find these inner experiences very distressing and confusing. Some believe they ought to feel safe and secure (or excited) back with their families and are not aware that all three systems have been (re)wired and so it will take time for them to be “wired back” into civilian, social contexts. Explaining the three-circle model and the possible process of “rewiring” according to context, to them and their families, can be very helpful and deshaming. Trying to understand trauma only through focusing on threat processing will be limited without also discussing the notions of secure base, safe haven, and how the parasympathetic system is linked to the functioning of the soothing system. Indeed, understanding the importance of the “buddy system” has stimulated work on the value of recruiting buddies and fellow veterans in the treatment of trauma.\textsuperscript{41}

Some (neuro)physiological mediators of prosocial motives and emotions and mental health

There are a number of key physiology adaptations that have facilitated enhanced affiliative and care-focused relating. Amongst evolved challenges for mammalian sociality are: (i) for close proximity not to trigger fear/flight or anger/fight; and (ii) provide advantages that support survival. MacLean\textsuperscript{42} highlighted the fact that parents needed to stop treating their offspring as just another meal (as some fish do). In addition, play

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\caption{Three types of affect regulation system. Reproduced from ref 22: Gilbert P. The Compassionate Mind: a New Approach to the Challenge of Life. London, UK: Constable Robinson; 2009. Copyright © Constable Robinson Ltd 2009}
\end{figure}
became a key source for mammalian interaction, especially where offspring are living close together. Porges\(^\text{43}\) suggests that the evolution of the myelinated vagus nerve was one part of the solution to such challenges. He has been at the forefront of suggesting that the myelinated parasympathetic system provides the physiological bases to put a brake on predatory, fight-and-flight behavior when individuals are in close proximity, and instead facilitate soothing and calming in the context of close relationships. This provides physiological infrastructures for the development of caring and cooperation; to enable individuals to help each other. Although some of the details of polyvagal theory have been questioned,\(^\text{44}\) there is good evidence now that this branch of the parasympathetic system is associated with prosocial behavior and well-being (see Kogan et al\(^\text{15}\) for a major review). A common way to explore the sympathetic-parasympathetic balance is with measures of heart rate variability.\(^\text{55}\) There is now good evidence that heart rate variability\(^\text{44}\) is an indicator for a range of physical or mental health difficulties and is strongly linked to the quality of social relationships.\(^\text{46}\)

Another key evolved physiological factor in prosociality is the hormone oxytocin, a nine-amino-acid neuropeptide hormone, produced in the hypothalamus.\(^\text{45}\) Oxytocin plays a fundamental role in a range of physiological processes throughout the body and is a key hormone in prosocial and affiliative behaviors.\(^\text{45,47}\) Oxytocin was central to the evolution of the mammalian caring/attachment behavior and now supports conspecific recognition, monogamous bonding, kin-attachment and bonding, increases trust, improves competencies in mind reading tasks, increases feelings of liking others, and reduces activation in the amygdala to threat.\(^\text{48}\) Importantly, it plays a significant role in threat regulation in general, there being oxytocin receptors in the amygdala.\(^\text{49}\) However, oxytocin is not a “be nice to all” hormone. It is also linked with greater hostility to outsiders and maternal aggression to potential threats to their infants.\(^\text{50}\) From an evolutionary point of view, oxytocin guides people to be selective in the choice of targets on which they focus prosocial behavior.

**Problems with the neurophysiology of prosocial relating to self and others**

A central argument of this section is that understanding how affiliative and prosocial systems work is key to understanding threat processing and psychopathology; one cannot understand psychopathology by analyzing threat or symptoms alone. It’s important then to recognize that the (neuro)physiological mechanisms that support prosocial and affiliative behavior have been identified as problematic in many people with psychological difficulties. Given parasympathetic functioning, and in particular heart rate variability, is linked to prosociality and mental well-being,\(^\text{15}\) Kemp and Quintana\(^\text{46}\) have provided a major overview of the link between poor heart rate variability and a range of psychological and physical difficulties. Low resting heart rate variability has knock-on effects to cardiovascular and immune systems, as well as mood regulation. Not only is there a direct connection between feeling socially connected and heart rate variability; Gillie and Thayer\(^\text{51}\) review the evidence that parasympathetic tone is very important for executive control and the integration of frontal cortical systems with deeper brain systems. They describe how executive control is compromised in people with post-traumatic stress disorder, and identify difficulties in parasympathetic regulation as a potential source. Austin et al\(^\text{52}\) found that people with borderline difficulties (reflected in difficulties in regulating emotions, a fragile sense of self, and problems in interpersonal relationships) do not differ in terms of sympathetic activation to threat compared with controls, but differ significantly in the parasympathetic responses to potential helpfulness—actually showing a more fight-flight profile in situations of helpfulness. In a study looking at people’s response to compassion, which involved imagining receiving kindness and compassion from others, Rockliff et al found that, when trying to imagine a compassionate other, low self-criticism and secure attachment were associated with improved/increased heart rate variability, but high self-criticism and insecure attachment were associated with a worsening of heart rate variability. In an fMRI study exploring the neurophysiological patterns of self-criticism and self-reassurance to threatening events, Longe et al\(^\text{44}\) found that high and low self-critics differed fundamentally in their neurophysiological profiles. For low self-critics, self-reassurance was associated with brain areas for calming. However, for those with higher self-criticism, efforts to be self-reassuring were associated with threat areas, such as the amygdala. Hence, for some individuals, efforts to be compassionate, reassuring, and kind to oneself activate threat systems. So, there are many studies suggesting that some
of the core physiological systems for prosocial emotion, thinking, and behavior are compromised in people with mental health problems. People are not able to use the parasympathetic-based soothing system for affect regulation and executive control.55,55

Looking at another major physiological system for prosociality, oxytocin, Yuen et al56 found that plasma oxytocin may be lowered in depression. This may account for some of the depressed person’s feelings of social disconnection, being cut off and different from others, separated, isolated, and lonely. Stanley and Siever57 suggested that a number of the interpersonal and emotion regulation difficulties associated with borderline personality disorder are indications of problems in oxytocin. Ebert et al58 developed a game to measure interpersonal trust and explored the impact of oxytocin (OT) in controls and people with borderline personality difficulties. One of their main findings was that “OT had a trust-lowering effect in highly traumatized patients.” Rockliff et al59 explored the impact of nasal oxytocin and placebo on the ability to generate and feel reassured by compassionate images. While oxytocin increased the experiences of compassion for many, some individuals with high self-criticism actually felt worse.

Training in compassion and prosocial behavior

Given that compassionate and prosocial behavior have such powerful influences on a range of physiological, psychological, and social processes, it follows that training people to cultivate compassion motives and emotions may be therapeutic. This raises the question about the focus for compassion, because compassion can be explored in relation to compassion we have for others, the way we respond to the compassion from others and self-compassion.11,22 There is increasing evidence that forms of meditation practices involving imagining compassion for others creates beneficial changes in the frontal cortex and immune system, as well as feelings of well-being.60 Hutcherson et al found that a brief loving-kindness meditation increases feelings of social connectedness and affiliation towards strangers. Fredrickson et al61 found that six 60-minute weekly group sessions with home practice based on a CD of loving kindness meditation (compassion directed to self, then others, then strangers) increases positive emotions, mindfulness, feelings of purpose in life, and social support, and decreases illness symptoms compared with a control group. Weng et al62 found that compassion training increases people’s prosocial behavior and neurophysiological responses to suffering in others. Hoge et al63 found that women with experience of loving-kindness meditation had longer relative telomere length than controls. The beneficial effects of compassion cultivation are not just linked to meditations but to values, and to the ways we live our lives.18

Psychotherapy has also begun to focus on compassion and prosocial cultivation as therapeutic targets in their own right.11,19,65,66 Focusing on the experience and development of compassion has been found to reduce depression, anxiety, and self-criticism in people presenting to a community mental health team,67 in people with long-term mental health problems,68 and people in a high-security psychiatric setting.69 Compassion-focused therapy (CFT) has been shown to be helpful for people with psychosis70,71; and for people with emotional difficulties and personality disorders.72 Ashworth et al73 found CFT to be a valuable addition in helping people with acquired brain injury.

Some researchers have focused on a particular and specific kind of self-compassion that involves cultivation of mindfulness (rather than attentional absorption in difficulties), a sense of common humanity (rather than a sense of shame and isolation), and non-judgement (rather than self-criticalness).74 Recent trials in nonclinical populations have shown this to be beneficial to well-being.75 For depressed people, Kuyken et al76 found that in a mindfulness trial, self-compassion was the significant mediator between mindfulness, change, and recovery from depression. A recent meta-analysis of compassion focused interventions found good evidence of effectiveness.77

Although compassion cultivation training can be helpful, therapists need to be aware that they can run into serious obstacles along the way. As noted above, there are a range of physiological systems that may be compromised and make compassion processing difficult. A series of studies suggest that some patients have negative beliefs about compassion and generally being kind and supportive to oneself. These include ideas about not deserving it, no trusting it, or seeing it as a weakness or an indulgence.78 In addition, when some individuals, especially those from a neglectful and abusive background, start to experience compassion, this
can ignite a powerful grief process.\textsuperscript{33,27} Importantly too, early trauma can create body memories that can block compassion and make experiencing caring and affiliation from others frightening.\textsuperscript{79}

**Conclusion**

We should not be surprised by the power of prosocial motives and emotions to create contexts for health, because supportive affiliative and helpful relationships provide major benefits for survival and reproduction. The mammalian and human brain and body are highly adapted to be regulated through social relationships. Moreover, it has been known for a long time that secure attachment and ongoing support throughout life provides major buffers against stress and vulnerability.

Despite this, it is comparatively recently that researchers have begun to look at people’s psychological and physiological capacities and competencies for prosocial processing as a way of helping to stabilize affect regulation and sense of self. Most pharmacological models ignore these complexities and focus mostly only on threat the physiologies of processing, eg, of anxiety or depression, rather than their regulators, such as social contexts, sense of self-identity, shame, trauma memories, or prosocial competencies and motives.

As we understand more about the regulating processes underpinning prosocial relating, we will be better able to develop therapies for cultivating them, and not simply rely on trying to tone down the threat system, be it with drugs, various forms of exposure, or cognitive reappraisals.

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Emociones y motivos prosociales y de afiliación en salud mental

Este artículo plantea que los estudios de salud mental y bienestar pueden ser contextualizados dentro de una perspectiva evolutiva que pone de relieve los procesos de co-regulación de las emociones y los motivos. En particular sugiere que, aunque muchos síntomas de salud mental comúnmente están relacionados con procesos de amenaza, la atención también necesita estar dirigida a los principales reguladores del procesamiento de la amenaza, es decir, las interacciones prosociales y de afiliación con uno mismo y con los demás. Teniendo en cuenta que la socialización humana ha sido un factor central para toda una serie de adaptaciones humanas, se requiere de una mejor comprensión de los efectos de las interacciones prosociales sobre la salud, y se deben integrar en las formulaciones e intervenciones psiquiátricas. La comprensión de los procesos de co-regulación de los motivos y las emociones, especialmente las prosociales, ofrece mejores formas de entender los problemas de salud mental y su prevención y alivio.

Émotions et motivations prosociales et affiliatives en santé mentale

Cet article traite des études de santé mentale et de bien-être pouvant être contextualisées dans une approche évolution qui souligne les processus de co-régulation des émotions et des motivations. Il indique en particulier que malgré la relation courante de nombreux symptômes de santé mentale avec le traitement de la menace, il faut aussi prendre en compte les régulateurs majeurs de ces processus, c'est-à-dire les interactions prosociales et affiliatives avec soi-même et avec les autres. La sociabilité humaine étant un fil conducteur pour une grande partie des adaptations chez l'homme, les effets des interactions prosociales sur la santé demandent à être mieux compris et intégrés dans les interventions et formulations psychiatriques. Mieux connaître les processus de co-régulation des motivations et des émotions, en particulier les processus prosociaux, permet de mieux comprendre les difficultés de santé mentale, ainsi que leur prévention et leur soulagement.

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