Psychoneuroendocrinology 105 (2019) 138–146

Contents lists available at ScienceDirect

Psychoneuroendocrinology

journal homepage: www.elsevier.com/locate/psyneuen

Embodied stress: The physiological resonance of psychosocial stress

Veronika Engert[a,*], Roman Linz[a], Joshua A. Grant[b]

[a] Max Planck Project Group Social Stress and Family Health, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany
[b] Max Planck Research Group Pain Perception, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany

ARTICLE INFO

Keywords:
Empathy
Contagion
Resonance
Empathic stress
Cortisol
Sympathetic nervous system

ABSTRACT

Psychosocial stress is a ubiquitous phenomenon in our society. While acute stress responses are necessary and adaptive, excessive activation of neurobiological stress systems can predispose an individual to far-reaching adverse health outcomes. Living in a complex social environment, experiencing stress is not limited to challenges humans face individually. Possibly linked with our capacity for empathy, we also display the tendency to physiologically resonate with others' stress responses. This recently identified source of stress raises many interesting questions. In comparison to the wealth of studies that have advanced our understanding of sharing others' affective states, the physiological resonance of stress has only recently begun to be more closely investigated. The aim of the current paper is to review the existing literature surrounding the emerging area of "stress contagion", "empathic stress" or "stress resonance", as it has been variably called. After a brief introduction of the concepts of stress and empathy, we discuss several key studies that paved the way for the merging of empathy with the concept of physiological resonance. We then delineate recent empirical studies specifically focusing on the physiological resonance of stress. In the final section of this review, we highlight differences between these studies and discuss the variability in terminology used for what seems to be the same phenomenon. Lastly, potential health implications of chronic empathic stress are presented and possible mechanisms of physiological stress transmission are discussed.

1. Introduction

The stress response is a healthy and adaptive function in situations of acute challenge. However, prolonged stress exposure may cause permanent dysregulation of the neurobiological stress systems, thereby leading to wear and tear on the body and brain termed allostatic load (McEwen et al., 2015). The respective physiological changes, specifically within the sympathetic nervous system (SNS) and hypothalamic-pituitary-adrenal (HPA) axis, have been linked to detrimental health effects, including cardiovascular, metabolic, autoimmune and mental diseases (Chrousos, 2009; McEwen, 2008; Sapolsky, 2004). While chronic stress can undoubtedly arise from traumatic life events, examining extreme adversity has taken us only so far in understanding why individuals living in less demanding conditions are also susceptible to stress-related conditions. One potential explanation is that allostatic load can accumulate in the presence of non-traumatic but persistent stressors (Almeida, 2005; DeLongis et al., 1982; Lazarus and Folkam, 1984). Above and beyond the daily hassles experienced firsthand, stress can be transmitted between individuals. Understanding this physiological resonance of stress may be a key aspect to explaining how the daily environment, without being traumatic, can significantly impact our health and wellbeing.

In the current paper, we review the newly emerging area of physiological stress resonance. Accordingly, studies were selected if they examined physiological resonance in two or more individuals, one of whom was subjected to stress or a stress-like challenge. Studies addressing resonance with other emotional states such as sadness or pain were not included (e.g. Harrison et al., 2006; Hein et al., 2011). Also, research addressing physiological responses to others' suffering, but without accounting for resonance between the suffering target and empathizing observer, were excluded (e.g. Liew et al., 2003, 2011). Although not all of the summarized work related physiological stress resonance to self-report measures of empathy, the original results were generally discussed in the context of empathy research. Thus, we touch on three independent research fields: stress, empathy, and physiological resonance. While it is beyond the scope of this review to provide a comprehensive theoretical background on each of these fields, a brief synthesis of basic concepts and ideas is given. We begin with an overview of the stress system and a definition of empathy and related terms. From there, a short history is presented featuring a number of seminal

* Corresponding author at: Max Planck Institute for Human Cognitive and Brain Sciences, Max Planck Project Group Social Stress and Family Health, Stephanstr. 1a, 04103, Leipzig, Germany.
E-mail address: engert@cbs.mpg.de (V. Engert).

https://doi.org/10.1016/j.psyneuen.2018.12.221
Received 13 June 2018; Received in revised form 12 November 2018; Accepted 16 December 2018

neural and peripheral-physiological studies that helped establish the notion of physiological resonance as an embodied substrate of empathy. Despite the fact that empathy research has evolved around negative states such as pain and disgust, the idea of empathy for another's stress is quite new. We will review the work of several groups, differentiating between studies examining stress resonance within the autonomic nervous system and the HPA axis. In a final section, we address unresolved issues in the area of embodied stress research. More specifically, we will highlight methodological differences between existing studies, discuss inconsistencies with regard to terminology, focus on potential mechanisms or channels of stress transmission, and lastly point to putative health implications for individuals resonating with chronically stressed others.

2. Stress

Stress is defined as a state in which an organism's homeostasis is threatened (or perceived to be threatened) by external or internal effects (Chrousos, 2009). Homeostasis is re-established by a complex repertoire of behavioral and physiological adaptive responses. The principal end-effectors of the stress system are cortisol, released by the HPA axis, and the catecholamines norepinephrine and epinephrine, released by the SNS. These end-effectors regulate behavioral, metabolic, cardiovascular, immune, and gastrointestinal functions, among others (Chrousos, 2009; McEwen, 2008). An acute stress response is a highly adaptive cascade of events providing the organism with the necessary motivation and energy to "fight-or-flight" in the face of adversity (Cannon, 1915). However, the very mechanisms that are adaptive short-term may promote pathophysiologic changes when experienced chronically. This fact is particularly relevant to socially complex species such as primates that can generate chronic stress for purely psychological reasons (Sapolsky, 2004).

3. Empathy and related phenomena

There are many definitions of empathy and contentious issues in the field of empathy research. Delving into these debates in too much detail risks losing the focus of the present review. Rather, we present a broad definition and then discuss how more narrow views differ with respect to that definition. In the process several unresolved issues will be raised.

The scientific endeavor to explain how we understand the feelings of others dates back to the German philosopher Theodor Lipps and his theory of *Einfühlung* ("feeling into"). *Einfühlung*, translated as "empathy" (Titchener, 1909), was suggested to result from the process of projecting oneself into an object of perception (Lipps, 1903). Following Lipps' early philosophical perspective, social psychologists (e.g. Batson, 1991, 2009; Davis, 1994; Eisenberg, 2000; Hatfield et al., 2009; Hoffman, 2000) and social neuroscientists (e.g. de Vignemont and Singer, 2006; Decety, 2011; Preston and de Waal, 2002) have been advancing the field of empathy. For the most part, researchers either explicitly claim that empathy is, or involves, sharing of an affective state between the person initially experiencing that state and a second person who observes the state in the other. However, the details on where to place empathy itself within the realm of several related phenomena, and what exactly constitutes empathy differs markedly between researchers.

Broad accounts describe empathy as a shared emotional experience, occurring when the perception of an object's emotional state leads to a similar emotional state in the subject (e.g. Hoffman, 2000; Preston, 2007). According to these broad conceptualizations, empathy is a superordinate category that subsumes phenomena such as emotional contagion, mimicry, sympathy and perspective taking (Preston and de Waal, 2002). De Waal and Preston (2017) argue that complex processes such as empathy are ultimately products of evolution, which have had many precursors in less cognitively-advanced species. As a result, humans are endowed with a toolbox of related processes which are distinguishable but largely inseparable. They argue that focusing on distinctions between the empathy-related phenomena risks losing sight of the "functionally integrated whole" (de Waal and Preston, 2017).

As pointed out by Levenson and Ruef (1992), the literature on empathy deals with several seemingly distinct aspects. First, empathy research has described the concept as knowing what a person is feeling, denoting a cognitive aspect. Secondly, empathy has been conceptualized as feeling what a person is feeling, involving a more experiential sharing. Thus, definitions or research agendas may be biased toward cognitive empathy (also referred to as perspective taking, theory of mind, or mentalizing) or emotional empathy (also called simply empathy, affective empathy, or affect sharing). There is now quite firm evidence that both exist and contribute to our ability to understand others. A meta-analysis of studies has demonstrated overlapping networks for what the authors referred to as affective-perceptual and cognitive–evaluative empathy (Fan et al., 2011). Distinct results have also been reported by Singer and colleagues (Kanske et al., 2015) using a task specifically designed to tease apart the affective and cognitive paths to understanding the states of others.

Singer and colleagues have put forth a narrow definition, with explicit distinctions made between empathy and related concepts. Empathy is restricted to the process of inferring the affective state of another person by generating an isomorphic state in the self, while realizing that the source of that state lies in the other person and not in oneself (de Vignemont and Singer, 2006; Singer and Lamm, 2009). Emotional contagion, in this account, involves affect sharing but does not require knowledge of the source of the state (i.e. no self-other distinction). Sympathy, in Singer's account, refers to an affective state in an observer that arises from another person's state but which is not isomorphic. Finally, in cognitive perspective-taking, the mental state of another is represented, yet this representation lacks emotional involvement. The implications of how one decides to structure empathy-related phenomena are substantial.

Do human infants or animals have the capacity for empathy? The answer to this question depends on how one defines the concept. If conscious awareness is necessary, specifically, if one must be aware that the origin of an empathic state is a conspecific, then we would conclude that neither human infants nor animals are capable of empathy. If, on the other hand, a broad conceptualization of empathy is held, then both infants and animals demonstrate empathy-related behavior.

4. Neural mechanisms of empathy

Regardless of the differences touched upon above, the predominant mechanistic view of contemporary empathy theories revolves around the idea of shared neural networks. "Neural resonance" accounts of empathy are based largely on brain imaging findings of overlapping activation patterns when observing or actually experiencing a given state (Zaki and Ochsner, 2012). Neural resonance has been shown between the observation and execution of motor tasks, but also in the somatosensory domain (Keysers et al., 2010) and for visceral states such as pain and disgust (Lamm et al., 2011; Lamm and Singer, 2010). Supporting the hypothesized link with empathy, studies have also provided evidence for an association between questionnaire measures of trait empathy (Davis, 1983; Mehrabian and Epstein, 1972) and shared brain networks in the domains of touch (Kuehn et al., 2013), pain (Singer et al., 2004) and disgust (Jabbi et al., 2007; Wicker et al., 2003). Decety and Sommerville (2003) point out that the first-hand and vicarious representations observed in brain imaging studies usually do not fully overlap and suggest this may be important with regard to allowing individuals to distinguish between oneself and other people.

A formalized account of how such findings may come about was put forth in 2002. The perception-action (PA) model of empathy (Preston and de Waal, 2002) attempts to explain how emotional and mental states, and possibly physiology, could be shared between individuals.

Briefly, PA models posit that the neural representations underlying actions and perceptions are not independent, contrary to earlier models, which placed cognitive events between perceptual and motor acts. In PA models, activation of perceptual representations, if attended to, automatically activates motor representations, and vice versa. PA models can explain, for example, why observing a facial expression often results in a highly similar pattern of muscle activity in the observer's face. Importantly, that effect is proposed to occur automatically and presumably also initiates the corresponding autonomic patterns underlying the transmitted state. Thus, PA models have been invoked to explain many empathy-related phenomena.

From a cellular point of view, a major breakthrough in our understanding of how experiences may be shared between individuals came with the discovery of "mirror neurons" in macaque monkeys by Giacomo Rizzolatti and colleagues. The team of neurophysiologists found robust activation of cells in the premotor cortex of an alert monkey while it observed an experimenter making a grasping movement. Remarkably, the same neurons discharged when the monkey performed the grasping movement itself (Di Pellegrino et al., 1992). While mirror neurons have been proposed as the basis of neural resonance and perception action models of empathy, what exactly mirror neurons do is still intensely debated (Hickok, 2013).

5. Peripheral-physiological resonance of stress

5.1. Examination of autonomic nervous system activity

Peripheral-physiological resonance refers to synchronous patterns of physiological activation that arise as a result of an observer watching a target. Compared to neural resonance, it has received relatively little attention in the domain of empathy research. This is surprising given that autonomic measures react quickly to affective change, can be recorded with high temporal resolution and are relatively inexpensive. The first demonstration of autonomic linkage was conducted with therapist-patient dyads in studies of psychotherapy (Di Mascio et al., 1957, 1955) and between members of small peer groups (Kaplan et al., 1964). However, in these early studies, autonomic linkage was not conceptually associated with an independent measure of empathic capacity. Twenty years later, Levenson and Gottman began studying autonomic linkage between spouses during marital conflict situations (Gottman and Levenson, 1985; Levenson and Gottman, 1983). Importantly, the group soon developed a behavioral procedure to assess participants' ability to accurately detect the feelings of another person (Levenson and Ruef, 1992). Observers viewed video sequences of spouses engaged in naturalistic marital interactions and continuously rated the affect experienced by a designated target spouse. The observers' ratings were then compared to the targets' actual affective ratings, which had been previously assessed. Autonomic physiology (heart rate, skin conductance level, general somatic activity, pulse transmission time to the finger and finger pulse amplitude) was also recorded and compared for both individuals. For the first time, the physiological linkage between an observer and a target could thus be related to the observer's emotional rating accuracy. Results supported the idea of a peripheral-physiological substrate for empathy. In both men and women, greater overall physiological linkage between observers and targets (driven by the sympathetic measures of skin conductance and pulse transmission to the finger) predicted greater accuracy of the observers' ratings of the targets' negative affect (Levenson and Ruef, 1992). Several studies have since demonstrated autonomic linkage while observing others' affective states such as sadness or pain (e.g. Harrison et al., 2006; Hein et al., 2011).

Following Levenson and Ruef's (1992) study, another 20 years passed until the topic of peripheral-physiological resonance was taken up in the context of stress research (see Table 1 for a summary of studies). In what we deem to be the first study of "empathic stress", "stress contagion" or "stress resonance", Ebisch et al. (2012) used non-intrusive thermal imaging to test whether there was physiological sharing of autonomic responses ("autonomic contagion" in their words) when mothers witnessed distress in their children. To induce an ecologically valid stressful experience, three-year-old children were exposed to the mishap paradigm, where they were falsely led to believe they broke a toy provided by the experimenter (Cole et al., 1992). Behavioral cues confirmed an increase in children's distress starting with the mishap (as opposed to the stress-free introduction and playing phases of the paradigm). Simultaneously, an increase in sympathetic activation became apparent in both the children and mothers. Sympathetic fluctuations in the mother-child dyads were significantly correlated, providing first evidence for stress contagion as an embodied autonomic process. Using similar methodology, Manini et al. (2013) extended the previous finding by showing that autonomic contagion is not limited to mother-child dyads. Albeit less pronounced compared to mothers, autonomic responses in women correlated with those of unknown children they were observing during distress.

Waters et al. (2014) provided intriguing evidence for what the authors termed sympathetic "stress contagion" in mother-infant dyads. In their study, mothers were randomly exposed to either social evaluation with negative feedback (negative stressor), social evaluation with positive feedback (positive stressor) or no evaluation while separated from their infants. Upon reunion, the mothers' stress levels were transmitted to the infants such that higher sympathetic activation in the mothers (measured in terms of pre-ejection period of the heart) triggered higher heart rate in the infants. This mother-child covariation was strongest after the experience of a negative stressor and strengthened over time. Moreover, infants' behavioral avoidance of the experimenter was stronger if mothers had experienced (either negative or positive) evaluative stress. Unlike in the study by Ebisch et al. (2012), physiological covariation in Waters and colleague's paradigm likely developed without infants' conscious awareness of the source of their affective state. Furthermore, infants did not observe the first-hand stressor itself. Stress-induced changes in mothers' facial expression, vocal tone, prosody, posture, odor and touch were all suggested as possible channels through which stress may have been communicated from mother to child (Waters et al., 2014).

In subsequent work, Waters et al. (2017) revisited the topic of affect and stress contagion, with an additional focus on the mechanism of transmission. Using a similar experimental setup, sympathetic and parasympathetic covariation between mothers and infants were assessed after either social evaluation with negative feedback (negative stressor) or the induction of a low arousal positive state (relaxation) in the mothers. As a possible pathway of transmission, the opportunity for physical contact between the mothers and infants upon reunion was experimentally manipulated. Suggesting that a low-arousal positive state can also be shared, parasympathetic covariation between mothers and infants was stronger when mothers experienced relaxation as opposed to negative stress. Surprisingly, the manipulation of touch had no influence on parasympathetic covariation. On the other hand, and consistent with the author's prior results, sympathetic covariation was found to be stronger when mothers experienced negative stress rather than relaxation. The manipulation of touch played a significant role for sympathetic covariation, albeit only in dyads with stressed mothers. While stress contagion occurred regardless of mother-infant touch, the strength of sympathetic covariation was greater, and increased over time, if the infants were held by their mothers. Without the possibility of mother-infant touch, sympathetic covariation in the stressed dyads decreased over time. On a behavioral level, infants whose mothers completed the relaxation task were rated by the experimenter as more comfortable than infants whose mothers were exposed to negative stress. Overall, these results support the idea that touch is an important pathway via which sympathetic stress activation is transmitted and synchronization is maintained. Touch does not seem to be necessary for sympathetic resonance to arise in the first place, however. Also, parasympathetic resonance seems to operate differently than sympathetic

Table 1
Summary of available studies on the physiological resonance of stress. Studies were included if they implemented an experimental stress induction task, and assessed physiological activity simultaneously in observers and targets.

Authors; sample	Term for resonance	Physiological measures	Empathy measures	Induction
Autonomic nervous system				
Ebisch et al. (2012) N = 12 mother-child dyads (9 female) Mothers: 31–46 years Children: 38–42 months	Autonomic contagion	Facial thermal imprints (various indicators of autonomic activity)	None	Acute distress (mishap paradgim; Cole et al., 1992)
Manini et al. (2013) N = 18 mother-child dyads; N = 18 mothers and N = 14 children (7 female) Mothers: 23–43 years Children: 39–45 months	Vicarious autonomic response	Facial thermal imprints (various indicators of autonomic activity)	None	Acute distress (mishap paradgim; Cole et al., 1992)
Waters et al., (2014) N = 69 mother-infant dyads (45% female) Infants: 12–14 months Mothers: X̄ = 33.6 years	Stress contagion	Mothers: preejection period (sympathetic activity); Infants: heart rate (predominantly sympathetic activity)	None	Acute stress (modified Trier Social Stress Test; Kirschbaum et al., 1993)
Waters et al. (2017) N = 105 mother-infant dyads (49% female) Infants: 12–14 months Mothers: X̄ = 33.77 years	Affect contagion; stress contagion	Mothers: respiratory sinus arrhythmia (parasympathetic activation); preejection period (sympathetic activity) Infants: respiratory sinus arrhythmia (parasympathetic activation); interbeat interval (predominantly sympathetic activity)	None	Acute stress (modified Trier Social Stress Test; Kirschbaum et al., 1993); acute relaxation (low-arousal positive video)
Dimitroff et al. (2017) N = 63 observers-target dyads; N = 63 observers (41 female) and N = 21 targets (11 female) Observers: X̄ = 20.5 years Targets: 18–22 years	Stress contagion	Interbeat interval (predominantly sympathetic activity)	Questionnaire of Cognitive and Affective Empathy (Reniers et al., 2011)	Video stimulus set featuring minimal stress, high stress and stress recovery
Hypothalamic-pituitary-adrenal axis				
Buchanan et al. (2012) N = 152 observer-target dyads; N = 20 observers (11 female) and N = 112 targets (55 female) Observers: 18–28 years Targets: 18–50 years	Empathic resonance of stress	Salivary cortisol; salivary alpha-amylase	Interpersonal Reactivity Index (Davis, 1983)	Acute stress (Trier Social Stress Test; Kirschbaum et al., 1993)
Engert et al. (2014) N = 211 observer-target dyads; N = 211 observers (149 female) and N = 151 targets (31 female) 18–35 years	Empathic stress: vicarious stress vs. stress resonance	Salivary cortisol; salivary alpha-amylase; heart rate	Interpersonal Reactivity Index (Davis, 1983); Emotional Response Scale (Batson et al., 1997)	Acute stress (Trier Social Stress Test; Kirschbaum et al., 1993)
Engert et al. (2018) N = 44 couple dyads 19–35 years	Diurnal cortisol covariation	Salivary cortisol	None	Acute stress (Trier Social Stress Test; Kirschbaum et al., 1993)

resonance.

In another recent study, Dimitroff et al. (2017) showed that the phenomenon of “stress contagion”, investigated in adult dyads, may be more complex than previously recognized. The authors tested the extent to which observers’ cardiac responses were associated with the cardiac responses of stressed targets displayed via pre-recorded video. Further, they tested whether this relationship was dependent on levels of self-reported empathy in the observers (assessed with the Questionnaire of Cognitive and Affective Empathy; Reniers et al., 2011). Videos depicted targets speaking in three conditions: without exposure to a social stressor (no stress), during a social stressor (stress) or after experiencing a social stressor (recovery). Cardiac activity for both observers and targets was recorded on a beat-to-beat basis (inter-beat interval) allowing the determination of autonomic contagion with high temporal resolution. While observers exhibited distinct patterns of cardiac reactivity depending on the observation condition, the direction of effects was unexpected. More specifically, the inter-beat-interval remained at baseline when observers viewed non-stressed targets, increased (i.e., heart-rate slowed down) when viewing overtly stressed targets and decreased (i.e., heart-rate increased) when observing the recovery condition. In line with previous literature (Lang et al., 1993), the authors suggest the cardiac deceleration when observing others’ stress may be indicative of a freezing response. Neither the stress condition deceleration, nor the recovery condition acceleration were related to self-reported affective empathy (i.e., sharing another’s affect) or cognitive empathy (i.e., representing the state of another through top-down processes). Also, despite the condition-wise effects, the targets’ actual stress levels were not predictive of the degree of cardiac contagion. Lastly, and perhaps most importantly, the level of observers’ affective empathy predicted the time required to reach maximum correlation with the target in the stress recovery condition. In other words, participants who reported being more affectively empathetic synchronized with the targets’ cardiac rhythm faster than participants scoring lower in trait affective empathy.

In summary, studies employing autonomic measures have repeatedly demonstrated stress contagion between individuals. There appear to be different mechanisms of transmission (e.g. touch and visual) and variability of results depending on the type of state induced, the context and the specific physiological indices employed. We now move to studies including measurements of endocrine stress reactivity.

5.2. Examination of hypothalamic-pituitary-adrenal axis activity

The term stress is used in many ways, however in stress research its definition is quite strict. Beyond the requirement of SNS system activation as an unspecific sign of general arousal, stress experience requires activation of the HPA axis, resulting in cortisol release (Chrousos, 2009; Hellhammer et al., 2009). Thus, true stress contagion or empathic stress should also involve resonance of cortisol activity. The first study to investigate the physiological resonance of stress at the level of the endocrine system was published by Buchanan and colleagues in 2012. Salivary cortisol and alpha-amylase (a marker of sympathetic activity; Nater and Rohleder, 2009) were measured simultaneously in both the stressed targets and observing committee members of the Trier Social Stress Test (TSST; Kirschbaum et al., 1993). The TSST is a standardized laboratory task in which participants perform a free speech and mental arithmetic task while allegedly being video- and audio-recorded, as well as evaluated by a panel of one or more committee members. The committee members are part of the research team and trained to withhold any social engagement or positive feedback, thereby creating an element of social-evaluative threat. Demonstrating “empathic resonance of stress", Buchanan et al. (2012) found that observers (i.e., committee members) showed increases in cortisol release that were proportional to the cortisol release of the stressed targets (i.e., participants). Moreover, observers’ cortisol responses were positively associated with their own aptitude for empathic concern and perspective taking, as measured by a multidimensional trait empathy index (Interpersonal Reactivity Index; Davis, 1983). Lastly, observers’ cortisol responses were unrelated to targets’ alpha-amylase release or self-reported affect. With respect to sympathetic resonance, stress-induced alpha-amylase release was uncorrelated between observers and targets. Interestingly, however, observers’ alpha amylase levels were positively associated with their own empathic concern and perspective taking, and correlated with targets’ self-reported affect.

Taken together, Buchanan and colleagues results suggest that both the endocrine and sympathetic dimensions of stress resonate with empathic observers, but tap into different systems. Observers’ cortisol responses resonate with targets’ cortisol levels, but their sympathetic responses resonate with the targets’ self-reported affect. While some of the endocrine activation, and even the resonance, in the committee members may have originated from first-hand stress as a result of actively stressing out another individual, this study provided the first demonstration of “full-blown” physiological stress resonance implicating both HPA axis and sympathetic reactivity.

Our own work extended Buchanan’s by differentiating between two aspects of what we referred to as “empathic stress” (Engert et al., 2014): vicarious and resonant. More specifically, vicarious stress was suggested to develop through the projection of the observer’s own perspective onto the target. Accordingly, an observer who appraises the target’s situation as stressful would mount a cortisol stress response irrespective of the target’s actual state. In stress resonance, on the other hand, the observer was suggested to explicitly share the target’s stress response. Thus, as was the case in Buchanan’s study, observer’s and target’s stress-induced cortisol release would be proportional to one another. To test this, and several potential modulatory factors of empathic stress, we systematically manipulated the familiarity between observers and targets (partners vs. strangers), as well as the modality of observation (real-life vs. virtual) and the observer sex (male vs. female). In the real-life observation modality, observers watched the TSST through a one-way mirror. In the virtual observation modality, they watched via live video feed. In all cases, observers watched an opposite-sex target being stressed. We assessed salivary cortisol, alpha-amylase and heart rate simultaneously in both dyad members. The study results revealed that overall, 26% of observers showed empathic stress (i.e., vicarious or resonant) in terms of a physiologically relevant cortisol increase of at least 1.5 nmol/l above baseline levels (Miller et al., 2013). Empathic cortisol stress responses were more pronounced in partners than strangers (40% vs 10%) and in the real-life representation of the stressful situation compared to the video feed (30% vs 24%), but not restricted to these conditions. Actual cortisol stress resonance, however, emerged primarily in partners and in the real-life representation of the stressful situation. Sex had no influence on either aspect of the empathic cortisol stress response. Our measure of self-reported empathy influenced both vicarious and resonant stress. Vicarious cortisol responses were positively associated with state empathic concern, while resonant responses were associated with trait and state empathic concern, trait perspective taking, trait fantasy and state personal distress. Alpha-amylase and heart rate, as markers of sympathetic arousal, only partially mirrored the cortisol results. While vicarious sympathetic arousal was stronger in emotionally close observer-target dyads and the real-life observation modality, unlike cortisol, there was no evidence for sympathetic resonance. Neither sex nor self-reported trait or state empathy had an influence on the sympathetic domain of either vicarious or resonant empathic stress.

The results of our study nicely replicated Buchanan et al.’s (2012) finding of cortisol stress resonance. We further demonstrated that observers can be entirely passive witnesses of others’ stress, and that observers are prone to resonate stronger when emotionally close to a target, when observing the stressful situation in person, and when exhibiting higher self-reported empathy. Our results are also consistent with Buchanan’s in terms of the specificity of the endocrine vs. sympathetic domains of empathic stress. More specifically, both studies show it is rather the cortisol than the sympathetic responsiveness that links individuals during stress. Overall, the emerging research suggests that the family unit – providing maximal emotional and spatial closeness between individuals – would seem to offer ideal conditions for the emergence of stress resonance.

While highly controlled laboratory experiments are critical, naturalistic methods may provide a truer reflection of relationship processes (Laurenceau and Bolger, 2005; Scollon et al., 2003). In a follow-up study (Engert et al., 2018), we therefore investigated the ecological validity of laboratory-induced cortisol stress resonance. We tested whether an individual's tendency to synchronize to their partner's acute cortisol stress response is related to their degree of everyday diurnal cortisol covariation. A sub-sample of 44 opposite-sex couples involved in the aforementioned empathic stress protocol (Engert et al., 2014) provided diurnal cortisol samples over the course of two non-consecutive weekdays. Partner presence at the time of saliva self-sampling was assessed. Of those 44 couples, all men had previously held the role of the target, and all women that of the observer when participating in the empathic TSST. We found that diurnal cortisol levels of male and female partners were positively associated, and that the degree of cortisol stress resonance during the TSST was linked to the strength of the inter-couple diurnal cortisol covariation. In detail, women with higher stress resonance, i.e., synchronized release of cortisol when passively witnessing their partners undergo stress in the laboratory, also exhibited greater inter-couple diurnal cortisol covariation in their daily lives. Whether partners were physically together when taking a cortisol sample had no influence on inter-couple covariation. Next to showing that stress resonance in the laboratory has ecological validity, these results suggest that our daily endocrine functioning reflects not only our own experiences. Rather, our diurnal cortisol rhythm is influenced by those close to us, particularly for individuals prone to empathically synchronize with their partner in situations of acute stress.

Related studies investigating cortisol synchrony in daily life, albeit without considering empathy per se, deserve mentioning here. Significant diurnal cortisol correlations have been reported in families with adolescent children, where the within-family synchrony was found to increase in moments of heightened negative affect (Papp et al., 2009). Coregulation of cortisol and negative mood has also been shown in adult couples, where higher covariation in mood fluctuations was linked to higher covariation in cortisol (Saxbe and Repetti, 2010). Pratt et al. (2017) reported stronger adrenocortical synchrony in mother-child dyads as a function of the children's diurnal cortisol secretion, with greater synchrony associated with higher cortisol. They suggest this may indicate that higher childhood stress increases susceptibility to the influences of maternal physiological stress. However, it seems equally likely that mothers of stressed children might themselves tune into their children out of concern. Although these studies did not specifically induce or even target stress, they indicate that resonance in daily life HPA axis activation of close conspecifics is particularly pronounced when negative affect is increased.

6. Issues and outlook

6.1. Inconsistencies between studies

The delineated studies have in common that physiological activity was assessed simultaneously in observers and targets after experimental stress induction tasks. However, methodologies differed quite significantly between studies, raising the question of whether distinct types of physiological stress resonance may have been captured. Regarding the relationship of the tested dyad, for example, physiological stress resonance in strangers may serve as a warning of imminent danger, allowing the observer to seek safety. Physiological stress resonance between mother-child or partner dyads may, in addition, serve the function of strengthening the dyad's bond and/or providing the observer with the necessary energy to support the target.

The role of the observer presumably also affects the emerging type of physiological stress resonance. In everyday life we are rarely restricted to an exclusively observing role. Thus, whether we are in a position to help the stressed target, be it by means of speaking or concrete actions, or whether we are directly involved in eliciting the target's stress may be of critical importance for the resulting nature of physiological resonance. On that note, the role of the observer differs considerably in the study by Buchanan et al. (2012) compared to all other studies. Here, observers (the TSST committee members) were not passive witnesses of targets' suffering but, in fact, actively induced it. Therefore, physiological synchrony may have reflected the extent to which committee members were stressed themselves by having to induce stress in the target – the more so, the more the target was visibly affected by the TSST.

Studies also differed substantially with respect to the potential mechanisms of transmission between target and observer. Being in physical contact with a stressed target, as in the studies by Waters and colleagues, raises the possibility that the somatosensory system plays a role in transference of stress-related states. However, there are clearly other pathways. Observing another's stress visually, in person through a one-way mirror or distantly via video transmission, all triggered stress resonance. Whether different modes of transference activate the same or different branches of the stress system is a question which needs to be addressed. It is noteworthy that perception/action models would suggest that any sensory modality that activates stress-associated representations should also trigger the corresponding physiological patterns underlying those associations.

Overall, future studies should begin to examine whether, next to the strength of a synchronized physiological response, patterns of sympathetic, parasympathetic and endocrine resonance differ systematically depending on the investigated type of dyadic relationship, role of the observer, or mode of observation or transmission. In order to actually reveal such subtle systematic differences in physiological responding, it may be critical to assess pure measures of either sympathetic (e.g., pre-ejection period) or parasympathetic activation (e.g. high frequency heart rate variability).

6.2. Terminology

Terminology in the area of empathy research seems to have been an issue right from the start (Batson, 2009; Levenson and Ruef, 1992). The current review clearly illustrates that different authors use different names for what could be the same phenomenon. For example, Ebisch et al. (2012), Waters et al. (2014, 2017) and Dimitroff et al. (2017) refer to autonomic or stress contagion, Buchanan et al. (2012) to the empathic physiological resonance of stress, and we (Engert et al., 2014) to vicarious or resonant empathic stress (see Table 1 for a summary of the utilized terms). Yet, in each study (except Waters'), the responses of adult observers to a target's acute stress response during a standardized psychosocial laboratory stressor were examined.

The differences in terminology are most easily explained by differences in the underlying definitions of empathy adopted. However, if explicit definitions are not provided it becomes exceedingly difficult to determine whether conceptualizations within the research area are in agreement or not. One key distinction among the definitional approaches to empathy, for example, is whether they consider empathy to encompass (e.g. Preston and de Waal, 2002) or be distinct from phenomena such as emotional contagion, sympathy and perspective taking (de Vignemont and Singer, 2006; Singer and Lamm, 2009). Holding the former point of view would allow one to label the same phenomenon as both contagion and empathy, whereas the latter view would insist it cannot be both simultaneously.

Another important aspect that differs across definitions of empathy or related concepts is the requirement that the observer be aware of the empathic process taking place. The question of whether observers are aware of sharing the targets' feelings of stress has not been explicitly addressed to date. However, the studies by Waters et al. (2014, 2017) testing infants that likely lacked the conceptual understanding of what was happening, would suggest awareness is not essential for stress transmission to arise. This, in turn, raises the question of whether the infants' responses to their mothers' stress should be considered empathic. Notably, the authors refer to their effects as stress contagion, not empathic stress. Generally, there seems to be consensus that "contagion" is a low-level or bottom-up process, which precludes the necessity of conscious awareness. The term "emotional contagion", for example, has been used by Hatfield et al. (1993) to indicate a largely non-conscious process whereby one person quickly and automatically catches the emotional state of another. Similarly, de Waal and Preston (2017) suggest conscious awareness is an aspect of top-down empathic processes such as perspective taking that rely more on reasoning or conceptual knowledge than the quick, automatic, bottom-up empathic processes such as contagion. The same rational (i.e., that awareness is not a necessary condition for stress transmission to arise) applies to recent animal studies showing that behavioral, autonomic, endocrine (Carnevali et al., 2017) and even synaptic changes (Sterley et al., 2018) similar to those found in actively stressed mice can be automatically transmitted to naïve conspecifics.

The issue of whether there needs to be awareness of the transmission process is further complicated by the fact that stress transmission following a laboratory paradigm may differ from empathy-dependent covariation of stress-reactive systems in everyday life. While it seems likely that the blatancy of the laboratory situation boosts the observer's awareness of sharing another's experience, cortisol covariation in everyday life (which exists independent of whether two individuals are physically together when taking their respective cortisol samples; Engert et al., 2018), may be less conscious. Furthermore, it is possible that a given subject may be aware of the source of resonant stress in one instance but unaware under slightly different circumstances, depending on where attention is deployed. Thus, using conscious awareness as a criterion, it would seem possible to label the same phenomenon "empathic" in one situation and "non-empathic" in another, despite the same underlying mechanisms.

Ultimately, as plainly stated by Batson (2009), there is "…no clear basis – either historical or logical – for favoring one labeling scheme over another. The best one can do is recognize the different phenomena, make clear the labeling scheme one is adopting, and use that scheme consistently." We suggest that future studies explain their respective naming choice so that in the long run and with growing knowledge of the phenomenon, a more consistent terminology can be established.

6.3. Potential implications of the physiological resonance of stress

At the most broad level, physiological resonance can be viewed as form of non-verbal communication with a host of implications for both the observer and target. Likely, first-hand and resonant phenomena also share a purpose. The function of a first-hand stress response is to provide the organism with the necessary motivation and energy to "fight-or-flight" in the face of adversity (Cannon, 1915). Similarly, physiological stress resonance may serve an adaptive function by allowing the silent transmission of threat from one individual to another. Consequent central and peripheral changes such as increased arousal, vigilance and oxygenation of brain, heart and skeletal muscles (Chrousos, 2009) would thus enable the empathic observer to escape adversity, or alternatively, help the distressed target. As has been suggested for the general human ability to share another's affective state (Butler, 2011; Hatfield et al., 1993), physiological resonance may also be critical to facilitate social connection and coordination.

Given the severe health consequences of long-term stress system activation (Chrousos, 2009; McEwen, 2008; Sapolsky, 2004), scenarios are conceivable where physiological stress resonance would turn maladaptive, however. Humans experience maximal emotional and spatial closeness, and hence the ideal conditions for stress resonance, in their family unit. Children or partners caught in a stress-charged family environment may accordingly be at risk of detrimental health effects following long-term stress resonance and associated physiological overactivation. While the health consequences of long-term stress resonance remain to be investigated, a survey by the American Psychological Association illustrates clearly that children are aware of and emotionally suffer from their parents' stress. The vast majority of children and teenagers are saddened, worried or frustrated by their parents' stress, and children who perceive their parents as constantly stressed are more likely to report being stressed themselves (American Psychological Association, 2010).

There is much work to be done in this newly solidifying area of physiological stress resonance, with the great potential for making a significant impact. Future studies should investigate the link between susceptibility for stress resonance (e.g. high cortisol stress resonance in the laboratory, high-stress family environment) and health. Next to examining typical health markers like low grade inflammation, metabolic indices and psychological wellbeing, it would be intriguing to test whether the typically flat diurnal cortisol profiles associated with chronic stress exposure (Miller et al., 2007) are reflected in the partners and children of chronically stressed individuals.

While studying the health consequences of stress resonance has obvious importance, we may be able to learn from investigating individuals who do not show resonance. For example, those who fail to resonate may lack empathy, but they may likewise deploy a protective strategy in the face of adversity. Notwithstanding the positive aspects of empathy, it can also lead to burnout and exhaustion, and bias moral decision-making (Bloom, 2017). An interesting alternative to help overcome such negative side-effects of empathy may be the Buddhist concept of compassion, defined as the feeling of concern for the suffering of others associated with the motivation to help (Keltner and Goetz, 2007). Unlike the training of empathy, training compassion was shown to strengthen the activation of brain networks implicated in affiliation and reward, and promoted prosocial behavior rather than empathic distress (Klimecki et al., 2013, 2014). Moreover, compassion training reduced acute stress reactivity to firsthand stress (Engert et al., 2017). In going beyond the excessive sharing of negative affect that is linked to empathy, training compassion may endow the individual with the ability to foster positive affect, to help, yet not become burdened by the hardship of others.

6.4. Mechanisms of stress transmission

There has been a call for research to move beyond the examination of whether contagion of affective states occurs, to how it occurs (Timmons et al., 2015). Indeed, understanding the mechanisms of empathic transmission processes would be a prerequisite for the future prevention of harmful stress resonance. Thus far, only two studies have explicitly addressed the topic of how stress can be transferred (which is also discussed in some detail in a review by White and Buchanan, 2016). In their 2017 study, Waters et al. showed that touch is an important channel of autonomic stress contagion between mother and infant. In all other reviewed studies, the investigated dyads were separated throughout the testing procedure. Thus, touch is clearly not the only mechanism of transmission. By comparing the one-way mirror and video feed conditions in our study (Engert et al., 2014), we could assess whether the surrounding context or the facial detail of the transmitted information had an influence on stress resonance. While the one-way mirror allowed for integration of multifaceted contextual information (including body posture, motion and visual presence of the committee), the video feed presented close-up recordings of the targets' faces allowing more detail of facial expression to be gleaned. We found that cortisol stress resonance in the total sample of 211 stranger and partner dyads was stronger in the one-way mirror condition, when multiple stress-related cues could be processed. However, when focusing on only

44 partner dyads (Engert et al., 2018), the video condition was equally permissive for cortisol resonance. This may indicate that partners have learned to interpret each other's facial expressions and can therefore make optimal use of the subtle stress cues transmitted in the video (e.g. pupil dilation, blushing, sweating) to accurately assess and resonate with their partners' state. When observing a stranger, on the other hand, it seems context is important to facilitate a fine-tuned empathic response.

Although the question of transmission was not explicitly addressed in our study on inter-couple diurnal cortisol covariation (Engert et al., 2018), it is intriguing to note that covariation between partners was not modulated by partners' current togetherness (i.e., covariance occurred whether or not partners were physically together when taking a cortisol sample). In this daily context it seems likely that cues transmitted via vocal tone and prosody during phone calls would play a central role in the process of stress transmission.

7. Conclusion

In sum, it has been established that the physiological resonance of stress includes both the sympathetic nervous system and the HPA axis. It is conceivable that such second-hand stress could become chronic, leading to accumulation of allostatic load and ultimately detriment of health, particularly when coupled with one's own first-hand stress experiences. Efforts should be made to elucidate the underlying mechanisms of stress transmission (e.g. facial expression, vocal tone, prosody, posture, odor and context). Ultimately, it may be possible to shield oneself from the adverse effects of stress resonance, yet remain close and supportive of stressed loved ones.

Contributors

V.E. conceptualized the theoretical framework. V.E., R.L. and J.A.G. wrote the paper and approved the final manuscript.

Conflict of interest

The authors have no conflict of interest relevant to this article.

Acknowledgements

I (V.E.) would like to thank Dirk Hellhammer for guiding and supporting me over the years, and for setting an example of excellence as a researcher and mentor. The authors are supported by the Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany.

References

Almeida, D.M., 2005. Resilience and vulnerability to daily stressors assessed via diary methods. Curr. Dir. Psychol. Sci. 14, 64–68.

American Psychological Association, 2010. Stress in America: Key Findings. American Psychological Association, Washington DC.

Batson, C.D., 1991. The Altruism Question: Toward a Social Psychological Answer. Erlbaum, Hillsdale, NJ.

Batson, C.D., 2009. These things called empathy. In: Decety, J., Ickes, W. (Eds.), The Social Neuroscience of Empathy. MIT Press, Cambridge, MA.

Batson, C.D., Early, S., Salvarini, G., 1997. Perspective taking: imagining how another feels versus imagining how you would feel. Pers. Soc. Psychol. Bull. 751–758.

Bloom, P., 2017. Empathy and its discontents. Trends Cogn. Sci. 21, 24–31.

Buchanan, T.W., Bagley, S.L., Stansfield, R.B., Preston, S.D., 2012. The empathic, physiological resonance of stress. Soc. Neurosci. 7, 191–201.

Butler, E.A., 2011. Temporal interpersonal emotion systems: the "TIES" that form relationships. Pers. Soc. Psychol. Rev. 15, 367–393.

Cannon, W.B., 1915. Bodily Changes in Pain, Hunger, Fear and Range: an Account of Recent Researches into the Function of Emotional Excitement. Appleton-Century-Crofts, New York and London.

Carnevali, L., Montano, N., Statello, R., Coude, G., Vacondio, F., Rivara, S., Ferrari, P.F., Sgoifo, A., 2017. Social stress contagion in rats: behavioural, autonomic and neuroendocrine correlates. Psychoneuroendocrinology 82, 155–163.

Chrousos, G.P., 2009. Stress and disorders of the stress system. Nat. Rev. Endocrinol. 5, 374–381.

Cole, P.M., Barrett, K.C., Zahn-Waxler, C., 1992. Emotion displays in two-year-olds during mishaps. Child Dev. 63, 314–324.

Davis, M.H., 1983. Measuring individual differences in empathy: evidence for a multidimensional approach. J. Pers. Soc. Psychol. 44, 113–126.

Davis, M.H., 1994. Empathy: a Social Psychological Approach. Westview Press, Madison.

de Vignemont, F., Singer, T., 2006. The empathic brain: how, when and why? Trends Cogn. Sci. 10, 435–441.

de Waal, F.B.M., Preston, S.D., 2017. Mammalian empathy: behavioural manifestations and neural basis. Nat. Rev. Neurosci. 18, 498–509.

Decety, J., 2011. The neuroevolution of empathy. Ann. N. Y. Acad. Sci. 1231, 35–45.

Decety, J., Sommerville, J.A., 2003. Shared representations between self and other: a social cognitive neuroscience view. Trends Cogn. Sci. 7, 527–533.

DeLongis, A., Coyne, J.C., Dakof, G., Folkman, S., Lazarus, R.S., 1982. Relationship of daily hassles, uplifts, and major life events to health status. Health Psychol. 1, 119–136.

Di Mascio, A., Boyd, R.W., Greenblatt, M., Solomon, H.C., 1955. The psychiatric interview: a sociophysiologic study. Dis. Nerv. Syst. 16, 4.

Di Mascio, A., Boyd, R.W., Greenblatt, M., 1957. Physiological correlates of tension and antagonism during psychotherapy: a study of "interpersonal physiology". Psychosom. Med. 19, 99–104.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., Rizzolatti, G., 1992. Understanding motor events: a neurophysiological study. Exp. Brain Res. 91, 176–180.

Dimitroff, S.J., Kardan, O., Necka, E.A., Decety, J., Berman, M.G., Norman, G.J., 2017. Physiological dynamics of stress contagion. Sci. Rep. 7, 6168.

Ebisch, S.J., Aureli, T., Bafunno, D., Cardone, D., Romani, G.L., Merla, A., 2012. Mother and child in synchrony: thermal facial imprints of autonomic contagion. Biol. Psychol. 89, 123–129.

Eisenberg, N., 2000. Emotion, regulation, and moral development. Annu. Rev. Psychol. 51, 665–697.

Engert, V., Plessow, F., Miller, R., Kirschbaum, C., Singer, T., 2014. Cortisol increase in empathic stress is modulated by emotional closeness and observation modality. Psychoneuroendocrinology 45, 192–201.

Engert, V., Kok, B.E., Papassotiriou, I., Chrousos, G.P., Singer, T., 2017. Specific reduction in cortisol stress reactivity after social but not attention-based mental training. Sci. Adv. 3, e1700495.

Engert, V., Ragsdale, A.M., Singer, T., 2018. Cortisol stress resonance in the laboratory is associated with inter-couple diurnal cortisol covariation in daily life. Horm. Behav. 98, 183–190.

Fan, Y., Duncan, N.W., de Greck, M., Northoff, G., 2011. Is there a core neural network in empathy? An fMRI based quantitative meta-analysis. Neurosci. Biobehav. Rev. 35, 903–911.

Gottman, J.M., Levenson, R.W., 1985. A valid procedure for obtaining self-report of affect in marital interaction. J. Consult. Clin. Psychol. 53, 151.

Harrison, N.A., Singer, T., Rotshtein, P., Dolan, R.J., Critchley, H.D., 2006. Pupillary contagion: central mechanisms engaged in sadness processing. Soc. Cogn. Affect. Neurosci. 1, 5–17.

Hatfield, E., Cacioppo, J.T., Rapson, R.L., 1993. Emotional contagion. Curr. Dir. Psychol. Sci. 2, 96–99.

Hatfield, E., Rapson, R.L., Le, Y.L., 2009. Emotional Contagion and Empathy. MIT Press, Cambridge, MA.

Hein, G., Lamm, C., Brodbeck, C., Singer, T., 2011. Skin conductance response to the pain of others predicts later costly helping. PLoS One 6, e22759.

Hellhammer, D.H., Wust, S., Kudielka, B.M., 2009. Salivary cortisol as a biomarker in stress research. Psychoneuroendocrinology 34, 163–171.

Hickok, G., 2013. Do mirror neurons subserve action understanding? Neurosci. Lett. 540, 56–58.

Hoffman, M.L., 2000. Empathy and Moral Development: Implications for Caring and Justice. Cambridge University Press, Cambridge, UK.

Jabbi, M., Swart, M., Keysers, C., 2007. Empathy for positive and negative emotions in the gustatory cortex. NeuroImage 34, 1744–1753.

Kanske, P., Bockler, A., Trautwein, F.M., Singer, T., 2015. Dissecting the social brain: introducing the EmpaToM to reveal distinct neural networks and brain-behavior relations for empathy and Theory of Mind. NeuroImage 122, 6–19.

Kaplan, H.B., Burch, N.R., Bloom, S.W., 1964. Physiological covariation and sociometric relationships in small peer groups. Psychobiological Approaches to Social Behavior. pp. 92–109.

Keltner, D., Goetz, J.L., 2007. Compassion. In: Baumeister, R.F., Vohs, K.D. (Eds.), Encyclopedia of Social Psychology. Sage Publications, Thousand Oaks, CA, pp. 159–161.

Keysers, C., Kaas, J.H., Gazzola, V., 2010. Somatosensation in social perception. Nature reviews. Neuroscience 11, 417–428.

Kirschbaum, C., Pirke, K.M., Hellhammer, D.H., 1993. The' Trier Social Stress Test'–a tool for investigating psychobiological stress responses in a laboratory setting. Neuropsychobiology 28, 76–81.

Klimecki, O.M., Leiberg, S., Lamm, C., Singer, T., 2013. Functional neural plasticity and associated changes in positive affect after compassion training. Cereb. Cortex 23, 1552–1561.

Klimecki, O.M., Leiberg, S., Ricard, M., Singer, T., 2014. Differential pattern of functional brain plasticity after compassion and empathy training. Soc. Cogn. Affect. Neurosci. 9, 873–879.

Kuehn, E., Trampel, R., Mueller, K., Turner, R., Schütz-Bosbach, S., 2013. Judging roughness by sight—a 7-tesla fMRI study on responsivity of the primary somatosensory cortex during observed touch of self and others. Hum. Brain Mapp. 34, 1882–1895.

Lamm, C., Singer, T., 2010. The role of anterior insular cortex in social emotions. Brain Struct. Funct. 214, 579–591.

Lamm, C., Decety, J., Singer, T., 2011. Meta-analytic evidence for common and distinct neural networks associated with directly experienced pain and empathy for pain. NeuroImage 54, 2492–2502.
Lang, P.J., Greenwald, M.K., Bradley, M.M., Hamm, A.O., 1993. Looking at pictures: affective, facial, visceral, and behavioral reactions. Psychophysiology 30, 261–273.
Laurenceau, J.P., Bolger, N., 2005. Using diary methods to study marital and family processes. J. Fam. Psychol. 19, 86–97.
Lazarus, S., Folkam, S., 1984. Stress, Appraisal, and Coping. Springer Publishing Company, New York.
Levenson, R.W., Gottman, J.M., 1983. Marital interaction: physiological linkage and affective exchange. J. Pers. Soc. Psychol. 45, 587.
Levenson, R.W., Ruef, A.M., 1992. Empathy: a physiological substrate. J. Pers. Soc. Psychol. 63, 234–246.
Liew, J., Eisenberg, N., Losoya, S.H., Fabes, R.A., Guthrie, I.K., Murphy, B.C., 2003. Children's physiological indices of empathy and their socioemotional adjustment: does caregivers' expressivity matter? J. Fam. Psychol. 17, 584–597.
Liew, J., Eisenberg, N., Spinrad, T.L., Eggum, N.D., Haugen, R.G., Kupfer, A., Reiser, M.R., Smith, C.L., Lemery-Chalfant, K., Baham, M.E., 2011. Physiological regulation and fearfulness as predictors of young children's empathy-related reactions. Soc. Dev. 20, 111–113.
Lipps, T., 1903. Einfühlung, innere Nachahmung und Organempfindung. Archiv für die gesamte Psychologie 1, 465–519.
Manini, B., Cardone, D., Ebisch, S.J., Bafunno, D., Aureli, T., Merla, A., 2013. Mom feels what her child feels: thermal signatures of vicarious autonomic response while watching children in a stressful situation. Front. Hum. Neurosci. 7, 299.
McEwen, B.S., 2008. Central effects of stress hormones in health and disease: understanding the protective and damaging effects of stress and stress mediators. Eur. J. Pharmacol. 583, 174–185.
McEwen, B.S., Bowles, N.P., Gray, J.D., Hill, M.N., Hunter, R.G., Karatsoreos, I.N., Nasca, C., 2015. Mechanisms of stress in the brain. Nat. Neurosci. 18, 1353–1363.
Mehrabian, A., Epstein, N., 1972. A measure of emotional empathy. J. Pers. 40, 525–543.
Miller, G.E., Chen, E., Zhou, E.S., 2007. If it goes up, must it come down? Chronic stress and the hypothalamic-pituitary-adrenocortical axis in humans. Psychol. Bull. 133, 25–45.
Miller, R., Plessow, F., Kirschbaum, C., Stalder, T., 2013. Classification criteria for distinguishing cortisol responders from nonresponders to psychosocial stress: evaluation of salivary cortisol pulse detection in panel designs. Psychosom. Med. 75, 832–840.
Nater, U.M., Rohleder, N., 2009. Salivary alpha-amylase as a non-invasive biomarker for the sympathetic nervous system: current state of research. Psychoneuroendocrinology 34, 486–496.
Papp, L.M., Pendry, P., Adam, E.K., 2009. Mother-adolescent physiological synchrony in naturalistic settings: within-family cortisol associations and moderators. J. Fam. Psychol. 23, 882.
Pratt, M., Apter-Levi, Y., Vakart, A., Kanat-Maymon, Y., Zagoory-Sharon, O., Feldman, R., 2017. Mother-child adrenocortical synchrony; Moderation by dyadic relational behavior. Horm. Behav. 89, 167–175.
Preston, S.D., 2007. A perception-action model for empathy. Empathy in mental illness. pp. 428–447.
Preston, S.D., de Waal, F.B., 2002. Empathy: its ultimate and proximate bases. Behav. Brain Sci. 25, 1–20 discussion 20-71.
Reniers, R.L., Corcoran, R., Drake, R., Shryane, N.M., Völlm, B.A., 2011. The QCAE: a questionnaire of cognitive and affective empathy. J. Pers. Assess. 93, 84–95.
Sapolsky, R.M., 2004. Social status and health in humans and other animals. Annu. Rev. Anthropol. 33, 393–418.
Saxbe, D.E., Repetti, R.L., 2010. For better or worse? Coregulation of couples' cortisol levels and mood states. J. Pers. Soc. Psychol. 98, 92–103.
Scollon, C.N., Kim-Prieto, C., Diener, E., 2003. Experience sampling: promises and pitfalls, strengths and weaknesses. J. Happiness Stud. 4, 5–34.
Singer, T., Lamm, C., 2009. The social neuroscience of empathy. Ann. N. Y. Acad. Sci. 1156, 81–96.
Singer, T., Seymour, B., O'Doherty, J., Kaube, H., Dolan, R.J., Frith, C.D., 2004. Empathy for pain involves the affective but not sensory components of pain. Science 303, 1157–1162.
Sterley, T.L., Baimoukhametova, D., Fuzesi, T., Zurek, A.A., Daviu, N., Rasiah, N.P., Rosenegger, D., Bains, J.S., 2018. Social transmission and buffering of synaptic changes after stress. Nat. Neurosci. 21, 393–403.
Timmons, A.C., Margolin, G., Saxbe, D.E., 2015. Physiological linkage in couples and its implications for individual and interpersonal functioning: a literature review. J. Fam. Psychol. 29, 720–731.
Titchener, E.B., 1909. Lectures on the Experimental Psychology of the Thought-processes. Macmillan.
Waters, S.F., West, T.V., Mendes, W.B., 2014. Stress contagion: physiological covariation between mothers and infants. Psychol. Sci. 25, 934–942.
Waters, S.F., West, T.V., Karnilowicz, H.R., Mendes, W.B., 2017. Affect contagion between mothers and infants: examining valence and touch. J. Exp. Psychol. Gen. 146, 1043.
White, C.N., Buchanan, T.W., 2016. Empathy for the stressed. Adapt. Human Behav. Physiol. 2, 311–324.
Wicker, B., Keysers, C., Plailly, J., Royet, J.P., Gallese, V., Rizzolatti, G., 2003. Both of us disgusted in my insula: the common neural basis of seeing and feeling disgust. Neuron 40, 655–664.
Zaki, J., Ochsner, K.N., 2012. The neuroscience of empathy: progress, pitfalls and promise. Nat. Neurosci. 15, 675.