Effects of Acute Psychosocial Stress on Cognitive and Affective Empathy

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Abstract

Empathy, broadly defined as the ability to understand and appropriately respond to what others are feeling, is critical for establishing and maintaining social connections and navigating our social world. There are two well-established routes for gathering information about others—by simulating/mimicking their emotional states (emotion contagion/affective empathy), and/or by mentalizing about their thoughts and feelings (cognitive empathy). Importantly, these processes rarely occur under optimal conditions; instead, contextual factors such as the experience of acute stress might change the way we perceive and interact with others. Despite increased research on the effects of acute stress on empathy, much remains unknown. This may be due to the fact that existing research in this domain has used the many facets of empathy synonymously or assumed that acute stress would result in similar effects across domains, thus obfuscating how acute stress might influence empathy. Furthermore, there is a need to use more naturalistic tasks that are less prone to range restrictions. Here, I addressed these shortcomings in two important ways. First, I provide a comprehensive overview of the research on empathy within the context of acute stress and highlight gaps in the literature, as well as emerging patterns and contextually relevant conditions that might need to be considered. Second, the empirical work in this thesis aims to address some of the gaps that were identified in the existing literature, by implementing more naturalistic tasks that more closely resemble real-life interactions that evoke empathic responses. Through these investigations I demonstrate that acute stress is associated with changes in empathic abilities in a domain specific way. The first major finding (Chapter 2) showed that acute stress improved cognitive empathy—measured using an empathic accuracy task—in men, while having no effects on cognitive empathic abilities in women. Moreover, stress induced glucocorticoid response was found to be positively associated with cognitive empathic abilities

in men. The second major finding (Chapter 3) showed that stress selectively impaired facial mimicry. Specifically, acute stress impaired facial mimicry for positively valenced stimuli (i.e., smiles)—affiliative mimicry—but did not impact mimicry for negatively valenced expressions (i.e., frowns). Importantly, this reduction in affiliative mimicry occurred both in male and female participants and was tied to stress induced levels of cortisol.

Together, the research presented here demonstrates that acute stress affects empathic abilities in a domain specific way and represents an important step towards enhancing our understanding of how acute stress impacts empathy. Given that humans are a social species, understanding how stress impacts our social togetherness has important consequences for our social life and well-being.

Résumé

L'empathie, c'est-à-dire la capacité de comprendre ce que les autres ressentent et d'y répondre de manière appropriée, est essentielle pour le développement et le maintien des liens sociaux, et nous aide à naviguer notre milieu social. Il existe deux processus bien établis par lesquelles un individu s'imprègne de l'état émotionnel d'une autre personne - en simulant/mimant leurs états émotionnels (contagion des émotions/empathie affective) et/ou en se représentant mentalement leurs pensées et leurs sentiments (empathie cognitive). Il est important de noter que ces processus se produisent rarement dans des conditions optimales ; des facteurs contextuels tels que l'expérience d'un stress aigu peuvent modifier nos perceptions et nos comportements envers les autres. Malgré un intérêt croissant pour les effets du stress aigu sur l'empathie, beaucoup de questions restent sans réponse. Cela peut être dû au fait que les recherches existantes dans ce domaine ne distinguent pas entre les différentes composantes de l'empathie, ou supposent que le stress aigu aurait des effets similaires dans tous les domaines, masquant ainsi la façon dont le stress aigu pourrait influencer l'empathie. En outre, il est nécessaire d'utiliser des tâches plus naturalistes, ayant une fourchette de valeurs moins restreinte. Dans le présent article, je propose deux solutions pour remédier ces problèmes. Premièrement, je présente un aperçu complet de la recherche sur l'empathie dans le contexte du stress aigu, et je souligne les lacunes de cette littérature, ainsi que les tendances générales qui ont émergé par rapport aux conditions contextuelles qui pourraient être pertinentes. Deuxièmement, le travail expérimental de cette thèse vise à combler les lacunes identifiées dans la littérature existante, en utilisant des tâches plus naturalistes qui ressemblent plus aux interactions de la vie quotidienne. Grâce à ces recherches, je démontre que le stress aigu est associé à des changements dans les capacités empathiques d'une manière spécifique au domaine. Le premier résultat majeur (chapitre 2)

montre que le stress aigu améliore l'habileté empathique cognitive chez les hommes, mais n'a aucun effet sur les capacités empathiques cognitives chez les femmes. De plus, chez les hommes, la réponse glucocorticoïde induite par le stress est positivement associée aux capacités d'empathie cognitive. Le deuxième résultat majeur (chapitre 3) démontre que le stress aigu affecte sélectivement la mimique faciale. Plus précisément, le stress aigu affecte la mimique faciale pour les stimuli à valence positive (c.-à-d. la mimique affiliative, ou les sourires réciproques) mais n'a aucun effet sur la mimique des expressions à valence négative (c.-à-d. les froncements de sourcils). Cette réduction du mimique affiliative s'est produite tant chez les hommes que chez les femmes et était liée aux niveaux de cortisol induits par le stress.

L'ensemble des recherches présentées ici démontre que le stress aigu affecte les capacités empathiques d'une manière spécifique à un domaine, et représente un pas important vers l'amélioration de notre compréhension de l'impact du stress aigu sur l'empathie. L'être humain étant une espèce sociale, l'impact du stress sur notre vie sociale peut avoir des conséquences importantes sur le bien-être.

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Statement of original contribution

How does the experience of stress impact our ability to empathize? Humans are social animals, and we rely on others for our health, well-being, and ultimately our survival. As such, we have developed a vast repertoire of abilities that help us understand and interact with our social environment. Among these abilities is empathy—an umbrella term that encompasses a set of aptitudes that help us to understand others, either through shared emotions or through gaining cognitive understanding of their mental states. However, empathy rarely occurs under optimal conditions, instead, contextual factors such as the experience of acute stress can change the way we perceive and interact with others. While, over the last decade there has been an increase in research on how stress affects our ability to connect with others, we still do not have a good understanding of these effects—with research often reporting detrimental, beneficial, or no effects. There are several reasons for this, for one, research has used the many facets of empathy synonymously or assumed that acute stress would result in similar effects across domains, consequently obfuscating patterns of how acute stress might influence empathy. As such, a consolidation of research findings is needed in the form of a review. Second, previous research has often relied on simplistic tasks that are prone to ceiling effects and might not generalize to the real-world. Thus, research including more naturalistic tasks that more closely resemble real-life interactions is needed.

To this end, the first aim of this thesis was to synthesize previous research findings. As such, the introduction of this thesis reviews the effects of acute stress on affective empathy and cognitive empathy. This is the first systematic review of the literature and I provide novel insights into emerging patterns, and boundary effects, and make recommendations for how research in this area can and should proceed.

The second aim of this thesis was to empirically extend previous work and address some of the gaps in the literature, through the use of naturalistic tasks to assess the different facets of empathy. Specifically, in Chapter 2, I tested the effect of acute stress on cognitive empathy, measured via a naturalistic, ecologically valid, empathic accuracy task. In two independent experiments, I found that acute stress improves men's ability to make inferences about another person's feelings, an effect that was tied to stress induced increases in cortisol. For women, however, acute stress did not affect empathic accuracy, possibly indicating more robust abilities that are less prone to contextual effects. Furthermore, the findings indicate that across conditions (stress and control), women using hormonal oral contraceptives performed worse on the empathic accuracy task compared to regularly cycling women.

In Chapter 3, I examined the role of acute stress on automatic facial mimicry, which is thought to be a component of affective empathy. Here, I found that the experience of acute stress results in a reduction in affiliative mimicry, specifically smile reciprocity. Of note, this effect was associated with stress induced glucocorticoid response, a finding that highlights the importance of the biological stress response system in this basic element of social–emotional experience. Overall, the results from Chapter 3 indicate that acute stress might reduce affiliative behaviours.

In sum, the research presented in this thesis demonstrates that acute stress impacts empathic abilities in a domain specific way. The findings presented here represent an important contribution towards enhancing our understanding of how acute stress impacts empathy. Given that humans are a social species, understanding how stress impacts our social togetherness has important consequences for our social life and well-being.

Contribution of Authors

This thesis includes two original manuscripts and an abridged version of a review paper. One manuscript has been published, and the other is currently under revision at a peer reviewed journal. The review paper is currently in preparation. Listed below are details of individual contributions towards each manuscript.

1. **Nitschke, J.P**., Bartz, J.A. (*in preparation*). Association between Acute Stress and Affective and Cognitive Empathy: A Literature Review.

Jonas Nitschke conducted the literature review, wrote and edited the manuscript.
Jennifer Bartz provided feedback and edited the manuscript.

2. **Nitschke, J.P.,** Pruessner, J.C., Bartz, J.A. (*revise and resubmit*). Stress and Stress-induced Glucocorticoids Facilitate Empathic Accuracy in Men, with no Effects for Women. DOI: 10.31234/osf.io/msxar

Jonas Nitschke conducted the literature review, developed the study concept, designed the study, collected and analysed the data, interpreted findings, and wrote and edited the manuscript.
Jens Pruessner contributed to study design and editing of the manuscript.
Jennifer Bartz developed the study concept and study design, contributed to interpretation of findings, and writing and editing of manuscript.

3. **Nitschke, J.P.,** Sunahara C.S., Carr. E.W., Winkielman, P., Pruessner, J.C., Bartz, J.A. (2020). Stressed Connections. Cortisol Levels Following Acute Psychosocial Stress Disrupts Affiliative Mimicry in Humans. *Proceedings of the Royal Society B: Biological Sciences*. DOI: 10.1098/rspb.2019.2941

Jonas Nitschke conducted the literature review, developed the study concept, designed the study, collected and analysed the data, interpreted findings, wrote and edited the manuscript.

Cecile Sunahara assisted with data collection and edited the manuscript.

Evan Carr facilitated the study design and implementation of the mimicry task.

Piotr Winkielman facilitated the study design and implementation of the mimicry task.

Jens Pruessner contributed to study design and editing of the manuscript.

Jennifer Bartz developed the study concept and study design, contributed to interpretation of findings, and writing and editing of manuscript.

List of Abbreviations

AUCi	Area-under-the-curve increase
CPT	Cold Pressor Task
fEMG	facial Electromyography
HPA	Hypothalamic-pituitary-adrenal
MASC	Movie for the Assessment of Social Cognition
MEM	Mixed-Effects Model
MET	Multifaceted Empathy Test
OC	Oral Contraceptive
rMEM	repeated measures Mixed-Effects Model
RMET	Reading the Mind in the Eye Task
sAA	salivary Alpha Amylase
SNS	sympathetic nervous system
TSST	Trier Social Stress Test

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Figure S5: Plotted salivary alpha amylase curves for Experiment-2, for men, RC women, and OC women. Error bars represent the standard error of the mean for each group.

Chapter 3

Figure 1. Timeline of the experimental procedure during visit-2, including cortisol and salivary alpha amylase (sAA) responses over time. Sampling times-points are indicated on the X-axis with ticks. Participants are introduced to the TSST setting ten minutes before going to the interview room (at 0 minutes). Twenty-five minutes after the end of the TSST participants started the facial mimicry task.

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Figure S1: The mean *zygomaticus* response to frowning faces (incongruent fEMG response); the dotted blue line represents the *zygomaticus* response to frowning faces on Day-1 (baseline), and the green line represents *zygomaticu*s response to frowning faces on Day-2 (TSST).

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Chapter 1: General Introduction

An extended version of the literature review section is currently in preparation, to be submitted to a peer reviewed journal.

Nitschke, J.P., Bartz, J.A. (*in preparation*). Association between Acute Stress and Affective and Cognitive Empathy: A Literature Review.

"Les signes [des autres] *rappellent donc les sensations; ils nous font sentir de nouveau. Il en est qui restent, pour ainsi dire, cachés dans l'intérieur, ils sont pour l'individu lui seul* [...] *A mesure que nos moyens de communication augment, cette faculté se développe de plus en plus, d'autre langue se forment; et bientôt, nous n'existons guère moins dans les autres que dans nous-mêmes"*

"The signs [of others] *thus recall sensations; they make us feel again. There are some which remain, so to speak, hidden within, they are for the individual alone* [...] *As our means of communication increase, this faculty develops more and more, other languages are formed; and soon we exist no less in the others than in ourselves"*

Pierre Jean Georges Cabanis on how we make sense of others' emotions (1802, pp. 88–89).

Humans are social animals, wired to engage with and understand others in our social world (Depue & Morrone-Strupinsky, 2005). Indeed, not only is understanding the feelings and thoughts of others critical for successfully navigating social life, it also helps with fostering and maintaining social connections (de Waal & Preston, 2017). Two well-established routes to gather information about others—commonly grouped under the umbrella term "empathy"—are by simulating/mirroring others' emotional states (emotion contagion/affective empathy), and/or by mentalizing about their thoughts and feelings (cognitive empathy). Unfortunately, there is a myriad of factors that can undermine these processes: some perceivers (i.e., the person doing the empathizing) are less skilled, some targets (i.e., the person who is the focus of empathy*)* are less readable, and even assuming perfectly skilled perceivers and decipherable targets, numerous situational factors can interfere with the accurate decoding of others' internal states. Here, I will focus on one factor that has received increasing research interest: the experience of acute stress.

1.1 Thesis Objectives

The overarching goal of this thesis is to understand how the experience of acute stress impacts empathic abilities. While research on this topic has accelerated over the past decade, I have identified three major gaps in the literature that I aim to address in my thesis.

Objective-1: <u>A review of the literature on the effects of acute stress on empathy</u>

The effect of acute stress on empathy—and its various facets—is an emerging area of study that has gained a great deal of attention over the past decade. The area is at a point in time that necessitates a review of the literature, to summarize existing findings and make recommendations on how to move forward. Empathy is a multifaceted construct; however, research has used the many facets of empathy synonymously or assumed that acute stress would

result in similar effects across domains, consequently obfuscating patterns of how acute stress might influence empathy. The objective of this review is to provide a synthesis of these research findings in order to shed light on emerging patterns in the literature, identify contextually relevant conditions, and boundary effects that may require further investigation. Moreover, by identifying gaps in the literature, recommendations can be made about directions for future research, which I hope will help the field as it moves forward.

Objective-2: To investigate how acute stress impacts cognitive empathy, in particular, "empathic accuracy', that is the ability to dynamically track another's emotions as they unfold over time, as well as how this process might differ between men and women.

Acute stress has been associated with changes in cognition in general, and both enhancing and impairing effects have been reported, depending on the situational context (Hermans et al., 2014; Schwabe, 2017; Shields et al., 2016; Wirz et al., 2018). However, to date only a handful of studies have measured the effects of acute stress on cognitive empathy, and findings have been mixed. Some studies report no difference in cognitive empathy between stress and control conditions, whereas others report either impairing or enhancing effects of stress. Moreover, most studies have largely relied on simplistic and static emotion recognition tasks (such as Reading the Mind in the Eye Task; Baron-Cohen et al., 2001) which are prone to range restrictions in scores, i.e., healthy individuals typically show ceiling effects. Additionally, these simplistic tasks do not capture the kind of mentalizing processes that are required in everyday social interactions, which tend to be multi-modal, dynamic, and fleeting. Moving forward it will be necessary to use tasks that afford more variability in responses and more closely resemble real-life situations. To this end, I use an empathic accuracy task (Zaki et al.,

2008), which is a more naturalistic task that allows for the tracking of momentary changes in others' emotional states as they unfold in real time. Specifically, in this task participants watch short videos of targets discussing real-life autobiographical experiences; importantly, after filming the targets watched their own videos and rated how they were feeling over the course of the video. By correlating target and perceiver ratings of how the target was feeling I can thus calculate an index of empathic accuracy. Not only is this task more akin to real life (i.e., multimodal, using autobiographical events, etc.), prior work indicates considerable range in empathic accuracy scores, thus addressing the aforementioned ceiling effect issue.

A second aim of this work is to investigate gender/sex differences. Research indicates that men and women show differences in biological stress-reactivity (Kudielka et al., 2004); moreover, there is some preliminary evidence that gender/sex can moderate the effects of stress on empathy, with stress facilitating cognitive empathy for men, but impairing it for women (Smeets et al., 2009). That said, the sample size in this initial study was very small, and the stress findings were ambiguous. Thus, in addition to using a more naturalistic, and ecologically valid task, I also recruited an adequately powered sample to specifically test the effect of gender/sex. Finally, to address the possibility of spurious effects, I conducted a replication study.

Objective-3: <u>To investigate how the experience of acute stress impacts affective empathy—that is, automatic facial mimicry. And whether possible gender/sex specific effects exist.</u>

To date, most studies investigating the effects of stress on affective empathy/emotion contagion, have largely focused on understanding the "spillover" of stress from stressed targets to *unstressed* perceivers. Results indicate that observing others (i.e., targets) in distress can lead to a stress response in the perceiver, an effect that seems to be associated with the familiarity of

the perceiver to the target, as well as other contextual factors. However, far less is known about how acute stress modulates emotion contagion in perceivers that are already stressed prior to engagement with others. Moreover, nearly all of the prior work has focused on the emotion contagion of negative emotions (i.e., pain, stress); thus, we know very little about whether, and how stress affects contagion of positive emotions. Further, the limited research that has been conducted has focused on what happens to a perceiver when sharing a pain experience with a target, thus using pain as a measure of emotion contagion. Research needs to extend beyond *empathy for pain* and look at behaviours related to other negative emotions, and importantly to positive emotions as well. As such, one of the goals of this work is to understand how individuals share emotions when they themselves are stressed when observing others. Specifically, the question I aim to answer is whether we share/engage in others' emotions to the same extent when we are stressed, as we are when we are unstressed? To investigate this, I employ a facial mimicry task, which assesses participants' tendency to mimic the facial expressions of targets on screen (angry faces, and smiling faces), using facial electromyography (fEMG) to measure the muscle activation of the "smiling" muscle (zygomaticus) and the frowning muscle (corrugator) (Carr et al., 2014). Here, I use a within-subjects design, in which participants come to the laboratory on two occasions, a stress day, and a non-stress day. This allowed me to account for individual differences in stress reactivity, as well as automatic facial mimicry.

Together, these investigations aim to improve our understanding of how acute stress impacts empathy, and consequently our social togetherness. In the following sections of this chapter, I first introduce the concept of acute stress. I describe the physiological and psychological stress

response, how acute stress is manipulated in the laboratory, and discuss evidence that suggests that men and women show differential responses to acute stress. Second, I provide an operational definition of empathy, highlighting both the cognitive component, and the affective component. Finally, I review the existing research investigating the effects of acute stress on cognitive and affective empathy, and identify the gaps in the literature that the studies in this thesis aim to fill.

1.2 Literature Review

1.2.1 Acute Stress

Acutely, stress is a momentary adaptive response to an adverse or challenging situation that aims to restore physiological and behavioural homeostatic balance (Lazarus, 2006). The acute stress response encompasses a synchronized activation of several biological systems. Two of them are frequently investigated for their effects on human behaviour: the fast-acting sympathetic branch of the autonomic nervous system, or sympathetic nervous system (SNS), and the slower acting hypothalamic-pituitary-adrenal (HPA) axis. Activation of the SNS results in, among other things, the release of catecholamines and increased heart rate. Activation of the HPA axis triggers a hormone cascade, and results in the release of the downstream glucocorticoid cortisol. Through a feedback-loop cortisol reaches the central nervous system where it binds to glucocorticoid and mineralocorticoid receptors and inhibits further release of cortisol by suppressing the release of corticotropin-releasing hormone (Chrousos, 2009).

Centrally, glucocorticoids exert their effects through non-genomic (rapid), as well as genomic (slow) effects (Hermans et al., 2014; McEwen et al., 2016). Research indicates that the immediate non-genomic effects change the way a situation is appraised and attended to (de Kloet

et al., 2005; Sapolsky et al., 2000), including how information about the situation is retained and retrieved. In this regard, under stress, attentional processes become more selective (Chajut & Algom, 2003; Hermans et al., 2011), resulting in a narrowing of attention, and reduced interference from irrelevant and distracting information (Plessow et al., 2011; Putman & Roelofs, 2011; Sänger et al., 2014), allowing the organism to cope with the stressor(s). In addition to this narrowing of attention, it is thought that acute stress elicits a shift from more cognitively demanding information processing to more habitual response patterns (Schwabe & Wolf, 2009; Wirz et al., 2018). This shift should enable more rapid information processing and, thus, might be beneficial for dealing with stressors (and ultimately, our survival), especially when quick decisions are necessary. However, this shift can also come at a cost, as mental flexibility is diminished under habitual-favouring strategies (Shields et al., 2016; Nitschke et al., 2019; Vogel et al., 2016).

Stress also shifts attention to what is salient in the environment—either to alert the organism to potential threats and challenges, or as a means to regulate and overcome the aversive situation. This shift may have important consequences for social information processing in general, and for cognitive and affective empathy specifically. For example, on the one hand, increased attention to potential threats in the environment may facilitate the identification of others' emotions, especially negative emotions (through vicarious means or by making cognitive inferences). On the other hand, when demands are high (i.e., the individual sustains high levels of acute stress), individuals will likely shift to more rudimentary and automatic strategies (that do not require high levels of mental flexibility), which, in turn, might lead to an inward focus towards ego-centric emotions rather than engaging with the social environment. This could make the identification and/or sharing of others' emotions more challenging. Given the ubiquity and

importance of social information to humans it is likely that some of these more automatic and habitual processes will involve the presence of others. If social information is processed differently—for example by relaying context specific threats and opportunities—one would expect that acute stress can enhance social inference making.

Manipulating Stress in the Laboratory

There are many ways by which stress can be elicited and measured in the laboratory, and consequently many ways stress can be defined. Importantly, research investigating the relationship between acute stress and empathy has generally relied on one of two approaches to elicit stress. First, as seen in many emotion contagion studies, researchers have measured the "spillover" from a stressed target to an (initially) unstressed perceiver. In these paradigms the stress response (i.e., biological and/ or psychological measures) in a perceiver is quantified as a correlation with a target's stress responses. Methodologically, it is difficult to distinguish if the measured stress response stems from the feelings of *personal distress* that are evoked within the perceiver, or via emotion contagion (i.e., stress that is grounded in the target's experience), given that an overlap in biological activation (e.g., increased cortisol in both target and perceiver) indicates a coinciding stress response, but does not clarify whether the stress response is shared or egocentric (cf. Lamm et al., 2016). This limits the interpretability of findings and claims about directionality. Thus, this approach (unstressed perceiver, stressed target) is not ideal for assessing the effects of acute stress on empathy; rather, what is needed is to elicit stress in the perceiver prior to the interaction with the target, using one of the paradigms described below. While another person's distress can make us stressed just by observing them, in real life, we often come into an interaction already stressed—what happens to empathic abilities in these instances? Thus, the second approach, to test causality utilizes laboratory stress paradigms to elicit a stress

response in the perceiver. Here, by manipulating acute stress prior to a social interaction we can gain further insight into the precise effects of stress on empathy.

Common indicators of an acute stress response are: an increase in glucocorticoids (resulting in elevated salivary cortisol); an increased activation of the sympathetic nervous system (resulting in increased heart rate, electrodermal activity, or salivary alpha amylase); and markers of emotional arousal (i.e., psychological distress). It is important to note however, that not all acute stressors result in the same stress profile; thus, some stressors might not be comparable. The most commonly used method to induce stress in the laboratory is the Trier Social Stress Test (TSST; Kirschbaum et al., 1993) which is designed to elicit a robust biological and psychological response—characterized by increased SNS activation, HPA stimulation, and feelings of distress. The defining characteristic of the TSST is its social-evaluative component, i.e., participants are being "judged". This social component may also have implications for subsequent social behaviours—as Dickerson and Kemeny note, because social stressors highlight aversive interpersonal interactions as the source of distress (Dickerson & Kemeny, 2004), they might affect social behaviours that follow. Many variants of the classic TSST exist, for example adaptations for the use in groups, which might highlight the already salient social nature of the situations (von Dawans et al., 2011), or for the use in a neuroimaging environment, such as the Montreal Imaging Stress Task (Dedovic et al., 2005).

Another common procedure to elicit stress in the laboratory is the cold pressor task (CPT; Hines & Brown, 1936). Here, participants are instructed to immerse their hand in ice-cold water (typically 4°C, or 39.2°F), sometimes repeatedly. As such, the CPT relies on an aversive physical experience (i.e., pain) to elicit the stress response. This immersion of the hand into ice-cold water

triggers a robust vasopressor effect, and subsequent sympathetic nervous system (SNS) activation, resulting in increased heart-rate and blood pressure. However, it is important to note that the CPT typically fails to elicit a robust HPA axis activation (Schwabe et al., 2008). A social variant of the CPT, the social-evaluative CPT, exists (Schwabe et al., 2008; Schwabe & Schächinger, 2018). Here, the aversive experience of immersing the hand in cold water is combined with a social-evaluative component. The social-evaluative CPT has been shown to result in an activation of the HPA axis. In this regard the addition of the socio-evaluative component makes the CPT more comparable to the TSST.

It is important to note that some effects of the acute stress tasks will last much longer than the actual task. For example, the TSST elicits a cortisol response that can last for up to 40-minutes after stress induction (Goodman et al., 2017); it is therefore possible to measure effects of acute stress after a longer delay. Although importantly, the acute stress response unfolds in several "stages" (Hermans et al., 2014) and we can expect to find different effects of glucocorticoids depending on whether they are measured after a short or a long delay (de Kloet et al., 2008; Henckens et al., 2011; Joëls et al., 2012). The timing of the dependent variable, in the case of the present research- the empathy task, in relation to the stress task therefore matters. Importantly, some studies have administered empathy tasks after a delay of more than 40 minutes after stress induction, potentially finding different effects of stress. Results from studies using a "short" delay (i.e., less than 40 minutes) after stress induction, and results from studies using "longer" delays (i.e., more than 40 minutes) should therefore be interpreted differently, or at least with greater consideration when comparing findings. In addition, studies often use modified versions of stress tasks (for various reasons), and these modified versions do not always result in similar stress-responses as the original tasks.

Gender/Sex Differences in Stress Reactivity

The acute stress response in humans shows different biological profiles depending on gender/sex, with men typically showing a pronounced and robust cortisol response, while women do not tend to show as robust a response (i.e., compared to men). Importantly, this effect extends beyond differences for men versus women (Kudielka & Kirschbaum, 2005), to differences based on the presence of other hormones—such as across the female menstrual cycle and the use of hormonal contraceptives (Childs et al., 2010; Duchesne & Pruessner, 2013; Kudielka & Kirschbaum, 2005)—and to differences based on perceived gender roles (Pruessner, 2018). It is therefore likely that all of these factors (i.e., gender/sex, hormonal levels) can impact empathic abilities. It is important to point out that the *perceived* complexity and variability in females' biology has led to an under-representation of female participants in psychopathology and neuroscience research (Bale, 2019; Riecher-Rössler, 2017; Shansky, 2019), including stress research. As such, much less is known about how acute stress impacts female participants, and what role cyclical variations in ovarian hormones play in the female stress response, and subsequent behaviour, and cognition.

1.2.2 Empathy

Empathy is a multifaceted construct, and definitions of empathy vary substantially between researchers (cf. Batson, 2009; Coll et al., 2017; Davis, 1983; Kogler et al., 2020; Stietz et al., 2019). Here, I broadly define empathy as a set of abilities that can help us identify, understand, and respond appropriately to another person's experience (cf. Baron-Cohen, 2002; de Waal & Preston, 2017).

One way to understand another's emotional state is through *cognitive* empathy. This includes more "top-down" processes, such as emotion recognition, mentalizing, and perspective taking, that allow us to understand someone else's emotions and intentions. As such, cognitive empathic abilities serve several important functions, but in particular they help reduce uncertainties in social interactions, and thus allow us to understand the intentions (and feelings) of another person (FeldmanHall & Shenhav, 2019).

Another way by which this understanding of others can be achieved is via *affective* empathy (encompassing among others: affect sharing and emotion contagion). Affective empathy is a more "bottom-up" process defined as the ability to share an emotional experience with another person. For example, when seeing someone else in distress there will be at least a partial transfer of that negative experience to the perceiver (e.g., seeing someone else step on a sharp object might trigger an unpleasant feeling in the perceiver). It is thought that this sharing of experience gives the perceiver valuable insight into the emotional state of another person and might help the perceiver to relate to that person.

Importantly, these two facets are not just conceptually distinct from one another, but partly rely on non-overlapping neural-computations (Schurz et al., 2020). Cognitive empathic process largely rely on top-down processes—such as increased activation in the dorso-lateral and ventro-lateral prefrontal cortices, and in the temporoparietal junction; whereas affective empathy (i.e., emotion sharing) is mostly mediated through bottom-up processes—such as increased activation in the amygdala, in thalamic regions, and in the anterior cingulate cortex. In addition, the anterior insula and the anterior middle cingulate cortex are commonly activated for both cognitive and affective empathy (de Waal & Preston, 2017; Lamm et al., 2019). Of note, more ecologically valid (i.e., naturalistic) empathy tasks, and, in particular, empathy tasks evoking

complex social cognitions that require the individual to draw inferences from various sources, have been shown to result in a coactivations of both cognitive and affective networks (Schurz et al., 2020).

The overall functions of these empathic abilities and behaviours are thought to increase social coherence, social bonding, and ultimately to enable group survival (for a review: de Waal & Preston, 2017). In this regard, it has been proposed that understanding others' thoughts and/or emotions can lead to an increase in empathic concern and sympathy (i.e., feeling *for* the other person), and ultimately to prosociality and helping behaviours. In this way, empathy can be seen as a complex set of competencies that help us cope with and interact in a complex social environment. However, the exact relationship between these facets of empathy is still unknown. Preston and de Waal (2002) have proposed the Perception-Action Model to integrate affective- and cognitive-empathy (a third concept in the model is prosociality). Within this model, empathy ranges from simple affect-driven, bottom-up processes such as affect sharing, to more complex, top-down regulated processes, such as perspective taking. Furthermore, the model includes helping behaviours as an ultimate consequence of understanding others. Implied in this model is the notion that humans draw from a variety of strategies, which allow them to flexibly process available information (Mitchell, 2005, 2009), in order to understand and react to their social environment.

I now turn to studies investigating the effects of stress on cognitive empathy, that is, the ability to identify and understand the thoughts, feelings, and intentions of another person.

1.2.3 The Effects of Stress on Cognitive Empathy

Cognitive empathy encompasses a variety of skills ranging from simple processes such as emotion recognition, to more complex mentalizing processes that require the integration of contextual information.

From what we know about the effects of stress on cognition in general, we can speculate about the effects of stress on cognitive empathy and make different predictions. On the one hand, research suggests that stress often leads to more habitual and automatic cognitions, and more gist-like information processing (Dandolo & Schwabe, 2016; Hermans et al., 2014; Nitschke, Giorgio, et al., 2020; Satpute & Lieberman, 2006; Schwabe & Wolf, 2009). This suggests that simple tasks, such as emotion recognition, might be enhanced under stress, at least in relevant contexts. However, these faster automatic processes also tend to lead to more rigid thinking. Given this, one might speculate that such facilitatory effects may not extend to more complex cognitions, which require more effortful and flexible control (Contreras-Huerta et al., 2020; Vogel et al., 2016). On the other hand, it has also been suggested that acute stress biases attention to contextually salient information in order to deal with the acutely aversive situation (Hermans et al., 2014). In this regard, social information might be of particular importance (Oliveira & Faustino, 2017; Olsson et al., 2020), given its inherent situational salience for social stress. The notion that stress increases attention to salient information in the environment, suggests that acute stress may augment cognitive empathy, both simplistic and more complex forms.

Emotion Recognition

In possibly the first study on stress and emotion recognition, Smeets and colleagues (2009) manipulated stress via the TSST and measured emotion recognition with the Reading the Mind in the Eyes Test (RMET; Baron-Cohen et al., 2001), in both men and women. In the RMET

participants are presented with photos of faces that are cropped so only the eye region can be seen. Participants must then indicate the target's emotion from a list of four possible responses. Here, the results showed no effect of stress induction on RMET performance (i.e., the number of correct responses). Wolf and colleagues (2015) conducted a similar study but used the Multifaceted Empathy Test (MET; Dziobek et al., 2008). The MET is similar to the RMET, but participants are shown photos depicting the whole face, and sometimes additional contextual information. As with Smeets et al., results showed no effect of stress on the cognitive component of the MET in a male sample. Wingenfeld et al. (2018) also looked at the effects of stress, induced via the TSST, on the MET performance in healthy women, and women diagnosed with borderline personality disorder (not discussed here). Similar to Smeets et al. and Wolf et al. (2015), they found no effect of stress induction on cognitive MET performance in healthy controls (Wingenfeld et al., 2018), although it is important to note that the authors administered the MET 65 minutes after stress induction, when cortisol levels would likely have abated. While these studies suggest that there is no effect of stress on basic emotion recognition, it should be pointed that both the RMET and the MET are rather rudimentary; and that such simplified tasks, with forced-choice answers, can be problematic as they are vulnerable to range restrictions (Oakley et al., 2016; Quesque & Rossetti, 2020).

Other studies have focused on the ability to distinguish between different emotions. For example, Decker et al. (2015) presented participants (n= 24 healthy controls, all female; note: this study also included borderline patients, and patients with Cluster C personality disorders) with video-vignettes of faces morphing from neutral to one of six emotions (anger, disgust, fear, happiness, sadness, and surprise). Participants had to classify the emotions displayed on two

occasions, prior to stress induction (via the TSST), and then again after stress. Compared to baseline, stressed participants had a higher recognition rate for emotions of any valence. Although this study suggests that stress may indeed facilitate emotion recognition, learning effects cannot be ruled out since changes were compared to pre-stress levels of recognition.

This issue was resolved in a recent study by Domes and Zimmer (2019), who exposed one group of their all male participants to the TSST and the other to a control task . All participants then viewed a series of faces and were instructed to identify one of two emotions (happy, angry) at different degrees of morph with a neutral face (low, medium, or high). To quantify accuracy, Domes and Zimmer calculated a sensitivity score (d'). Results showed that participants in the TSST group had a higher sensitivity (d') for identifying emotions of any valence, compared to control participants. Participants in the TSST group also had lower response latencies for identifying negatively valenced emotions—an observation that is consistent with research that stress increases attention to threat cues. Using a different stressor (group version of the TSST), the same research group however reported somewhat contradictory results (von Dawans et al., 2020). In this study stressed male participants had a higher sensitivity (d') for positive emotions, but a lower sensitivity for negative emotions of high intensity compared to control participants. Finally, Daudelin-Peltier and colleagues (2017) investigated the effects of stress on the ability to differentiate emotions from one another. Here, the stimuli consisted of two different emotions presented simultaneously (e.g., fear and disgust) at different proportions (e.g., 86% fear and 14% anger; 50% fear and 50% anger etc). Participants (all men) were asked to make judgments on which prototypical expression the image most resembled. The authors found that stressed individuals (group TSST; vs. control) were more likely to mis-categorize similar emotional facial expressions; specifically, faces expressing disgust or

surprise were more often confused with other emotions. This might suggest that under stress emotions are processed in a more gist-like manner, and consequently results in emotion confusion.

However, not all studies have found an effect of acute stress on emotion recognition. Graumann and colleagues (2021) had healthy female participants (same sample as Wingenfeld et al., 2018) either undergo a stress (TSST) or control task before conducting a facial emotion recognition task (completed 65 minutes after the stressor). Here, participants had to correctly identify neutral as well as two negatively valenced faces (sadness and anger) faces at different levels of intensity (low: 40% intensity, high: 80% intensity). A subsequent sum-score was calculated for all correctly identified emotions at each level of intensity. The authors did not find an effect of stress versus control, for emotion recognition rate, for either low or high emotional intensity.

Overall, results from research looking at simple emotion recognition accuracy are mixed, although the bulk of the evidence suggests that acute stress increases emotion recognition abilities, at least to some extent. That said, there are only a handful of studies on this topic, and the sample sizes are not large. Moreover, the use of different emotion recognition tasks and how emotion recognition is operationalized makes it difficult to compare the findings across the studies.

Beyond Emotion Recognition: Mentalizing, Theory of Mind

Cognitive empathy, of course, extends beyond basic emotion recognition abilities; it also involves inference making about others' thoughts and intentions. Moreover, as noted, such mental state attribution processes social cognitive abilities in real-life situations require the

integration of contextual information, and the updating of information when a situation inevitably changes. As such, the ability to "read" another person necessitates more complex cognitive processes than those engaged in the RMET or similar tasks. To date, research investigating the effect of acute stress on "higher inferential" mentalizing is very limited.

In the aforementioned study by Smeets et al. (2009), the authors also looked at the effects of stress on emotion inference with the Movie for the Assessment of Social Cognitions task (MASC; Dziobek et al., 2006). Specifically, 30-minutes after the TSST, participants were instructed to watch a 15-minute movie of a dinner party involving four characters. At various time-points the video stopped, and participants were asked to make inferences about the feelings and intentions of the characters involved (e.g., "What is Betty feeling?"), from a selection of answer choices (e.g., happy vs. sad). Results showed that stress indeed influenced performance on the MASC; however, the effect of stress depended on gender/sex, with stress improving MASC performance for men, but impairing MASC performance for women. It is important to note that in this study, there was no main effect of the stress condition; rather the effects were driven by the magnitude of the cortisol response in the TSST group. Specifically, for men in the TSST condition, high cortisol responders performed better than low cortisol responders on the MASC (median-split; n=8 high; n=8 low), however, high cortisol responders to the TSST did not perform better than the males in the control condition, which makes the interpretation of these findings less straightforward as it is not simply about the presence/absence of stress. For women in the TSST condition, the opposite effect was observed: here, *low* cortisol responders performed better on the MASC than high cortisol responders; again, though, the effect was specific to the TSST group as high cortisol responders did not differ from women in the control condition (although low cortisol responders did).

The study by Smeets et al. was the first to report gender/sex differences in the effects of stress on cognitive empathy. In some ways this is not entirely surprising; as noted, evidence suggests that there are gender/sex differences in stress reactivity, with men typically showing greater cortisol reactivity in response to stress compared to women (Kudielka & Kirschbaum, 2005). That said, the results are ambiguous given that there was no main effect of the stress manipulation. That is, the effect is not due to the stressor per se; rather it is *how people respond* to a stressor that appears to be important for cognitive empathy.

In summary, there is currently a lack of research on acute stress on social cognitive abilities, and in particular on complex social inference making abilities. The study by Smeets and colleagues is an important first step, one that intriguingly shows gender/sex specific effects that might be tied to the HPA stress response. This is in line with research that suggests that acute stress, and specifically increases in stress induced glucocorticoids such as cortisol, can lead to a large network adjustment from cognitively demanding cognitive process to more automatic and salient driven attentional processes (Hermans et al., 2014; Wirz et al., 2018). There is a need for additional research to utilize adequately powered samples with both male and female subjects, and secondly, to use tasks that are less prone to ceiling/floor effects and more closely resemble real-life situations. Chapter 2: Acute Stress and Cognitive Empathy, will discuss this approach in detail and test the association between acute stress and continuous social inference making using an empathic accuracy task, with a specific focus on gender/sex specific effects.

1.2.4 Effects of Stress on Emotion Contagion/Affective Empathy

Emotion contagion/affective empathy is generally thought to be a relatively automatic, spontaneous process (Preston & de Waal, 2002; Prochazkova & Kret, 2017). We observe someone else's plight and experience a similar affective state. This process can be observed in real-life social interactions (i.e., a close other is crying, and we feel sad), but also in a more abstract fashion (i.e., we see a movie character crying, and we choke up). Many processes can be included under the umbrella of affective empathy; this ranges from putative mirror neuron activation eliciting vicarious emotional states through shared brain activation (Gallese, 2003; Keysers & Gazzola, 2009), to more implicit bodily reactions such as mimicry (Hatfield et al., 1993; Hoffman, 2001; Lipps, 1906; McDougall, 1908). As noted, cognitive empathy and affective empathy are believed to be distinct both at the psychological and biological levels. For this reason, we may not necessarily assume that the effects of stress on affective empathy/emotion contagion will be similar to the effects of stress on cognitive empathy.

To date, much of the work on affective empathy has focused on documenting emotion contagion in humans; specifically, showing the "spillover" of stress from stressed targets to unstressed perceivers (first demonstrated by Buchanan et al., 2012). In general, these studies support the existence of emotion contagion, with some notable boundary conditions (for recent reviews: Engert et al., 2019; White & Buchanan, 2016). For example, vicarious responses appear to be weaker when observing strangers, compared to familiar others (Engert et al., 2014; Schury et al., 2020), and for less visceral situations (Engert et al., 2014; Erkens et al., 2019; Schury et al., 2020). In addition, there is some evidence indicating a divergent emotional response in perceivers (Dimitroff et al., 2017; Young et al., 2017). This divergent response may reflect the perceiver's efforts to down-regulate their own (dis)stress. That is, the experience of seeing others

in distress might be so overwhelming that it triggers egocentric self-regulation and social withdrawal (Porges, 2003; Sandi & Haller, 2015); this response appears to be especially likely for those individuals who are susceptible to intense emotional distress—that is, with high levels of anxiety (Hagenaars et al., 2014), highly sensitive to vicarious affect sharing (Young et al., 2017), and low trait self-concept clarity (Krol & Bartz, 2021). Importantly, these studies do not address the question of whether and how acute stress affects emotion contagion/affective empathy, because stress is the measure of emotion contagion. Further research is therefore needed to delineate when stress leads to vicarious other-centric emotion sharing, and when it leads to ego-centric emotion regulation.

Only a handful of studies have investigated the effects of acute stress on affective empathy by directly manipulating the acute stress response in perceivers to test the causal effect on emotion contagion/affective empathy. In one of the first studies (the first set of experiments was with mice, and the second set of experiments was in humans) on this topic, Martin and colleagues (2015) investigated the effects of stress on emotion contagion. This study followed up on previous work showing that mice experience emotion contagion during interactions with familiar others but not with strangers (Langford et al., 2006). Martin et al. (2015), had male and female friend-dyads and stranger-dyads undergo the CPT to induce stress. During the CPT participants repeatedly immersed their hand in cold (4°C) water for 30 seconds; after each immersion participants rated how much pain they were experiencing. Consistent with Langford et al. 's findings, and the aforementioned work on emotion contagion, pain ratings were significantly higher when a friend was present compared to when a stranger was present, as well as compared to the alone condition, indicating greater shared emotional experience among familiar others.

This emotion contagion finding was also replicated in a subsequent experiment which manipulated familiarity by having stranger dyads play a collaborative video game prior to the CPT (Martin et al., 2015). Similar findings were reported in a recent study by Nahleen and colleagues (2019). Here, participants (all female) first got to know another participant (in actuality, a research confederate) in order to build rapport. Following this, participants either did a version of the CPT (7℃) for 1 minute alone, or in the presence of the confederate. As with Martin et al., participants in the shared condition reported higher levels of sensory pain and higher levels of perceived stress, compared to the alone condition. Finally, Gonzalez-Liencres and colleagues (2016) manipulated acute stress in a sample of men and women using the TSST, compared to a control condition; they then measured empathy for pain by showing participants pictures of others in pain and having them rate how unpleasant the pictures made them feel. Consistent with Martin et al. and Nahleen et al., results showed significantly higher pain ratings in the TSST compared to the control condition, suggesting a causal role for the effect of *first-hand* stress on emotion contagion.

At first blush, these studies seem to suggest that first-hand stress facilitates emotion contagion; however, a closer analysis suggests the effect is not so clear cut. Specifically, Martin et al.'s study (2015) also found evidence to suggest that stress, and specifically the stress hormone cortisol, that was elicited in the stranger condition, actually blocked emotion contagion (an effect that was reversed by the administration of the drug metyrapone, which blocks the synthesis of cortisol). The notion that acute stress may dysregulate the mechanisms that modulate the automatic sharing of emotions is also echoed in work by Tomova and colleagues (2017), who manipulated acute stress by exposing male participants to either a modified version of the Montreal Imaging Stress Task (Dedovic et al., 2005), or a control task, while undergoing

functional neuroimaging. They then showed participants a series of pictures that depicted targets undergoing either a painful procedure (needle injection), or one of two control pictures (target's hand was "anesthetized", or a q-tip "prick"). Results showed that participants in the stress (vs. control) condition showed greater activation in brain areas associated with pain-processing, suggesting greater emotion contagion/affective empathy. Interestingly, stressed (vs. control) participants also showed greater activation in the pain network when viewing the anesthetized hand—a condition that should not result in increased activation. This suggests that acute stress may dysregulate the mechanisms that otherwise modulate the automatic sharing of emotions (i.e., pain), as is also evident from increased engagement of brain areas implicated in emotion regulation and cognitive control during presentation of these stimuli. Of note, this dysregulation was also linked to difficulties in differentiating self- and other-experienced negative affect, suggesting that acute stress leads to more self-centred information processing, or at the very least a blurring of self and other.

Thus, the findings from Martin et al. (2016) and Tomova et al. (2017) suggest that the effects of stress on emotion contagion are not straightforward and may often depend on features of the context (e.g., presence of strangers); moreover, they highlight the difficulty of disentangling the stress response from the emotion contagion response.

In summary, these findings suggest that individuals do experience emotion contagion, especially with familiar others and in more visceral contexts. In contrast to the work on stress and cognitive empathy though, some studies suggest that stress, and specifically the stress hormone cortisol, may disrupt emotion contagion/affective empathy. That said, there is very little work on this

topic. Chapter 3: Acute Stress and Affective Empathy, will discuss this approach in detail and test the association between acute stress and affective empathy using a facial mimicry task.

Chapter 2: Acute Stress and Cognitive Empathy

This chapter has been submitted for peer-review.

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Preface to Chapter 2

Research on the effects of acute stress suggests that stress undermines cognitive abilities, especially those involving executive functioning (Shields et al., 2016). Given this, one might expect acute stress to similarly impair cognitive empathy. However, research indicates that humans process social information differently from non-social information (FeldmanHall & Shenhav, 2019; Oliveira & Faustino, 2017; Olsson et al., 2020), as social information might carry particular relevance for understanding the environment, its threats, dangers, and opportunities. As such, acute stress might enhance attention to social information, rather than impairing it—as noted, in Chapter 1, there is some preliminary evidence to support this assumption (cf. Smeets et al., 2009). Here, we examine the possibility that stress induced glucocorticoid levels might have beneficial effects on cognitive empathy.

With regards to social cognitive abilities, there is limited research investigating the effects of acute stress, and the evidence from these studies is mixed, with most reporting null-effects, while others report gender-specific effects with both enhancing and impairing effects. These inconsistencies likely have several reasons. First, studies have largely relied on simplistic tasks that are prone to ceiling/floor effects, such as the RMET and the MET. In these tasks participants make decisions about the (often stereotypical) emotions expressed by others by picking a correct choice from a set of predetermined answers. Whether or not these simplistic tasks are valid measures for cognitive empathic abilities is thus still a matter of debate (e.g., Oakley et al., 2016; Quesque & Rossetti, 2020). Second, studies have relied on single gender/sex samples to study the effects of stress on cognitive empathy. This makes it difficult to understand these findings in context of gender/sex effects, especially given that there seem to be gender/sex differences in stress reactivity. Third, the one study that has used a more complex task to assess

cognitive empathy in men and women (Smeets et al., 2009) relied on a small sample (after a median split) and results were ambiguous: (there was no main effect of stress vs. no stress; rather, there was only an effect of cortisol in the stress condition). As such there is a need for higher powered studies, in order to test for stress induced effects, including potential gender/sex specific effects, as well as studies with more naturalistic emotion identification tasks.

To test the effect of stress on social cognitive abilities, we used a naturalistic task, empathic accuracy task, that requires participants to continuously rate the emotions expressed by a target (real individuals talking about autobiographical events). In this way we were able to investigate how stress will impact social inference making in situations that are more akin to those we encounter in every-day life. Critically, we included both men and women in our sample. Moreover, to account for the varying levels of endogenous sex-steroids within women, we included a subsample of regularly cycling women in the luteal phase, women in the follicular phase, as well as women using oral contraceptives.

Stress and Stress-induced Glucocorticoids Facilitate Empathic Accuracy in Men, with no Effects for Women

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Abstract:

Empathy, the ability to understand what others are feeling, is critical for establishing and maintaining social connections and navigating our social world. We investigated the effects of acute stress on cognitive empathy. Given that acute stress, and resulting increased glucocorticoids, triggers a shift in two large-scale brain networks, prioritizing salience over executive control, we predicted that stress would facilitate empathic accuracy (EA). We also investigated the effects of gender/sex, given evidence of differential stress reactivity. Results from two independent studies (N= 267 students; 2,256 observations) showed that acute stress facilitated EA for men, an effect that was partly driven by their glucocorticoid response. Conversely, stress had no effect for women, who also showed a blunted cortisol response. Exploratory analyses further revealed that women taking oral-contraceptives performed worse on the EA task than regularly-cycling women. This research highlights the important, but complex, role of stress in cognitive empathy.

Keywords: Stress; Emotion; Tracking; Social Cognition; Empathic Accuracy; Gender/Sex; Social Interactions

Statement of Relevance:

Research on the effects of acute stress suggests that stress undermines cognitive abilities, especially those involving executive functioning. Given this, one might expect acute stress to similarly impair cognitive empathy. However, research indicates that humans process social information differently from non-social information. Here, we examine the possibility that stress induced levels of glucocorticoids might have beneficial effects on cognitive empathy. Results from two studies showed that acute stress facilitated empathic accuracy for men, an effect that was partly driven by their glucocorticoid response. Conversely, stress had no effects on empathic accuracy for women, who also showed a blunted cortisol response. Exploratory analyses revealed that women taking oral contraceptives, in general, performed more poorly on the empathic accuracy task than regularly cycling women. This research highlights the important, but complex, role of stress in cognitive empathy and the importance of considering gender/sex specific effects.

1. Introduction

The ability to understand the emotions of others is critical to navigating daily life and facilitates predictions about future interactions (FeldmanHall & Shenhav, 2019). Moreover, mentalizing, and empathy in particular, plays a vital role in the development and maintenance of social bonds (de Waal & Preston, 2017), and may even contribute to our unrivalled success as a species (Tomasello, 2020; Zaki & Ochsner, 2012). To date, a great deal of research has been devoted to understanding the factors that can facilitate, or hinder, empathy. One factor that has received relatively little attention is acute stress, an ubiquitous feature of the human experience.

Acute stress is a momentary adaptive response to an adverse or challenging situation that aims to restore a physiological and behavioural homeostatic balance (Lazarus, 2006). The stress response results in the activation of numerous biological systems. Two of them are frequently investigated for their effects on human behaviour: 1) the fast-acting autonomic nervous system, indicated by increased heart rate, electrodermal activation, and the release of catecholamines and 2) the slower acting hypothalamic-pituitary-adrenal (HPA) axis leading to an increase of its downstream marker cortisol. Through a negative feedback loop, cortisol reaches the central nervous system and is thought to cause a shift in neural activation meant to further an adaptive response in order to deal with the stressor. As Hermans and colleagues (2014) theorize, acute stress triggers the reconfiguration of two large-scale neural networks. Immediately following the stressor, resources are reallocated from the executive control network to the salience network; this reallocation of resources facilitates vigilance to contextual cues, especially threat cues, which, presumably, helps the organism to cope with the challenge at hand. Once the immediate threat has passed, resources are shifted back to the executive control network. Meta-analytic data support the idea that these two systems are modulated in a reciprocal manner following stress:

performance on attentional vigilance tasks is generally elevated when such tasks are administered immediately following a stressor (within ~1 hour) and decline afterwards, whereas performance on executive control tasks is typically lower when such tasks are administered immediately following a stressor but improves as the time relative to stressor onset increases (Hermans et al. (2014). To the extent that mentalizing, and cognitive empathy in particular, relies on the salience network, we might expect acute stress will have beneficial effects on this kind of information processing.

In the present research, we aimed to investigate the effects of acute psychosocial stress on empathic accuracy—i.e., the ability to dynamically track the emotional state of another individual over time. To this end, we conducted two studies in which we induced acute psychosocial stress with the Trier Social Stress Test (TSST)(Kirschbaum et al., 1993), and then had participants complete an empathic accuracy task (Zaki et al., 2008) in which they watched videos of targets discussing negative autobiographical events and rated, continuously, how they thought the target was feeling. Critically, the targets also rated how they were feeling, which allowed us to calculate an index of empathic accuracy by correlating perceiver and target ratings of the target's affect overtime. Because empathic accuracy relies on the ability to update one's representations based on (often) subtle changes in the target's affect, it should be particularly sensitive to glucocorticoid-induced changes in attentional vigilance for negatively valenced or threatening information (Hermans et al., 2014).

We also aimed to investigate whether the effects of acute psychosocial stress on empathic accuracy depends on gender/sex. To date, women are under-represented in stress research, largely because cyclical variation in ovarian hormones makes it difficult, methodologically, to study them (Riecher-Rössler, 2017; Shansky, 2019). As Kudielka et al. (2004) have shown,

women typically show an attenuated cortisol response (an effect that is linked to ovarian hormones) to that of men. This difference in stress reactivity could have important implications for cognition, and empathic accuracy in particular. If the aforementioned stress-induced shift in cognition is thought to be driven by cortisol, and women show a more blunted cortisol response, women may be less likely than men to show facilitatory effects of stress on empathic accuracy. In fact, there is preliminary evidence that gender moderates the effects of stress on more general social cognition (Smeets et al., 2009).

Finally, we also took this opportunity to explore the role of women's oral contraceptive use. Women taking oral contraceptives are especially likely to be excluded from stress research because they show an even more blunted cortisol response than regularly cycling women, due to the higher availability of corticosteroid-binding globulin caused by exogenous oestrogen administration (Kirschbaum et al., 1995; Meulenberg et al., 1987). Thus, very little is known about how women taking oral contraceptives respond to stress and how the two might interact to influence social cognition. Given the significant number of women taking oral hormonal contraceptives—approximately 25% of college aged (i.e., 20 to 30 years) women in the US (Kavanaugh & Jerman, 2018)—this is a serious gap in our understanding.

2. Experiment-1 (between-subjects)

2.1 Overview

In Experiment-1 we randomly assigned participants to the TSST or a control condition (placebo TSST; see below); participants then completed the empathic accuracy task as well as tasks assessing different research questions (Nitschke & Bartz, 2020). See Figure-1 for timeline.

2.2 Sample

One-hundred and fifty-eight participants were recruited from classifieds-ads and online advertisements posted on McGill University forums; as noted, we recruited men, regularly cycling ("RC") women, and women taking oral contraceptives ("OC"); in order to reduce variance associated with cyclical changes in oestrogen, RC women were asked to come during the luteal phase of their menstrual cycle. For sample size considerations see Supplemental Materials. Three women were excluded: one opted out of the study following the TSST, and two others—one TSST and one control—had no empathic accuracy data due to computer malfunction. Thus, the final sample consisted of 61 men (mean age= 22.4; SD = 3.43), and 97 women (mean age= 22.1; SD= 3.42; 48 RC and 49 OC). There were 78 participants in the TSST condition (30 men, 23 RC and 25 OC women) and 80 participants in the control condition (31 men, 25 RC and 24 OC women; see Supplemental Online Materials for detailed participant demographics). The study was approved by the McGill University Institutional Review Board and conducted in accordance with the Declaration of Helsinki, as was Experiment-2.

2.3 Measures

Empathic Accuracy Task (EA) (Zaki et al., 2008). Participants watched six videos of real individuals ("targets") discussing negative autobiographical life events (e.g., losing one's job, death of parents, rejection). While watching each video, participants used key presses on a computer keyboard to continuously rate how they thought the target felt during the narrative based on a 9-point Likert-scale, ranging from 'very negative' to 'very positive' (Zaki et al., 2008). Importantly, the targets also rated their own emotional experience while discussing the events on the same 9-point Likert scale. Empathic accuracy is operationalized as the correlation

between the continuous ratings made by perceivers and targets (ratings were z-scaled within participants to account for individual differences). To ensure that any effects we observed were not due to the idiosyncratic nature of particular videos, we randomly assigned participants to watch one of two video sets (with an equal number of male and female targets).

Trier Social Stress Test (TSST) (Kirschbaum et al., 1993)**.** The TSST is a mock-job interview followed by an oral arithmetic task, and has been shown to reliably induce a cortisol (Goodman et al., 2017), sympathetic nervous system (Rohleder et al., 2004), and subjective stress (Ali et al., 2017) response. For participants in the control condition we used the placebo version of the TSST (Het et al., 2009). The placebo TSST (from here on, “control condition”) is matched to the characteristics of the TSST without eliciting an acute stress response: participants are instructed to talk about a recent life event for 5-minutes in an empty room. Following this, participants are instructed to count upwards in 15 step increments. In 10-minute intervals (starting 10-minutes prior to the TSST or control task), we took saliva samples (i.e., "Salivette"; Sarstedt AG & Co, Nümbrecht, Germany) to assess cortisol; at these time-points we also measured salivary alpha amylase (sAA; a marker of sympathetic activation) (Ali & Nater, 2020), and subjective-stress using a visual analogue scale (i.e., “how stressed do you feel?”). Our primary hypotheses concerned cortisol; interested readers are referred to the Supplemental Online Materials for additional analyses including sAA and subjective stress.

Analytic Approach. We first sought to confirm successful stress manipulation. To this end, we conducted a repeated measures mixed-effects model (rMEM) (Gueorguieva & Krystal, 2004) to test for differences in stress responsivity (cortisol levels at each measurement time-point)

between the stress and control condition. Condition (0= control, 1= stress), Gender/Sex (men, RC women, and OC women; see below), and sampling-time were included as predictors, as well as all 2-way interactions, and the 3-way Condition × Gender/Sex × sampling-time point interaction. Time was nested within Subject-ID as a random-factor (see Supplemental Online Materials, Note 1).

To test our main hypothesis—the effect of acute psychosocial stress on empathic accuracy—we ran a mixed-effects model (MEM) (Holmes Finch et al., 2014) with empathic accuracy scores as the dependent variable, and the fixed-factors Condition (0= control, 1= stress) and Gender/Sex (men, RC, and OC women; see below); we also included the Condition × Gender/Sex interaction term to test for differential effects of stress on empathic accuracy for men, RC and OC women. AICs were used to test whether the inclusion of the interaction term resulted in a more parsimonious model fit (i.e., variance explained versus model complexity; see Supplemental Online Materials) (Cohen et al., 2003). Finally, we included two random factors, Subject-ID and Video-ID, in our model. For this and all subsequent analyses, the planned contrasts (Helmert-coding) for the Gender/Sex variable were defined as following: contrast-1, testing men vs. all women (men= 1, RC= -0.5, OC= -0.5), and constrast-2, testing RC vs. OC women (Men= 0 (excluded), RC= 1, OC= -1). Finally, we also included a covariate to account for video sets in this and all subsequent models.

We then tested the effect of stress-induced cortisol on empathic accuracy. We first calculated AUCs for cortisol (i.e., changes from pre-stress levels until immediately after the empathic accuracy task) using the formula described by Pruessner et al. (2003). We then conducted MEMs as described above but in addition included cortisol AUC (z-transformed) as a fixed-effect. Of note, it has previously been reported (Nitschke et al., 2019; Smeets et al., 2009)

that cortisol may have a nonlinear association with (social) cognitive abilities; thus, in an exploratory step we included a second-degree polynomial effect of cortisol.

All confidence intervals were bootstrapped. All statistical analyses were conducted in R (Version: 3.6.3) (R Core Team, 2020), and the lme4 (Bates et al., 2015) and lmerTest (Kuznetsova et al., 2017) packages for mixed-effects models. Significant interaction effects from the MEMs were decomposed using the emmeans package (Lenth et al., 2018).

3. Results

Manipulation Check for Stress Induction: Cortisol

The rMEM testing for an effect of stress induction on cortisol levels revealed a significant triple interaction between Condition, Gender/Sex, and sampling-time $F(14, 703.75)= 3.81$, $p< 0.001$. Specifically, results showed significantly higher cortisol levels in the stress versus control conditions and, thus, successful stress induction; moreover, consistent with prior work (B. M. Kudielka et al., 2004), results showed that men had a higher cortisol response compared to women (contrast-1) at time-points, 3, 4, 5, 6, and 7 (all ps < 0.05; see Supplemental Online Materials for details). We did not observe cortisol differences between RC and OC women (contrast-2) at any time-point. For visualisation of the cortisol response see Supplemental Online Materials.

Effect of Stress Induction on Empathic Accuracy

Next the MEM predicting empathic accuracy with Condition and Gender/Sex and their interaction as fixed-factors, and Subject-ID and Video-ID as random effects, revealed a significant interaction effect for contrast-1 (men versus women), b= 0.052 (SE= 0.02;

95%CI[0.003, 0.097]), *t*(156.12)= 2.184, *p*= 0.031. Specifically, men in the stress condition had significantly higher empathic accuracy scores than men in the control condition, b= 0.063 (SE= 0.03; 95%CI [0.006, 0.119]), *z*=2.195, *p*= 0.029. By contrast, there was no difference in empathic accuracy performance between women in the control condition and women in the stress condition, b= 0.015 (SE=0.02; 95%CI[-0.029, 0.059]), *z*= -0.661, *p*= 0.51. Results also showed that women had significantly lower empathic accuracy scores than men in the stress condition, b= -0.073 (SE= 0.03; 95%CI[-0.023, -0.124]), *z*= 2.867, *p*= 0.005. Finally, there was no difference in empathic accuracy performance between women and men in the control condition, b= 0.004 (SE= 0.03; 95%CI[-0.046, 0.054]), *z*= -0.153, *p*= 0.878; See Figure 2 for a graphic depiction of the results, and Table S1 (Supplemental Online Materials) for a summary of the model.

Regarding contrast-2 (comparing RC and OC women), results showed no significant interaction, b= -0.032 (SE= 0.02; 95%CI[-0.07, 0.009]), *t*(156.12)= -1.456, p= 0.146; however, there was a significant conditional effect for contrast-2, b= 0.033 (SE= 0.015; 95%CI[0.005, 0.065]), *t*(156.12)= 2.153, *p*= 0.033, indicating that women taking oral contraceptives performed worse on the empathic accuracy task than regularly cycling women across both conditions (control and stress). See Figure 3 for a graphic depiction of the results.

Effect of Cortisol on Empathic Accuracy

We next investigated the effects of cortisol (AUC, z-transformed) on empathic accuracy. As the previous analysis indicated a differential effect of stress on empathic accuracy for men and women, and a significant difference in cortisol response for men and women, we ran two separate models, the first for men, and the second for women (we combined the RC and OC

women given that our main analyses showed no differential effects of stress for these two groups). The MEM for men showed a significant interaction between Condition and cortisol on empathic accuracy, b= 0.068 (SE=0.03; 95%CI[0.012, 0.126]), $t(56.00)= 2.270$, $p= 0.027$; for men in the stress condition, higher cortisol was associated with superior empathic accuracy performance, $b= 0.034$ (SE= 0.02; 95%CI[0.004, 0.065]), $z=2.267$, $p= 0.027$), whereas for men in the control condition, there was no association between cortisol and empathic accuracy, $b= -0.033$ (SE= 0.03; 95%CI[-0.085, 0.018]), $z= -1.298$, $p= 0.200$. The MEM for women did not result in a significant slope, $b= -0.015$ (SE= 0.023; 95%CI[-0.061, 0.033]), $t(92.99)= -0.647$, $p= 0.519$, indicating no association between cortisol and empathic accuracy. Finally, the inclusion of a polynomial cortisol effect did not show any significant result, suggesting that the association between cortisol and empathic accuracy is linear. In sum, these results indicate that the biological stress response—i.e., cortisol—facilitated empathic accuracy for men.

In sum, we show that acute psychosocial stress improves empathic accuracy performance for men, but has no effect on empathic accuracy for women. This finding does not appear to be due to ceiling effects on the empathic accuracy task for women—our results show no gender/sex difference in the control condition (cf. Christov-Moore et al., 2014); rather, men actually get a boost in performance from the stressor. Additional analyses reveal that the effects of stress on empathic accuracy for men is due, in part, to their enhanced cortisol response, an effect that was not observed for women. These findings are consistent with the notion that acute stress-induced glucocorticoid changes facilitate attentional vigilance for negatively valenced information (Hermans et al., 2014). Finally, intriguingly, we found that women taking oral contraceptives performed significantly worse than regularly cycling women on the empathic accuracy task, regardless of stress condition, suggesting a potential link between exogenous oestrogen

administration and social cognitive abilities.

4. Experiment-2 (within-subject)

4.1 Overview

In Experiment-2, we aimed to replicate the findings from Experiment-1. Although some prior work led us to expect that gender/sex might moderate the effect of stress on empathic accuracy, these findings nonetheless warrant replication. Moreover, in Experiment-1, we used a between-subjects design; however, this design is vulnerable to the influence of individual differences (e.g., in stress reactivity and/or empathic accuracy performance). Thus, in Experiment-2, we used a within-subjects design to control for these sources of influence. During the first visit ('Visit-1'), participants completed the empathic accuracy task in the absence of stress as well as other tasks and questionnaires reported elsewhere (Nitschke, Sunahara, et al., 2020; Nitschke & Bartz, 2020). Participants returned to the lab approximately 3 weeks later (or according to the menstrual cycle; see Supplemental Materials) for 'Visit-2'; they first underwent the TSST and, immediately after, completed the empathic accuracy task. The timing of the empathic accuracy task vis a vis stress induction was identical to Experiment-1. See Figure-1 for timeline.

4.2 Sample

As in Experiment-1, we recruited men, regular cycling (RC) women and women on oral contraceptives (OC)(For details see Supplemental Materials). We used the same inclusion and exclusion criteria as for Experiment-1. Ten female participants did not return to the lab for the second session; thus, the final sample consisted of 109 participants (men= 30; women= 79, 54

RCW, 25 OC). Participants were compensated $10 an hour for their time ($10 + $20).

4.3 Measures

Empathic Accuracy Task. We used the same empathic accuracy task described in Experiment-1. To avoid practice effects, participants watched different videos on Visit-1 and Visit-2. As in Experiment-1, we included a variable to account for possible differences between the two video sets in our statistical analyses.

Trier Social Stress Test. We again used the TSST to elicit a stress response during Visit-2, and followed the same stress marker protocol; all measures (cortisol, sAA, and subjective stress) were taken at seven time-points throughout Visit-2, starting 20-minutes before the stress induction, prior to stress (-10), and following stress at: 0, +10,+25, +40, and +50. Cortisol levels (nmol/l) were assessed using a time-resolved fluorescence immunoassay (Dressendörfer et al., 1992) and sAA (U/ml) levels were determined using the enzyme kinetic method (Engert et al., 2011). Again, for additional analyses including sAA and subjective stress see Supplemental Online Materials.

Analytic Approach. We followed the same analytic plan as in Experiment-1. We first ran a repeated measures MEM (Gueorguieva & Krystal, 2004) to test the effects of acute stress induction on cortisol levels for Visit-2 (stress day); we included Gender/Sex (same coding as Experiement-1), sampling-time, and the interaction between Gender/Sex and sampling-time as fixed-effects. Time was nested within Subject-ID as a random-factor.

Next we ran a MEM predicting empathic accuracy. Visit (0=Visit-1; 1=Visit-2) and

Gender/Sex (men, RC women, and OC women) were entered as fixed-factors. We included an interaction between Visit and Gender/Sex to test for differential effects for men, RC women and OC women. Subject-ID and Video-ID were entered as random factors. Visit was nested within Subject-ID.

Finally, as in Experiment-1, we followed-up these analyses with MEM analyses that also included cortisol AUC (z-transformed) as an independent variable (note: these analyses are restricted to Visit-2, as we did not measure cortisol on Visit-1).

5. Results

Manipulation Check for Stress Induction: Cortisol

The repeated measures MEM testing the effect of stress induction on cortisol levels revealed a significant interaction between Gender/Sex and sampling-time, $F(12, 373.09)= 2.474$, $p= 0.004$, indicating that Gender/Sex moderated the effect of the stress induction on cortisol; specifically, consistent with prior work, and as observed in Experiment-1, men had a higher cortisol response compared to women (contrast-1) at time-points, 3, 4, 5, and 6 (all ps < 0.05; see Supplemental Online Materials for details). We did not observe cortisol differences between RC and OC women (contrast-2) at any time-point. For plotted cortisol-curves see Supplemental Online Materials.

Effect of Stress Induction On Empathic Accuracy

The MEM with empathic accuracy as dependent variable and Gender/Sex, Visit, and the interaction between Gender/Sex and Visit as fixed-factors revealed a significant interaction for contrast-1 (men vs. women), b=0.047 (SE= 0.02; 95% CI[0.007, 0.083]), $t(108.13)= 2.467$, $p=$ 0.015. Specifically, as in Experiment-1, men showed a significant increase in empathic accuracy

performance from Visit-1 to Visit-2 (stress induction visit): b= 0.060 (SE= 0.02; 95%CI[0.013, 0.108]), *z*= 2.516, *p*= 0.013. By contrast, for women, there was no difference in empathic accuracy performance from Visit-1 to Visit-2, b= -0.01 (SE= 0.02; 95%CI[-0.039, 0.020]), *z*= -064, *p*= 0.523. Results also showed that men had significantly higher empathic accuracy scores than women during Visit-2: b= 0.064 (SE= 0.03; 95%CI[0.012, 0.116]), *z*= 2.418, *p*= 0.017. Finally, there was no difference in empathic accuracy performance between men and women at Visit-1/baseline: b=-0.01 (SE=0.02; 95%CI[-0.041, 0.054]), *z*= -0.266 *p*= 0.791. See Figure-4 and Table S2 (see Supplemental Online Materials).

The interaction for contrast-2 (RC versus OC women) was not significant, b= -0.015 (SE= 0.015; 95% CI[-0.044, 0.015]), *t*(108.03)= -0.970, *p*= 0.334. However, as in Experiment-1, we observed a significant conditional effect for contrast-2, b= 0.029 (SE= 0.01; 95%CI[0.004, 0.056]), *t(*108.34)= 2.252, *p*= 0.026, indicating that, again, women taking oral contraceptives performed worse on the empathic accuracy task than regularly cycling women across both visits. See Figure 3 for a graphic depiction of the results.

Effect of Cortisol on Empathic Accuracy

In a next step we assessed the impact of stress-induced cortisol (AUCi) on Empathic Accuracy during Visit-2. Again, because the previous analysis indicated a differential effect of stress on empathic accuracy for men and women, and a significant difference in cortisol response for men and women, we ran two separate models, the first for male participants, and the second for female participants. Replicating the findings from Experiment-1, the MEM for men showed a significant effect of cortisol on empathic accuracy: *b*= 0.046 (SE= 0.019; 95% CI[0.013, 0.083], *t*(27.28)= 2.501, *p*= 0.019), whereas the MEM for women did not show a significant association

(although the pattern was in the same direction): b= 0.024 (SE= 0.01; 95% CI[-0.003, 0.050]), t(77.24)= 1.758, p= 0.083. These results indicate that men benefited from increased levels of cortisol, while women did not. The inclusion of this curvilinear effect did not result in a significant predictor for either men or women, indicating a linear relationship between cortisol and EA for men.

In sum, in Experiment-2 we replicate several key findings from Experiment-1. Specifically, acute stress improved empathic accuracy performance for men, but had no effect on empathic accuracy performance for women (either RC or OC). Again, it was not that women performed better overall: there was no difference in empathic accuracy between men and women at Visit-1/the baseline testing day; rather, men showed selective gains in empathic accuracy following the stress induction. We also replicated the finding from Experiment-1 that women showed a more blunted cortisol response to the TSST compared to men, and that the magnitude of the cortisol response, for men, was associated with superior empathic accuracy. Finally, we replicate the intriguing oral contraceptives effect observed in Experiment-1, such that women taking oral contraceptives performed worse on the empathic accuracy task, in general, than did regularly cycling women.

6. Discussion

In two independent experiments we show that, for men, acute psychosocial stress improves empathic accuracy—i.e., the ability to accurately track another's emotional experience overtime; conversely, stress has no effect on empathic accuracy in women. Moreover, results show that men's empathic accuracy performance following stress was partially due to stressed-induced levels of the glucocorticoid cortisol. Recent accounts suggest that acute stress triggers a phasic

shift in two large-scale neural networks, prioritizing the salience network over the executive control network, at least immediately following the stressor. Our findings are consistent with this idea: If stress facilitates vigilance to contextual cues, and especially threat, then one would expect enhanced attention to, and processing of, the negative emotional experiences conveyed by our empathic accuracy targets. Here, it is interesting to note research showing that stress impairs set-shifting (Shields et al., 2016) and, more generally, is thought to undermine flexible and/or effortful behaviours (Nitschke, Giorgio, et al., 2020; Otto et al., 2013; Steinhauser et al., 2007; Wirz et al., 2018). The empathic accuracy task requires cognitive flexibility as participants must continually update their ratings as the target's emotional state evolves over time. Our findings may thus represent an exception to this prior work; in this case, increased vigilance to salient social-emotional information may compensate for any stress-induced cognitive rigidity.

In contrast to men, stress had no effect on empathic accuracy in women. This was not because women were simply better at the empathic accuracy task as there was no difference between men's and women's empathic accuracy performance in the placebo condition (Experiment-1) or at baseline (Experiment-2); this observation that goes against the popular, but empirically dubious (Christov-Moore et al., 2014), view that women are more empathic than men. Why did stress *not* enhance women's empathic accuracy performance? One possibility is that women may have experienced and/or coped with the stressor differently than men. For example, women may have been more likely to perceive the TSST as a threat rather than a challenge experience (Dickerson & Kemeny, 2004; Moons et al., 2010). That said, stress did not impair women's empathic accuracy performance (their performance did not change). It may be that women's social cognitive abilities are more robust than are men's, and/or are less affected by contextual shifts, such as acute stress, or other hormonal factors (Bartz et al., 2019). Another

possible explanation is that women did not mount a strong cortisol response to the stressor. In both Experiment-1 and -2, men showed a stronger cortisol response to the TSST compared to women, and the effects of stress on empathic accuracy, in men, was partly due to cortisol. If, as is thought to be the case, the re-balancing of the salience and executive networks following acute stress is driven by stress-induced changes in neurotransmitters and hormones, including cortisol (Hermans et al., 2014), then the absence of a strong cortisol response in women may explain the lack of an effect—indeed, the association between cortisol and empathic accuracy for women was positive but fell short of statistical significance in both Experiments and, in fact, was marginal in Experiment-2. While further research is needed to understand the mechanisms underlying gender/sex differences in response to stress, and how that affects social cognition, the differential gender/sex effects that we observed, across two independent samples, highlights the importance of including women in stress research. Given that acute stress can influence men and women differently (Ali, Nitschke, et al., 2020; Brigitte M. Kudielka & Kirschbaum, 2005; van den Bos et al., 2009), and our data, as well as other data showing that some cognitive processes might be impacted differently by stress (Starcke & Brand, 2016), we cannot assume that the effects observed in men will generalize to women.

Interestingly, our exploratory analyses showed that women taking oral contraceptives performed significantly worse on the empathic accuracy task than regularly cycling women. To date, evidence regarding oral contraceptive use and social cognition is mixed (Montoya & Bos, 2017), with some studies showing an effect (Hamstra et al., 2014), but not others (Radke & Derntl, 2016; Shirazi et al., 2020). Our findings are consistent with the former group. Interestingly, Hamstra and colleagues (2014) found that hormonal contraceptive use impaired emotion recognition abilities, particularly for negatively valenced emotions (cf. Pahnke et al.,

2018); this is noteworthy given that our empathic accuracy task only included videos of negative autobiographical experiences. Thus, valence may be an important factor to consider in future work comparing women taking oral contraceptives and regularly cycling women. We should note, however, that while we observe this effect in both experiments, if we do not include interaction-terms for our gender/sex variable (i.e., main effects models; see Supplemental Materials), then the oral contraceptive effect only holds for Experiment-2. Although this could indicate a spurious effect in Experiment-2, it is possible that the muted effect observed in Experiment-1 was due to our use of a between versus within-subject design, which would have reduced our statistical power and limited our ability to control for individual variation in hormones. That said, future studies should confirm and further investigate the effects of oral contraceptives on social cognition, given the fairly large number of women taking oral contraceptives (~25% of college age women in the United States)(Kavanaugh & Jerman, 2018).

Another question for future research is whether stress similarly affects empathic accuracy for positive emotional experiences. Stress is thought to bias attention to negative, threat related information to help the individual assess threat levels in the environment (Olsson et al., 2020). Supporting this, Bublatzky and colleagues (2020) showed that in a threat (vs. safety) condition, facial emotion recognition was biased towards negative emotions, especially more subtle expressions. Similarly, others (Ali, Cooperman, et al., 2020) have found that acute psychosocial stress increased threat perception for contextually relevant neutral facial stimuli, relative to baseline. In addition, there is research indicating that acute stress increases the speed at which negative emotions are recognized (Deckers et al., 2015; Domes & Zimmer, 2019). If the effects of stress on attention to threat accounts for the present findings, then it is unclear whether these effects would extend to the processing of more positive information. Similarly, research indicates

that one's own affective experience is an important source of information when we perceive another person's emotions (Silani et al., 2013; Steinbeis, 2016; Trilla et al., 2020); if such mood-congruent bias is at play, that would suggest caution when considering the effects of stress on the processing of positive social cues.

In sum, empathy and specifically the capacity to understand the emotional states of others, is a cornerstone of human social-emotional experience. Our findings show that acute psychosocial stress and, specifically, the stress hormone cortisol, facilitates empathic accuracy for men, but has no effect on empathic accuracy for women. This research adds to the growing body of literature showing that cognitive empathy is not only influenced by our psychology but is also tied to our biology.

Appendix

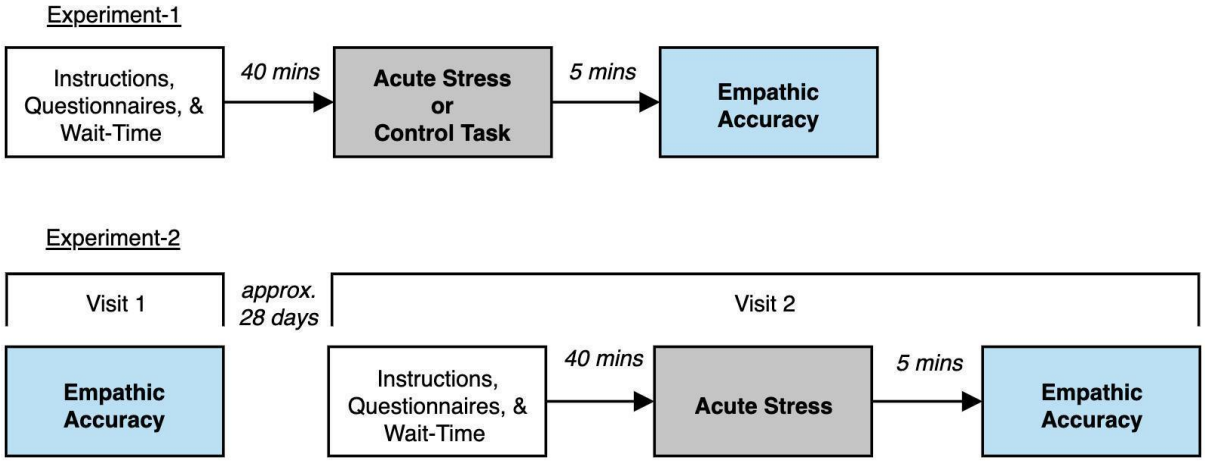

Figure 1: Study design for both Experiments. Experiment-1, participants were randomly assigned to either an acute stress paradigm or a control condition before doing the EA task. d. In Experiment-2, utilized a within-subject design; participants came to the lab on two separate occasions, separated by a ca. 28 delay (or based on the menstrual cycle), during visit-2 all participants underwent a stress task before doing the same EA task as in Experiment-1.

Figure 2. Experiment-1: Effects of acute psychosocial stress on empathic accuracy in men

and women. Group differences between the control and the Stress (TSST) groups.

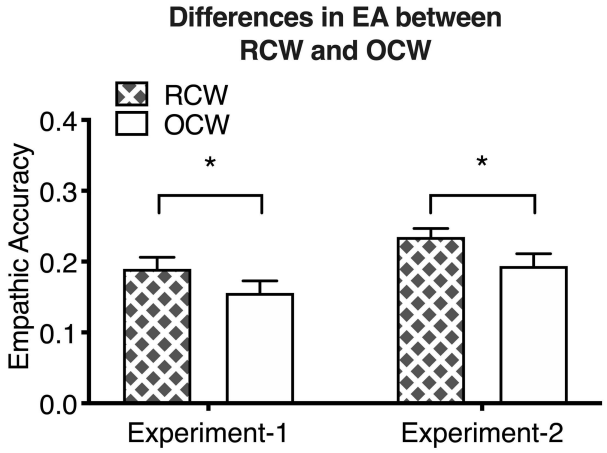

Figure 3. Differences between women using oral contraceptives (OCW) and regularly cycling women (RCW), across Conditions/Visits. Left panel, differences for Experiment-1. Right panel, differences for Experiment-2.

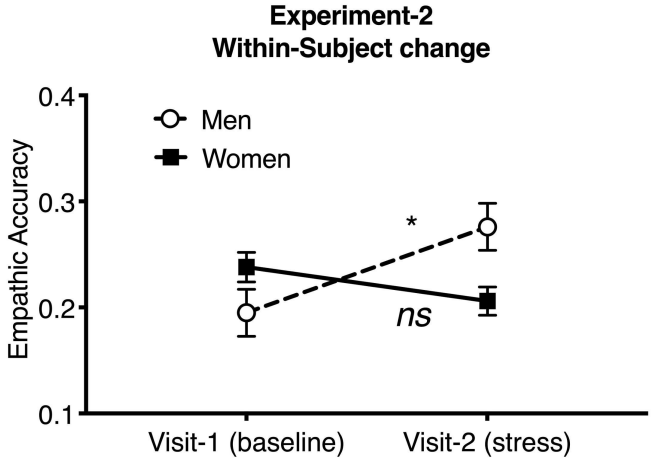

Figure 4. Experiment-2: Effects of acute psychosocial stress on empathic accuracy in men and women. During visit-1 participants did the empathic accuracy task in the absence of stress;

during visit-2 all participants did the TSST before re-doing the EA-Task (with different videos, counterbalanced).

Supplemental Materials

Stress and Stress-induced Glucocorticoids Facilitate Empathic Accuracy in Men, with no effects for Women

Content:

Notes

Note 1:

To reduce issues of convergence we used the bound optimization by quadratic approximation (i.e., BOBYQA) optimizer (Brauer & Curtin, 2018; Powell, 2009). This optimizer was used for all time-course cortisol analyses (Experiment-1 and Experiment-2), and for the main models predicting empathic accuracy (Experiment-1 and Experiment-2).

Sample Size Considerations

Given that no studies have yet investigated how acute stress affects empathic accuracy, we used findings from prior work examining the effects of stress on social cognition more generally (Smeets et al., 2009). Smeets and colleagues report differences for unstressed (m= 0.75, sem= 0.04) and (highly) stressed men (0.84, sem=0.05; d=0.57), as well as differences for unstressed (m= 0.79, sem= 0.03) and (highly) stressed women (m= 0.69, sem= 0.04; d= 0.80) (Rosenthal et al., 1994). Using the G*Power software (Faul et al., 2009), we calculated the following minimum sample sizes to detect an effect for stress versus control (α= 0.05; 1-ß= 0.8, f= 0.285) for a medium effect size: 30 participants per group and for each gender/sex for Experiment-1 (between-subjects, observations per subject= 6); and 29 for each gender/sex for Experiment-2 (within-subject, observations per subject= 12).

Menstrual Cycle Screening Procedure

Experiment-1:

Prior work has suggested that hormonal status, in particular the female menstrual cycle, can impact the biological stress response (for a review: Brigitte M. Kudielka et al., 2009). During

recruitment, female participants were asked to self-report hormonal contraceptive use. For this particular experiment we recruited two groups of women, regularly menstruating females (with cycle lengths of 21- 35 days) in their late follicular phase (for a 28 cycle, days 10-14) , and women using hormonal contraceptives. Women using oral contraceptives reported taking contraceptives for at least 1 year prior to testing. For each regularly cycling female participant, following recruitment, and prior to scheduling the first laboratory session, we tracked two full menstrual cycles in order to confirm their self-reported cycle length. For each regularly cycling female participant, following recruitment, and prior to scheduling the first laboratory session, we tracked the two full menstrual cycles in order to confirm their self-reported cycle length. It has been suggested that comparing OCW to women in the follicular phase is more informative than comparing women in the mid-luteal phase (Montoya & Bos, 2017), we therefore decided to only recruit women in the late follicular phase.

Experiment-2:

Similarly, for Experiment-2, for visit-1,we recruited both RCW and OCW. For Experiment-2, half of the regularly cycling female participants were scheduled during the late follicular phase of their menstrual cycle, and the other half during their mid-luteal phase (for a 28 cycle, days 18-26). Following the first session, participants were scheduled for visit-2 during the same menstrual cycle phase of the following month, according to the previously tracked cycle. Half the regularly cycling female participants were scheduled to participate during the late follicular phase of the menstrual cycle, while the other half was scheduled during the mid-luteal phase.

Menstrual Cycle

Additional analyses (Experiment-2):

Adding cycle phase as predictors to the models (instead of gender/sex) did not change the results; female participants showed similar behaviours across both menstrual cycle phases. To this aim we ran a mixed-effects model with a Helmert-coded grouping variable including both types of RCW (Contrast-1: men versus all women; Contrast-2: RCW versus OCW; Contrast-3: Late-follicular versus Mid-Luteal). The results of the MEM show a significant interaction for contrast-1 (men vs women), b=0.047 (SE= 0.010), t(108.134)= 2.499, p= 0.0139, but not for the other two contrasts. Instead, we find a significant conditional marginal effect for contrast-2, b=0.03(SE= 0.013), t(108.338)= 2.357, p=0.0202. The contrast-3 was not significant, b=-0.021(SE=0.0143), t(108.341)= -1.432, p= 0.155, indicating no significant differences for mid-luteal and late follicular women across conditions or in response to stress. See Figure S1 below.

Salivary Alpha Amylase

In order to quantify the sympathetic nervous system activation, we calculated AUCs (Pruessner et al., 2003) for the salivary alpha amylase (sAA) measures (i.e., changes from pre-stress levels until immediately after the empathic accuracy task). Following this AUC values were z-standardized for interpretability. We subsequently entered the values as predictors into an MEM predicting empathic accuracy, analogous to the cortisol analyses reported in the main manuscript.

Experiment-1:

For the MEM predicting empathic accuracy as a dependent variable, we entered group (control versus stress), AUC for sAA, and their interaction as fixed factors. Subject-ID and Video-ID were entered as random factors. We ran models separately for men and women.

The results of the MEM predicting empathic accuracy in men did not result in a significant interaction (b=0.004(SE=0.03), t(55.99)= 0.127, p=0.90), or conditional marginal effect (b=0.015(SE=0.016), t(56.00)= 0.963, p=0.340) for AUC sAA. Hence, levels of sAA did not have an influence on empathic accuracy performance for men. The results of the MEM predicting empathic accuracy in women did not result in a significant interaction (b=0.014(SE=0.03), t(90.99)= 0.525, p=0.60), or conditional marginal effect (b=-0.037(SE=0.02), t(90.996)= -1.683, p=0.096) for AUC sAA. Hence, levels of sAA did not have an influence on empathic accuracy performance for women.

Experiment-2:

For the MEM predicting empathic accuracy as a dependent variable, we entered AUC for sAA as fixed factors. Subject-ID and Video-ID were entered as random factors. We ran models separately for men and women.

The results of the MEM predicting empathic accuracy in men did not result in a significant effect for AUC sAA, b=-0.025 (SE=0.2), t(26.29)=1.376, p=0.181. Neither did the MEM predicting empathic accuracy in women with AUC sAA, b=0.0201 (SE=0.1), t(77.24)=1.538, p=0.128.

Subjective Stress (Visual Analogue Scales)

In order to quantify the sympathetic nervous system activation, we calculated delta-peaks for our subjective stress measures (Δ stress; change from baseline to peak-levels) (Visual Analogue Scales; 0 “not stressed” at all - 10 “very stressed”). Following this, Δ stress levels were z-standardized for interpretability. We subsequently entered the values as predictors into an MEM predicting empathic accuracy, analogous to the cortisol analyses reported in the main manuscript.

Experiment-1:

For the MEM predicting empathic accuracy as a dependent variable, we entered group (control versus stress) and Δ stress as fixed factors, and their interaction as fixed factors. Subject-ID and Video-ID were entered as random factors. We ran models separately for men and women.

The results of the MEM predicting empathic accuracy in men did not result in a significant interaction (b=-0.023(SE=0.04), t(55.00)= -0.621, p=0.53), or conditional marginal effect (b=0.012(SE=0.03), t(55.00)= 0.42, p=0.68) for Δ stress. The results of the MEM predicting empathic accuracy in men did not result in a significant interaction (b=-0.30(SE=0.03), t(87.99)= -1.06, p=0.294), or conditional marginal effect (b=0.003(SE=0.02), t(87.99)= 0.113, p=0.91) for Δ stress.

Experiment-2:

For the MEM predicting empathic accuracy as a dependent variable, we entered Δ stress as fixed factors. Subject-ID and Video-ID were entered as random factors. We ran models separately for men and women.

The results of the MEM predicting empathic accuracy in men did not result in a significant effect for Δ stress, b=0.006(SE=0.2), t(25.31)==2.99, p=0.768. Neither did the MEM predicting empathic accuracy in women with Δ stress, b=0.008 (SE=0.1), t(76.241)=-0552, p=0.583.

Overview of MEMs and model selection.

We used AICs to test whether the inclusion of the interaction resulted in a more parsimonious model fit (i.e., variance explained versus model complexity; Cohen et al., 2003)**.**

Experiment-1:

The model including the Gender/Sex × Condition interaction term (AIC=-71.625, BIC= -23.081) resulted in a better model fit, compared to the model including only main effects (AIC= -68.889, BIC= -30.054; χ^2=6.7355, *p*= 0.03447). See Table S1 for a summary of both models.

Table S1: Between-subjects models predicting empathic accuracy (Experiment-1)

	Main effects model			**Interaction model**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.15	0.00 – 0.29	0.053	0.15	0.00 – 0.29	**0.050**
set	0.06	-0.13 – 0.25	0.565	0.06	-0.13 – 0.25	0.574
Condition	0.01	-0.02 – 0.05	0.407	0.01	-0.02 – 0.05	0.541
C-1 (m vs w)	0.02	-0.00 – 0.05	0.064	-0.00	-0.03 – 0.03	0.877
C-2 (RCW vs OCW)	0.02	-0.00 – 0.04	0.114	0.03	0.00 – 0.07	**0.033**
Condition * C-1				0.05	0.00 – 0.10	**0.031**
Condition * C-2				-0.03	-0.08 – 0.01	0.156
N	158			158		
Observations	948			948		
AIC	-68.889			-71.625		
				χ^2=6.7355, *p*= 0.035		

Experiment-2:

The model including the Gender/Sex × Visit interaction term (AIC=-222.56, BIC= -160.44) resulted in a better model fit, compared to the model including only main effects (AIC= -218.52, BIC= -166.76; χ^2=8.041, p= 0.018). See Table S2 for a summary of both models.

Table S2: Within-subject models predicting empathic accuracy (Experiment-2)

	Main effects model			**Interaction model**		
Predictors	*Estimates*	*CI*	*p*	*Estimates*	*CI*	*p*
(Intercept)	0.16	0.04 – 0.31	**0.019**	0.16	0.03 – 0.29	**0.022**
set	0.03	-0.00 – 0.07	0.077	0.03	-0.00 – 0.07	0.069
Visit	0.01	-0.01 – 0.04	0.412	0.02	-0.01 – 0.04	0.184
C-1 (m vs w)	0.02	-0.01 – 0.04	0.248	-0.00	-0.03 – 0.03	0.788
C-2 (RCW vs OCW)	0.02	0.00 – 0.04	**0.043**	0.03	0.00 – 0.05	**0.026**
Visit * C-1				0.05	0.01 – 0.08	**0.015**
Visit * C-2				-0.01	-0.04 – 0.01	0.334
N	109			109		
Observations	1308			1308		
AIC	-218.519			-222.560		
				χ^2=8.041, p= 0.018		

Additional Figues

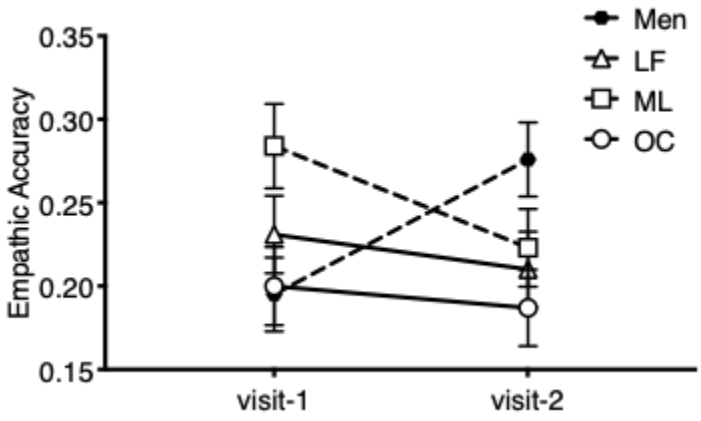

Figure S1: Results for Experiment-2 (within-subject) for each of the four groups; men, mid-luteal women, late follicular women, and women using oral contraceptives.

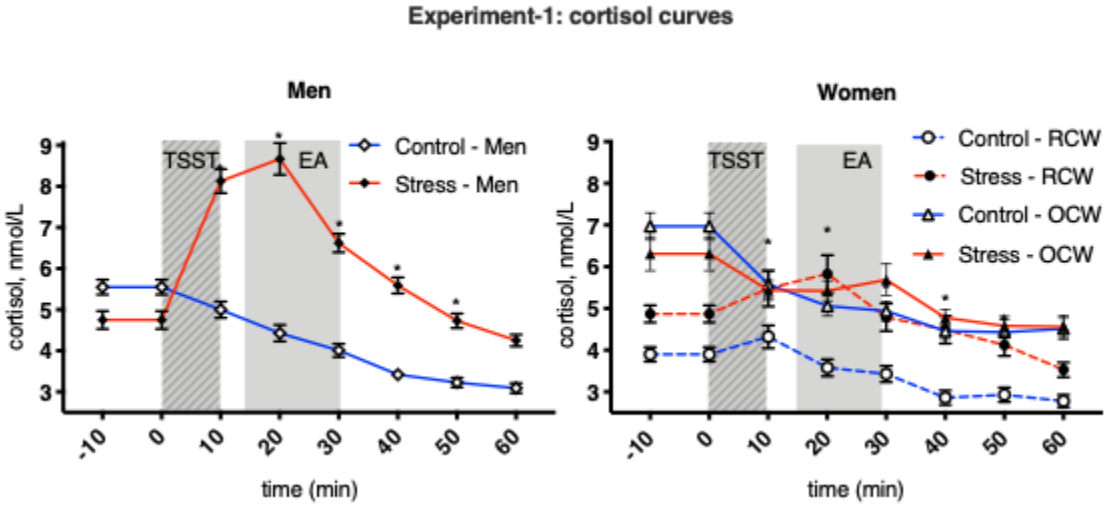

Figure S2: Plotted cortisol-curves for Experiment-1, for men, RC women, and OC women. Error bars represent the standard error of the mean for each group.

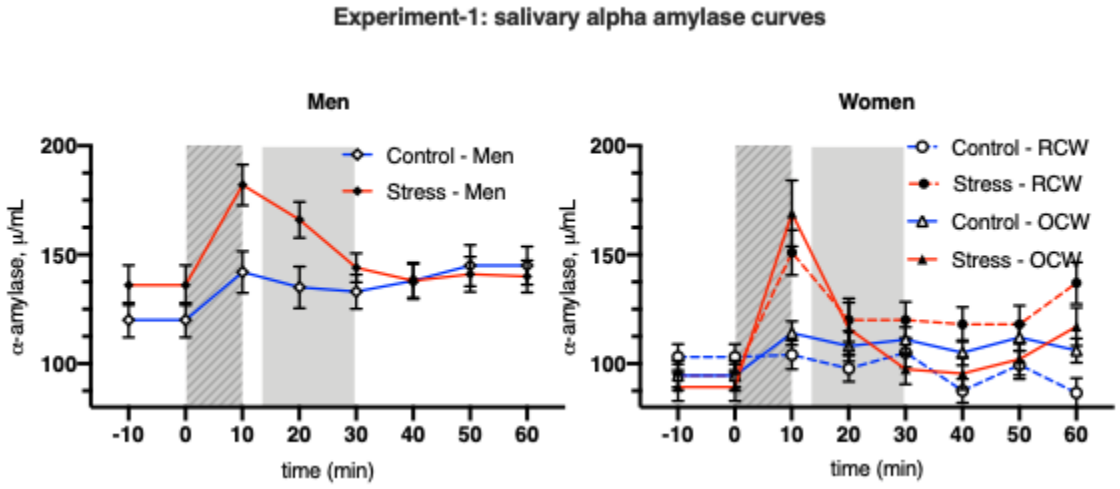

Figure S3: Plotted salivary alpha amylase curves for Experiment-1, for men, RC women, and OC women. Error bars represent the standard error of the mean for each group.

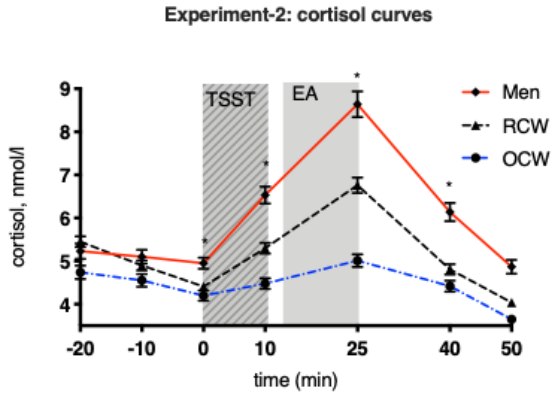

Figure S4: Plotted cortisol curves for Experiment-2, for men, RC women, and OC women. Error bars represent the standard error of the mean for each group.

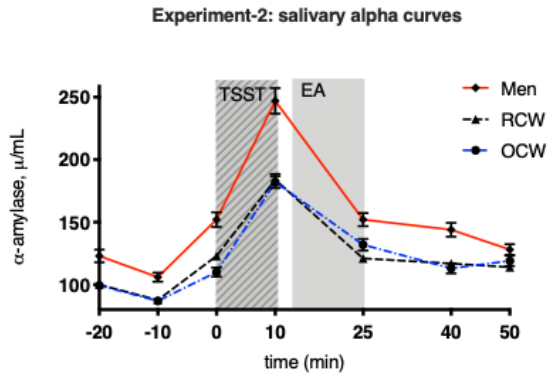

Figure S5: Plotted salivary alpha amylase curves for Experiment-2, for men, RC women, and OC women. Error bars represent the standard error of the mean for each group.

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Chapter 3: Acute Stress and Affective Empathy

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Preface to Chapter 3

The research described in Chapter 2 demonstrates that acute stress facilitates cognitive empathy, at least for men. In Chapter 3, I investigate the effects of acute stress on affective empathy. As noted in the General Introduction, cognitive and affective empathy are distinct—albeit somewhat overlapping—processes both at the neural and psychological level. As such, we may not expect stress to exert similar effects on affective empathy. Also as noted in the General Introduction, most research to date has focused on the effects of "spillover" stress—this research undoubtedly shows that people experience emotion contagion when another is in distress. However, because stress is the measure of emotion contagion, these studies do not directly speak to the effects of stress on affective empathy. The few studies that do investigate this (e.g., Martin et al., 2015 and Tomova et al., 2017) suggest a complicated picture, that stress might actually disrupt emotion contagion in the perceiver.

Affect sharing is a process that is thought to come online automatically, implicitly, and rapidly after another person's affective responses are observed (Preston & de Waal, 2002). One way to investigate the effects of stress on affect sharing more directly is by investigating behaviours that have been proposed to come online as a direct consequence of seeing someone else's affective state. In this regard, it has been proposed (cf. de Waal & Preston, 2017) that facial mimicry plays an important role in facilitating affect sharing, and is also a precursor to other empathic behaviours and cognitions—for example, triggering an emotional response that then has to be appraised and understood. Thus, in the research that is presented in Chapter 3, I have used a behavioural task that assess facial mimicry with fEMG as a measure of affective empathy.

Finally, as noted in Chapter 1, previous research has focused on negative emotions when assessing affect sharing (i.e., pain). However, affect sharing can include positive emotions as

well (i.e., joy) (Morelli et al., 2015). This might be of particular importance when studying mimicry in the context of acute stress, as smile reciprocity has been linked to signalling affiliative intent (Chartrand & Lakin, 2013; Hess et al., 1998). As such, changes in facial mimicry could be indicative of underlying motivational intentions.

Thus, the goal of the current study was to test the effects of acute stress on facial mimicry, for both negative and positive emotions. In doing so, this is the first study to empirically investigate the effects of stress on facial mimicry, a rudimentary and evolutionarily conserved element of social–emotional experience.

Stressed Connections: Cortisol Levels Following Acute Psychosocial Stress Disrupt Affiliative Mimicry in Humans

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Abstract

Mimicry, and especially spontaneous facial mimicry, is a rudimentary element of social-emotional experience that is well-conserved across numerous species. Although such mimicry is thought to be a relatively automatic process, research indicates that contextual factors can influence mimicry, especially in humans. Here, we extend this work by investigating the effect of acute psychosocial stress on affiliative facial mimicry. Participants performed a spontaneous facial mimicry task with facial electromyography (fEMG) at baseline and approximately 1-month later, following an acute psychosocial stressor (Trier Social Stress Test). Results show that the magnitude of the endocrine stress response reduced *zygomaticus major* reactivity, and specifically spontaneous facial mimicry for positive social stimuli (i.e., smiles): Individuals with higher levels of the stress hormone cortisol showed a more blunted fEMG response to smiles, but not to frowns. Conversely, stress had no effect on *corrugator supercilii* activation (i.e., frowning to frowns). These findings highlight the importance of the biological stress response system in this basic element of social-emotional experience.

Keywords: Stress; Mimicry; Affiliation; Emotion; Empathy; Cortisol; Social Support

Subject: Behaviour; Neuroscience; Evolution

1. Introduction

Spontaneous mimicry, that is, the automatic tendency of an observer to match the perceived behavior of a target, is considered to be a rudimentary element of social-emotional experience. Although mimicry can take various forms (matching postures, gestures, mannerisms, and even speech patterns), spontaneous facial mimicry is thought to be a particularly important conduit of social-emotional understanding and shared experience. As de Waal and Preston (2017) note, by physically replicating the facial expressions of others in our social world, we can simulate their emotional states to better understand what they are feeling. This affect sharing, in turn, can then facilitate downstream processes like empathy and prosocial action (de Waal & Preston, 2017; Prochazkova & Kret, 2017). In addition to facilitating social-emotional communication, mimicry (facial and other forms) has been shown to have more general effects on social cohesion, by increasing affiliation, interpersonal rapport, synchrony and liking (Chartrand & Lakin, 2013; Hess & Fischer, 2013). Indeed, some have argued that mimicry functions as a "social glue" that supports our fundamental need to belong (Lakin et al., 2003).

Mimicry, and specifically spontaneous facial mimicry, appears to be a conserved mechanism across a variety of species (Hecht et al., 2012). Indeed, spontaneous facial mimicry has been observed in several species of great apes, including orangutans (Davila Ross et al., 2008), chimpanzees (Palagi et al., 2019), and lowland gorillas as well as in some monkey species, including geladas (Mancini et al., 2013b) and macaques (Scopa & Palagi, 2016). There is also evidence for spontaneous facial mimicry in domestic dogs (Palagi et al., 2015). Like in humans, this mimicry appears to be a catalyst for social cohesion. For example, mimicry of the "play face" expression in dogs communicates positive mood during rough-and-tumble play and, in this way, prolongs the play session. Similarly, in primates, mimicry during playful interactions

has also been shown to extend the duration of social interactions (Davila-Ross et al., 2011; Mancini et al., 2013a).

To our knowledge, no study has yet investigated the effects of acute stress on spontaneous facial mimicry. However, research showing that stress can undermine emotion contagion suggests that stress may affect mimicry. Of course, mimicry is not identical to emotion contagion. Mimicry, by definition, reflects the tendency to behaviourally match others, whereas contagion reflects the tendency to experience the affective states of others, at both the psychological and physiological levels. That being said, some have argued that mimicry and emotion contagion rely on similar neural computational mechanisms (Iacoboni, 2009). Moreover, it has been argued that mimicry may facilitate emotion contagion, as the enactment of another's emotional expression may bring about the corresponding emotional experience (Winkielman et al., 2015, 2018). As noted, recent research suggests that stress can disrupt emotion contagion (2015). Recognizing that mice (and humans) are more likely to experience emotion contagion with familiar others (Langford et al., 2006), Martin et al. (2015) theorized that it is the stress of interacting with strangers that undermines emotion contagion. Supporting this, in a series of studies involving both mice and humans, they found that interactions with strangers (vs. familiar others) were associated with higher levels of the stress hormone cortisol, and that cortisol was negatively associated with emotion contagion. They also showed that blocking cortisol synthesis with the drug metyrapone increased emotion contagion with strangers, essentially making strangers look like friends, thus highlighting the important role of stress in emotion contagion. Buruck et al. (2014) also observed negative effects of stress on emotion contagion. They showed participants pictures of people in pain and asked them to rate the extent of visible pain. Stressed (vs. non-stressed) individuals reported lower ratings of perceived pain in

others. Taken together, these findings suggest that the experience of stress—and specifically the presence of the glucocorticoid cortisol—can attenuate emotion contagion (however see: Tomova et al., 2017).

The aim of the current study was to extend this prior work to investigate the effect of acute stress on mimicry and, specifically, spontaneous facial mimicry, which, as noted, is thought to be an evolutionarily conserved mechanism supporting social emotion experience in human and some non-human animals. Given the aforementioned research on stress and emotion contagion, we predicted that acute psychosocial stress would attenuate spontaneous facial mimicry. Furthermore, we hypothesized that individuals' physiological stress response would moderate the effects of stress on mimicry: following Martin et al. (2015), we predicted that those individuals who responded to the stressor with higher levels of cortisol would show the most pronounced reduction in facial mimicry following the TSST. Of note, we also measured salivary alpha amylase (sAA; a marker of sympathetic nervous system activation); however, we did not have specific predictions about sAA given that the mimicry task was timed to occur during peak levels of cortisol, when sAA levels would be expected to have started to decline (Engert et al., 2011; Nater et al., 2005). Finally, we also tested whether the effect of stress on mimicry depends on mimicry type (reciprocal smiling vs. frowning). Research suggests that *zygomaticus* activation is typically more flexible and reactive in social contexts (Hess & Fischer, 2013; Niedenthal et al., 2010)(Carr et al., 2014); consequently, the effects of stress might be specific to smile mimicry.

2. Methods

Participants

Seventy-three healthy participants (23 men: mean age = 22.8, SD ± 3.56; 50 women: mean age = 21.8, SD ± 3.11; $F(1,71) = 1.3$, $p = 0.26$), with no current history of medical or psychiatric illness were recruited from the McGill University campus. Recruitment criteria included: no recreational drug use, consuming less than ten alcoholic beverages a week, and smoking less than seven cigarettes a day (factors that have been shown to influence the HPA axis; Kudielka et al., 2009). Women were regularly menstruating and self-reported no chemical contraceptive use (see Supplemental Materials for detailed description of the procedures). All participants provided written informed consent and were compensated 10$/hr. The study was approved by the McGill University Faculty of Science Institutional Review Board.

Design & Procedures

We used a within-subjects design in which participants came to the lab on two occasions, on average four-weeks apart. Of note, this research was part of a larger program of research investigating the effects of stress on various aspects of social cognition. During the first visit ('Day-1'), participants completed self-report questionnaires, and an empathic accuracy task (Bartz et al., 2010; reported on elsewhere; Zaki et al., 2008), and then a task using facial electromyography (fEMG) to assess spontaneous facial mimicry (Carr et al., 2014; McIntosh, 2006). During the second visit ('Day-2'), we first induced acute psychosocial stress with the Trier Social Stress Test (TSST; Kirschbaum et al., 1993; see below), after which participants performed the same empathic accuracy and mimicry tasks they performed at baseline. We assessed subjective distress, cortisol, and sAA throughout Day-2.

Trier Social Stress Test (TSST)

The TSST (Kirschbaum et al., 1993) is comprised of a mock-job interview combined with an oral arithmetic task. Specifically, participants are instructed to identify a job they would like to interview for and are then given 10-mins to prepare for the "job interview". Following this anticipation period, participants perform, in front of a panel of expert judges (i.e., research confederates: one male, one female): 1) a 5-mins speech task in which they are instructed to describe why they are qualified for the job, and, then, 2) a 5-mins oral arithmetic task in which they must count backwards from 2023 in increments of 17. The TSST has been shown to reliably induce stress across a variety of markers including cortisol, sAA, and subjective experience (Ali et al., 2017; Goodman et al., 2017; Nater et al., 2005). Cortisol and sAA were collected via salivary samples (i.e., "Salivette"; Sarstedt AG & Co, Nümbrecht, Germany), and subjective stress was assessed using a visual analogue scale (i.e., "how stressed do you feel?"); all measures were taken at seven time-points throughout the Day-2 session, at 10-mins intervals starting 20-mins before the stress induction, and following stress at +10-, +25-, +40-, and +50-mins (hereto referred to as 'Sampling time'; see Figure 1 for timeline). Cortisol levels (nmol/l) were assessed using a time-resolved fluorescence immunoassay (Dressendörfer et al., 1992) and sAA (U/ml) levels were determined using the enzyme kinetic method (Engert et al., 2011).

Spontaneous Facial Mimicry Task (Carr et al., 2014)

This task uses facial electromyography (fEMG) to assess spontaneous facial mimicry. Specifically, participants were presented with 5-sec video-clips of individuals going from a neutral expression to either a smile or a frown, (two emotions that can reliably be assessed with fEMG; cf. McIntosh, 2006). Participants were instructed to simply observe the stimuli, and to press the spacebar every time a face appeared on the monitor. A total of 80 stimuli (40 smiling,

40 frowning faces) were presented in randomized order. During the stimulus presentation, we measured activity in the *zygomaticus major* muscle (engaged when people smile) and *corrugator supercilii* (engaged when people frown) to index mimicry (Ekman & Friesen, 1982). EMG data was obtained with bipolar electrode montage on the left side of the face (Fridlund & Cacioppo, 1986). Acquisition was controlled by a Biopac MP150 using Acqknowledge software (Biopac Systems Inc.). The amplified EMG signals were filtered online with a low-pass of 500 Hz and a high-pass of 10 Hz, sampled at a rate of 2000 Hz, and then integrated and rectified using Mindware EMG software (version 2.52, MindWare Technologies Ltd., Ohio, USA).

For each stimulus (i.e., 5-sec video-clip), EMG was measured for ten 500-ms windows. Prior to the stimulus presentation, a fixation cross was presented for 3-secs, resulting in six pre-stimulus recordings of 500-ms. These six recordings were averaged and used as a baseline measure for each stimulus. For each participant, we z-transformed the fEMG data and excluded extreme (± 3 SD) data points. This resulted in a loss of 2,751 (out of 180,480) data points (1.52% missing values). We used the MICE package (van Buuren & Groothuis-Oudshoorn, 2010) to impute the excluded data. Next, we corrected each data point according to its respective baseline measure, by subtracting the baseline measure from the value obtained during stimuli presentation (cf. Carr et al., 2014). These mean-rectified values were used for all subsequent analyses. Using the area under the curve (AUC) formula (Pruessner et al., 2003), we aggregated the 10 fEMG recordings of the *zygomaticus major* and *corrugator supercilii* in response to smiling and frowning faces. This resulted in a total of 160 AUCs for each participant: specifically, 80 *zygomaticus* (40 responses to smiles; 40 responses to frowns) and 80 *corrugator* (40 responses to smiles; 40 responses to frowns). Of note, AUCs are not measures of overall muscle activation, rather they quantify the amount of muscle activity in response to a stimulus presentation (i.e.,

smiles vs. frowns) compared to baseline (i.e., the fixation cross)(Fekedulegn et al., 2007).

Statistical Analyses

We first conducted manipulation checks to confirm that the TSST elicited a stress response. Specifically, we conducted repeated-measures Mixed-Effects Models (rMEM; Gueorguieva & Krystal, 2004) on the measures of cortisol, sAA, and subjective-stress. Sampling time and participant sex/gender (male=0, female=1), and the Sampling time x sex/gender interaction were entered as fixed factors. Sampling time was nested within-participant as a random factor (Barr et al., 2013). Raw cortisol and sAA data were log-transformed. Subsequently, we calculated areas under the curve (AUCs) for cortisol, sAA, and subjective stress using the formula described by Pruessner et al. (2003).

We then conducted rMEM analyses to test the effects of stress induction on *zygomaticus major* and, in a separate analysis, *corrugator supercilii* activity, using the AUCs for each muscle as the dependent variable (Note: as we were not interested in comparing *zygomatics* and *corrugator* activation, we ran our analyses for these muscles separately, as others have done (A. Arnold, 2019; Carr et al., 2014; Korb et al., 2016); however, results testing one overarching model that includes Muscle type as a third factor are comparable to those we report below; see Supplementary Materials). For each analysis, Stimulus type (0 = smile; 1 = frown) and Day (0 = Day-1/baseline; 1 = Day-2/TSST) were entered as fixed-effects, and stimulus presentation order and sex/gender were entered as covariates. In an additional step, we entered a higher order term for the Stimulus type x Day interaction. Subject-ID was entered as a random-effect. Following Barr et al. (2013; 2013), we included random slopes for our highest-order combination of within-subject factors subsumed by the Stimulus type x Day interaction to test for a maximally-defined model.

In addition to looking at overall muscle reactivity during stimulus presentation, we adopted a more fine-grained approach looking at muscle activations at each of the 10 EMG recordings to investigate whether stress differentially affects zygomaticus activation during earlier versus later phases of the stimulus presentation. To this end, we ran an MEM with *zygomaticus* activation in response to smiles (i.e., affiliative mimicry) as the dependent variable and Day and Time-course (i.e., 10 EMG recordings) as independent variables; as in the AUC analysis, stimulus presentation order and sex/gender were entered as covariates. We also included a Day x Time-course interaction term. For a maximally defined model, Day x Time-course was nested within participant as a random factor.

After testing the effect of the stress induction on mimicry, we then probed the effect of the three stress markers (cortisol, sAA, and subjective stress); here, we focused our analyses on data from Day-2 (TSST day), as we only assessed these markers on Day-2. Specifically, we ran a series of linear Mixed-Effect Models (MEM; Baguley, 2012; Holmes Finch et al., 2014), one for each stress marker. Respective AUCs of muscle reactivity were entered as the dependent variable, and Stimulus type (0 = smile; 1 = frown) and the stress marker of interest (AUCs) were entered as fixed-effects. We also included the interaction between these two fixed-effects (i.e., Stimulus type x stress marker), to ascertain whether the effect of stress was specific to one kind of stimuli (e.g., smiles). Stimulus presentation order and participant sex/gender were entered as covariates; subject-ID was entered as a random-effect. Of note, we initially included Stimulus type as a random slope (cf. Barr et al., 2013); the model converged for cortisol and sAA, but not for subjective stress. To facilitate comparisons, we reverted to a simple intercept model for all stress-marker analyses (Brauer & Curtin, 2018). This approach did not change the significance of the cortisol effects reported below.

All reported confidence intervals were bootstrapped. All statistical analyses were conducted using R (R Core Team, 2020) and the lme4-package (1.1-18-1) for the rMEM and MEM analyses (Bates et al., 2015). Significant effects from the MEM were decomposed using the formula described by Preacher et al. (2006).

3. Results

Stress Manipulation Check

The rMEMs revealed a significant effect of Sampling time for cortisol ($F(5, 214.55) = 25.52$, $p < 0.001$), sAA ($F(5, 259.48) = 42.57$, $p < 0.001$), and subjective-stress ($F(5, 342.62) = 80.86$, $p < 0.001$), thus indicating successful stress induction (see Figure 1). Results showed no effects for sex/gender, or the sex/gender x Sampling time interaction for cortisol or sAA; all ps > 0.1. However, there was a significant sex/gender effect for subjective stress: women reported higher subjective stress levels than men, $F(1,70) = 5.8$, $p = 0.02$ (women: mean = 3.69, SD = 2.7; men: mean = 2.31, SD = 2.25).

Effect of Stress Induction on Zygomaticus Major (Day-2 vs. Day-1)

The rMEMs evaluating *zygomaticus major* activation revealed a significant effect of Stimulus type (smile vs. frown), $F(1, 74.0) = 8.66$, $p < 0.01$; consistent with prior mimicry research, across days, participants smiled more to smiling faces (congruent: mean = 514.70, SEM = 42.41) than to frowning faces (incongruent: mean = 207.22, SEM = 40.54). Turning to the effect of stress, our key experimental question, results showed a main effect of Day on

zygomaticus activity, $F(1, 74.0) = 4.89$, p = 0.03, such that participants smiled less on the TSST day (mean = 246.33, SEM = 43.61) relative to baseline (Day-1: mean = 476.35, SEM = 39.26). The reported model (AIC = 213115) had a better fit than the intercept only model (AIC = 213120; $\chi^2(4) = 13.23$, $p = 0.01$). Adding the Stimulus type x Day interaction did not reveal a significant interaction ($F(1,73.1) = 0.11$, $p = 0.74$). Thus, our hypotheses about the effects of stress were partially supported: Stress did attenuate smiling, but this effect occurred for both smiling and frowning stimuli.

We now turn to the more fine grained time-course data looking at *zygomaticus* activity during each of the 10 fEMG recordings; here we focus specifically on the mimicry response—that is, *zygomaticus* activity to smiling faces; (readers interested in *zygomaticus* activity to frowns are referred to Figure S1 in the Supplementary Materials). Results from the MLM analysis showed a significant Day x Time-course interaction on *zygomaticus* activity in response to smiling faces, with higher activation on Day-1, compared to Day-2, at 2000ms, at 2000ms (b = -0.097 (SE ± 0.040; 95% CI [-0.173, -0.018]), $t(928.9) = 2.45$, $p = 0.014$) and 2500ms (b = -0.103 (SE ± 0.044; 95% CI [-0.185, -0.017]), $t(427.8) = 2.35$, $p = 0.019$). Thus, it appears that stress resulted in a delayed onset of smiling to smiling faces. (For details, see Figure S2, panel A, in the Supplementary Materials). The reported model had a better fit (AIC = 143671) compared to the intercept model (AIC = 143729; $\chi^2(21) = 100$, $p < 0.001$).

Effects of Stress Markers on Zygomaticus Major (Day-2)

Given that we observed an overall effect of the stress induction, we conducted additional analyses to examine the effects of cortisol, sAA, and subjective stress, respectively, on

zygomaticus major activity on Day-2 (the only day we assessed the stress markers). Results from the MEM using cortisol as a predictor revealed a significant Stimulus type x cortisol interaction, b = -14.37 (SE ± 5.20; 95% CI [-24.52, -4.73]), $t(5588.62) = -2.76$, $p < 0.01$. The reported model had a better fit (AIC=107583) than the intercept model (AIC = 107601; $\chi^2(5) = 27.4$, $p < 0.001$).

Post-hoc testing revealed a significant negative association between cortisol and *zygomaticus* activation for smiling stimuli ($z = -2.76$, $p < 0.01$), but not for frowning stimuli ($z = -0.379$, $p = 0.41$). As depicted in Figure 2, as cortisol levels increased, smiling to smiling faces decreased, but cortisol increases had no effect on smiling to frowning faces. These findings indicate that the biological stress response, as measured by cortisol, specifically attenuated mimicry, consistent with Martin et al. (2015) and supporting our hypothesis about the effects of stress on mimicry. In further support of this, analyses showed that participants who did not show a strong cortisol response (-1 SD) to the TSST showed significantly higher *zygomaticus* activation to smiles than to frowns on the TSST day ($z = 4.30$, $p < 0.005$); this suggests that participants had an intact mimicry response that was similar to the baseline/no stress testing day. By contrast, participants who showed a strong cortisol response (+1 SD) did not show higher *zygomaticus* activation to smiles than to frowns on the TSST day ($z = 0.393$, $p > 0.70$); again, indicating that cortisol blunted mimicry (see Figures 2 and 3). The MEM with the Stimulus type x cortisol interaction term (AIC = 107589) was significantly better than the non-interaction model (AIC = 107583; $\chi^2(1) = 7.63$, $p = 0.006$).

In contrast to cortisol, results from the MEM analyses using sAA and subjective stress as predictors revealed no significant effect for either variable on *zygomaticus major* activation (all ps > 0.05). The non-interaction models had significantly better fits than the interaction model, all ps > 0.2.

Effect of Stress Induction on Corrugator Supercilii (Day-2 vs. Day-1)

Turning to the *corrugator supercilii* analyses, the rMEM revealed no effect of Stimulus type or Day; nor was there a significant Stimulus type x Day interaction (all *p*s > 0.2). Intercept model (AIC = 213815); reported model (AIC = 213811; $\chi 2(4) = 12.07$, $p = 0.017$).

Since none of these effects on the *corrugator supercilii* were significant, we did not probe for the effects of the different stress markers on frowning mimicry on Day-2.

Thus, stress did not attenuate mimicry to frowns. The lack of effects on the *corrugator*, however, may be because, as noted, the *corrugator* is less reactive than the *zygomaticus* and, typically, also more rare. Indeed, consistent with this hypothesis, as can be seen in Figure S2, panel B, of the Supplementary Materials, the *corrugator* is less active than the *zygomaticus* on both days.

4. Discussion

The aim of the current study was to investigate the effects of acute psychosocial stress on spontaneous facial mimicry, a rudimentary and evolutionarily conserved element of social-emotional experience. Our results show that the experience of stress reduced *zygomaticus* reactivity, and specifically spontaneous facial mimicry for positive social stimuli (i.e., smiles), an effect that was driven by the endocrine stress response. Individuals with higher levels of the stress hormone cortisol showed a blunted fEMG response to smiles, whereas those with lower cortisol levels showed an intact affiliative response that was similar to their baseline response.

Our findings extend prior research on stress and emotion contagion (Buruck et al., 2014; e.g., Martin et al., 2015) by showing that the biological stress response also attenuates spontaneous facial mimicry. These findings may shed light on the observation that humans, and some non-human animals, are less likely to mimic outgroup members (Bourgeois & Hess, 2008; Campbell & de Waal, 2011). Consistent with Martin et al., it may be the stress elicited in such interactions that undermines mimicry (cf. Gray et al., 2008).

Of note, the effects of the endocrine stress response (i.e., cortisol) were specific to reciprocal smiling. There are a few possible explanations for this selective effect. First, the TSST, which is not a pleasant experience, may have primed participants to show negative emotions, in this way overriding the mimicry-attenuating effects of stress on frowns. This explanation, however, seems unlikely given that we did not observe greater *corrugator* activation on the stress-day versus baseline-day, nor was the *corrugator* more active than the *zygomaticus* on the stress-day. A more likely explanation, we think, has to do with the greater flexibility and reactivity of the *zygomaticus major* muscles (Niedenthal et al., 2010), a factor that could make them more vulnerable to the influence of stress. Relatedly, frowns are, in general, more rare than smiles (Carr & Winkielman, 2014; Niedenthal et al., 2010), so the selective effects could be due to a general absence of frowning. In fact, some have argued that mimicry to smiles and mimicry to frowns are not equivalent and support different (albeit sometimes overlapping) goals. According to Hess and Fischer (2013), smiling to a smile, or "affiliative mimicry," is one key way people communicate their interest because such positive feedback signals enjoyment of the activity/other conspecific, desire for continued interaction, and a strong emotional connection. Such positive mimicry is also a catalyst for social cohesion in some non-human animals (Palagi et al., 2015). By contrast, anger mimicry (i.e., responding to anger with anger) is often avoided in

social situations because it can antagonize a relationship. Future research is needed to better understand the (lack) of an effect of stress on anger mimicry; for example, by examining the effects of stress in situations where anger mimicry is more likely to occur (e.g., competitive situations; Hess & Fischer, 2013), one can ascertain whether stress selectively impairs affiliative mimicry, or whether it also affects anger mimicry under the right circumstances.

What might be the mechanism underlying the effect observed in the current research? It has been argued that stress can lead to social withdrawal in order for the organism to attend to its own affective state (for a review: Sandi & Haller, 2015). In this regard, there is evidence that the experience of acute stress leads to an increase in self-focus, particularly towards one's own emotional experience (Starcke et al., 2011; Tomova et al., 2014). Such egocentrism could prevent affiliative mimicry by reducing emotional engagement with the stimulus. Refusing to resonate happiness (i.e., smiling to a smile) might also be a way to solicit social support when one is distressed. Our effects could also be due to reduced attention, given prior research showing that negative emotional states can sometimes undermine both exogenous (stimulus-driven, bottom-up) and endogenous (top-down) attention to emotional faces (Mansell et al., 1999; Yiend, 2010), though there are also some attention capture phenomena. Future research using eye-tracking may shed light on this mechanism.

A few aspects of our procedures are worth noting. First, we found no effect of sAA or subjective stress on affiliative mimicry. However, our study design was guided by prior research linking cortisol to reduced emotion contagion (Buruck et al., 2014; e.g., Martin et al., 2015), and we timed the mimicry task to occur during peak cortisol levels; by this time, sAA levels had begun to decline. Similarly, subjective stress may also have begun to decline 20-mins after the TSST. That said, others have also shown a dissociation between subjective stress and the

physiological stress response (Ali et al., 2017; Buchanan et al., 2012). Future research should manipulate task timing to assess the role of other stress markers on facial mimicry. Second, we did not counterbalance the stress manipulation; thus, it is possible that learning or repeated exposure to the mimicry task may have attenuated participants' responses to the stimuli on Day-2. That said, it is not clear why learning or habituation would only occur for participants with higher cortisol levels. Third, we only assessed spontaneous facial mimicry to smiles and frowns (emotions that can reliably be assessed with fEMG; McIntosh, 2006). Of course, there are numerous other socially relevant emotions: sadness, fear, disgust, and guilt, just to name a few. Sadness or distress, in particular, is especially relevant given the significance of mimicry and emotion contagion in empathy; indeed, there is evidence of hormonal stress contagion (i.e., a rise in cortisol) when people observe another in distress (Buchanan et al., 2012; Engert et al., 2014). It would be interesting to know if pre-existing stress attenuates this emotion contagion effect (cf. Martin et al., 2015).

In closing, the present research indicates that the stress hormone cortisol can attenuate affiliative mimicry (smiling to smiles). Given the importance of mimicry and especially affiliative mimicry to bonding, our findings suggest that stress may undermine social connection (or, perhaps, more precisely, our research sheds light on one mechanism by which stress can undermine bonding). Corroborating this idea, recent research indicates that chronically lonely individuals, who often show alterations in the physiological stress response system (Hawkley & Cacioppo, 2003), show selective impairments in reciprocal smiling (A. Arnold, 2019). Additionally, to the extent that mimicry serves more sophisticated forms of empathy, our findings suggest that stress could undermine the quality of our social relationships and experience by attenuating emotion sharing and understanding (de Waal & Preston, 2017; Prochazkova & Kret, 2017). Although we focused

on humans in the present research, there is good reason to believe that these effects would extend to at least some non-human animals, given that the phenomenon of spontaneous facial mimicry is conserved across numerous species and the cortisol system is also well-conserved biologically.

Appendix

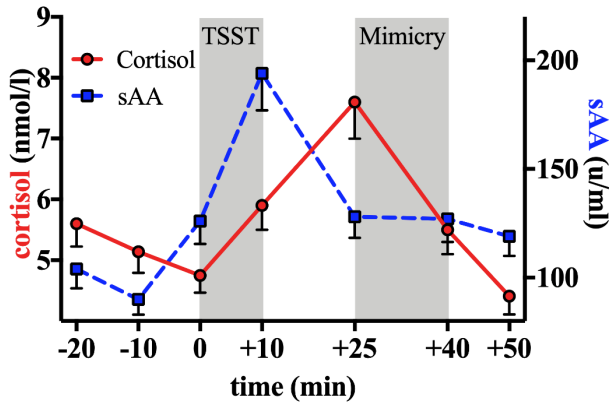

Figure 1. Timeline of the experimental procedure during visit-2, including cortisol and salivary alpha amylase (sAA) responses over time. Sampling times-points are indicated on the X-axis with ticks. Participants are introduced to the TSST setting ten minutes before going to the interview room (at 0 minutes). Twenty-five minutes after the end of the TSST participants started the facial mimicry task.

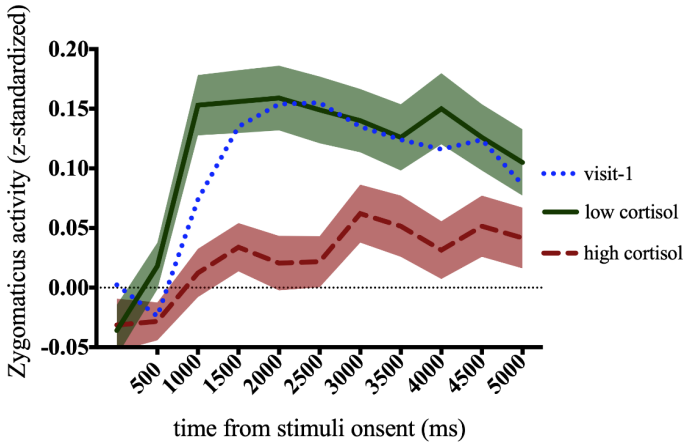

Figure 2: Activity of the zygomaticus major muscle following stimulus onset. Activity during visit-1 (no stress) is depicted by the blue dotted line. High-cortisol responders are represented by the red line and low-cortisol responders are represented by the green line (median-split for illustrative

purposes).

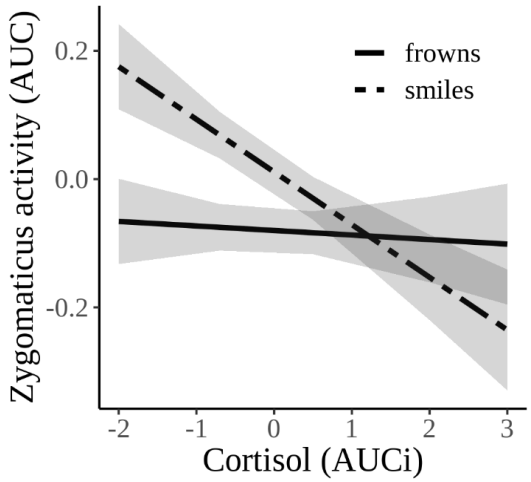

Figure 3: Results of the multilevel model analysis predicting zygomaticus activation with stimuli type (frowning faces and smiling faces) and cortisol levels. The shaded areas reflect the standard error of the mean. There was a significant slope for zygomaticus major activation in response to smiling faces, with higher levels of cortisol leading to a reduction in zygomatics activation. In addition, there was a significant difference in zygomatics activation in response to smiles and frowns (higher activation to smiles) for low cortisol responders, but not for high cortisol responders. All data converted to z-scores for illustrative purposes.

Supplemental Materials

Stressed Connections: Glucocorticoid Levels Following Acute Psychosocial Stress Disrupt Affiliative Mimicry

Content:

Supplemental Methods

Menstrual Cycle Screening Procedure: Prior work has suggested that hormonal status, in particular the female menstrual cycle, can impact the biological stress response(for a review: Kudielka et al., 2009). For this reason we wanted to keep our sample as homogenous as possible and recruited regularly menstruating women in either their late-follicular and mid-luteal phase of their menstrual cycle. During recruitment, female participants were asked to self-report hormonal contraceptive use. Only regularly menstruating females, with cycle lengths of 21- 35 days were recruited. For each female participant, following recruitment, and prior to scheduling the first laboratory session, we tracked the two full menstrual cycles in order to confirm their self-reported cycle length. For visit-1, half of the female participants were scheduled during the late follicular phase of their menstrual cycle, and the other half during their mid-luteal phase. Then, participants were scheduled for visit-2 during the same menstrual cycle phase of the following month, according to the previously tracked cycle. Half the female participants were scheduled to participate during the late follicular phase of the menstrual cycle, while the other half was scheduled during the mid-luteal phase. It is important to note that, adding cycle phase as predictors to the models (instead of gender/sex) did not change the results; female participants showed similar behaviours across both menstrual cycle phases.

Supplemental Results

1. Three- & Four-way interaction rMEM. Our overall aim in this research was to investigate the effects of stress on mimicry—that is, smiling to smiling faces and frowning to frowning faces. As we were not interested in directly comparing the timing of zygomatics and corrugator muscle

activation, we ran our analyses for these muscles separately, as others have done(A. J. Arnold & Winkielman, 2020; Carr et al., 2014; Korb et al., 2016) to keep our statistical model as simple as possible. Indeed, testing a 3- or 4-factor interaction models in the context of a multilevel model is very computationally intense—especially when also adhering to the implementing new recommendations about appropriately controlling for random error in multi-level models (e.g., Barr et al.(2013; 2013).

To simultaneously test the effects of acute stress induction on both muscles (*zygomaticus major, corrugator supercilii*) we attempted to run a repeated measures mixed-effects model predicting muscle activation with a including a three-way interaction between muscle * Stimulus-Type * Day as fixed effects. We also included gender/sex of participants as a covariat. We initially tried to add a nested random-slope nested within Subject-ID(Barr, 2013; Barr et al., 2013), including all within-subject factors subsumed in the interaction, however models could not be estimated. This was either due to a lack of computational power (we ran this model on a 32-core cluster with 1510 GB of RAM), or issues with the underlying lmer code. Following recommendations by Brauer and Curtin(2018) we simplified the model to include a random intercept only, Subject ID. Here, we estimated activation (of either muscle) with the fixed-factors: Day, Time-course, Muscle-type, Stimulus-type, and Gender (covariate). We estimated activation (of either muscle) with the fixed-factors: Day, Time-course, Muscle Type, Stimulus Type, and Gender (covariate). In response to your comments, we included the suggested 3-way interaction Day * Stimulus Type * Muscle Type. (Note: that we also ran a more conservative model that included all possible triple interactions, and the results reported below hold.)

The results revealed a significant Day * Stimulus-Type * Muscle Type interaction ($F(4, 25) = 42.92$, $p < 0.0001$). We then conducted post-hoc tests (all uncorrected) using the R-package 'emmeans' (Lenth, 2016) to probe the interaction effect. We focused on comparing the results obtained for this model to the results reported in the paper—that is, the two main effects of Day and Stimulus. Of note, the model was too complex to estimate degrees of freedom for the effects (again, RAM buffering errors).

First, in regard to the main effect of stress induction on muscle activation, the post-hoc test revealed a significant effect of day on zygomaticus activation: The average activation of the zygomaticus in response to smiles was higher on Day-1, compared to Day-2 ($z= 2.86$, $p= 0.004$). This is in line with the results reported in the manuscript; stress led to a reduction in mean zygomaticus activation in response to smiles. In addition, the average zygomaticus activation in response to frowns was higher on Day-2, compared to Day-1 ($z= 2.12$, $p= 0.034$).

Second, we find significant effects for differential muscle activation in response to stimulus presentation. Mean zygomaticus activation was higher for smiles, compared to frowns, on both days (Day-1: $z= 11.311$, $p< 0.0001$; Day-2: $z= 6.354$, $p < 0.0001$). This is in line with the findings reported in the manuscript, where we find a significant effect of stimulus on zygomaticus reactivity. Conversely, there was no difference in corrugator activation in response to smiles or frowns.

2. Additional Corrugator Supercilii Analyses. Given the repeated measures design of the current study, we followed suggestions by Gueorguieva and Krystal(2004) to run mixed-effects models instead of repeated measures ANOVAs. As described in the manuscript, these analyses, which controlled for error structures that included all within-subject effects, did not reveal any

congruent mimicry towards frowning faces (i.e., corrugator supercilii activity towards frowning stimuli). However, we also ran analyses controlling for random error structures resembling that of a repeated measure ANOVA (i.e., the random intercept only) for comparison. These analyses revealed an effect of frowning stimuli on mean-level corrugator activity, $F(1, 11204)= 4.07$, $p=0.04$, which may suggest the presence of mimicry towards frowning faces. Of note, however, there was still no effect of stress on corrugator activity.

3. Trait Empathy and Mimicry. In additional, exploratory analyses, we investigated the relationship between trait empathy and mimicry, using the Interpersonal Reactivity Index(IRI; Davis, n.d.), a questionnaire that assesses self-reported empathy on 4 different dimensions: perspective taking (example: "I sometimes try to understand my friends better by imagining how things look from their perspective"), emotional concern (example:"I am often quite touched by things that I see happen"), personal distress (example: "In emergency situations, I feel apprehensive and ill-at-ease"), and fantasy (example: "I really get involved with the feelings of the characters in a novel"). In order to test the association between IRI and mimicry we ran the same rMEM analyses described in the main manuscript; fEMG activations were entered as dependent variables, with stimulus valence, and testing day as fixed-effects, and stimulus presentation order and participant sex/gender were entered as covariates.Subject-ID was entered as a random-effect. In addition, we added each subscale of the IRI separately in order to investigate the effects of trait empathy on fEMG activation. In a second step we entered the interaction between the IRI and day of testing. The results revealed no significant association between trait measures of perspective taking, emotional concern, and personal distress, and fEMG activation for either of the two muscles (zygomaticus or corrugator), all ps > 0.05. There was however a significant effect of the fantasy subscale on zygomaticus activation F(1, 72.5) =

6.84, p=0.01, indicating that higher scores on this subscale were related to higher affiliative mimicry regardless of the day of testing. It has been suggested that fantasy measures the tendency to transpose oneself imaginatively into the feelings and actions of fictitious characters(Davis, n.d.), however, these theoretical assumptions have not held up in empirical studies, and it remains unclear what the subscale tap-into(Corte et al., 2007; Nomura & Akai, 2012). In the context of the current study it might measure the likelihood to engage with the stimuli presented on the computer screen (i.e., real individuals showing genuine expressions, however, not physically present or interpersonally reactive).

Additional Information

Information regarding this dataset: As noted in the main text, this dataset is part of a larger program of research into the effects of acute stress, as well as other hormones, on affiliative behaviours. In addition to the mimicry data presented here we collected data for assessing cognitive empathic abilities. The cognitive empathy task was conducted prior to the mimicry task.

Published research associated with the current dataset (day-1) can be found here:

- Nitschke, J. P., & Bartz, J. A.(2020). Lower digit ratio and higher endogenous testosterone are associated with lower empathic accuracy. *Hormones and behavior*, *119*, 104648.

Supplemental Figures:

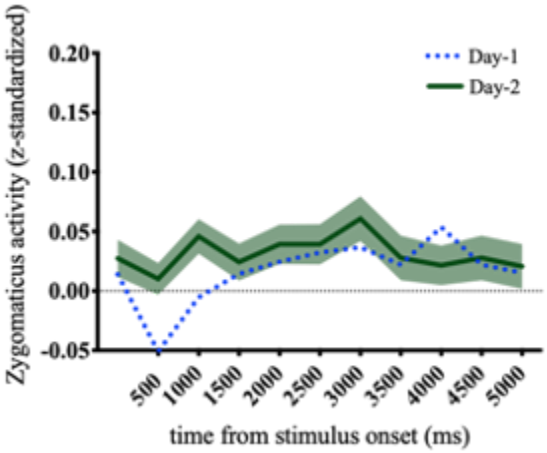

Figure S1: The mean *zygomaticus* response to frowning faces (incongruent fEMG response); the dotted blue line represents the *zygomaticus* response to frowning faces on Day-1 (baseline), and the green line represents *zygomaticu*s response to frowning faces on Day-2 (TSST).

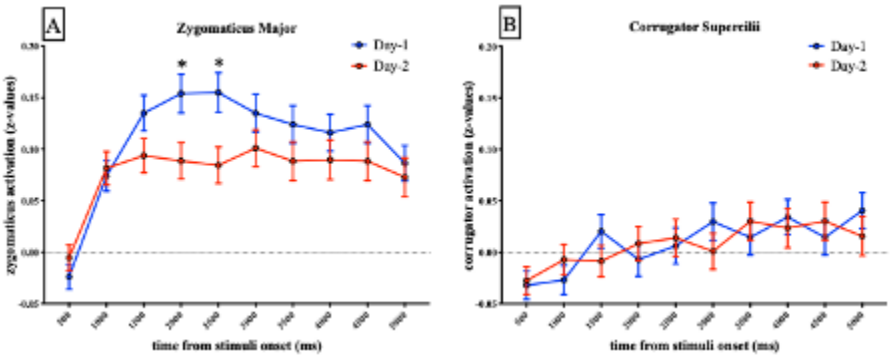

Figure S2: Time-course data of the mimicry response on Day-1 (i.e., the baseline day) and Day-2 (i.e., the TSST day). (A) depicts *zygomaticus major* activity to smiling faces, while (B) depicts *corrugator supercilii* activity to frowning faces. The blue lines represent activity during

Day-1, whereas the red lines represent activity during Day-2. Stars indicate significant differences between Day-1 and Day-2.

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Chapter 4: Discussion

4.1 Overview of Thesis Goals

The goals of this thesis were threefold: first, to provide an in-depth review of the existing literature on the relationship between acute stress and empathy in order to highlight discrepancies and identify gaps for future research; second, to test the effects of acute stress on cognitive empathy—specifically the naturalistic tracking of others' emotions—in men and women; third, to test the effects of acute stress on naturalistic emotion sharing using a facial mimicry task.

Over three chapters I accomplished these goals, first by conducting a literature review, followed by two behavioural studies that manipulated acute stress in the laboratory in order to examine the relationship between stress and cognitive empathic abilities (Chapter 2), and stress and affect-sharing/affiliative behaviours (Chapter 3). As a whole, this thesis highlights the need for a differentiative view of empathy and its subcomponents. In the following sections I will discuss these findings in more detail and within the broader context of empathy and stress research.

4.2 Summary of Results

First, in reviewing the literature in Chapter 1, I showed that the effects of acute stress on empathy—a multifaceted construct—are domain specific, and likely influenced by contextual factors. As such, research on *cognitive empathy* indicates that emotion recognition abilities can increase during acute stress, but there are no effects of stress on basic social cognitions measured using common paradigms such as the RMET. It is important to note that these tasks are prone to range restrictions, particularly ceiling effects. As such, there is some evidence that more complex mentalizing processes might be impacted by the occurrence of stress. Moreover, there is

evidence that acute stress might differentially impact more complex social cognitive abilities for men and women, with men sometimes benefitting, and women sometimes showing impairments due to acute stress. Research on *affective empathy* indicates that humans show stress-resonance when observing another person in distress. However, there appear to be boundary effects: we tend to empathize more when we are familiar with the stressed person. That said, these studies do not speak to the effects of stress on affective empathy, because the measure of affective empathy/emotion contagion, is stress. In fact, some research suggests that when we are stressed ourselves, we may disengage from the distress of other persons, and possibly focus on our own emotional state.

Second, as demonstrated in Chapter 2, acute stress enhances empathic accuracy in male, but not in female participants. In two independent studies, one using a within-subject design and the other using a between-subjects design, I showed that men's empathic accuracy abilities were enhanced under acute stress, compared to when they were not stressed. This increase in cognitive empathy was associated with elevated stress induced cortisol levels. For women, I found no effects of either acute stress, or stress induced cortisol on empathic accuracy. There were, however, differences in empathic accuracy between groups of women. Specifically, compared to regularly cycling women, women taking oral contraceptives performed significantly worse on the empathic accuracy task, regardless of whether they were under acute stress or not. This research highlights the crucial, but complex, role of stress in cognitive empathy and the importance of considering gender/sex specific and hormonal effects.

Third, as Chapter 3 showed, stressed individuals are less likely to mimic others' facial expressions—a putative marker of emotion sharing and affiliation—specifically positive emotions (i.e., smiling), compared to a no-stress condition. In addition, as in the findings from

Chapter 2, this effect was associated with the stress induced cortisol response, such that higher levels of cortisol resulted in less mimicry for smiles. Importantly, although I tested this effect for both men and women, I did not find any gender/sex specific effects: both men and women showed a reduction in smile mimicry following stress. This finding constitutes an important contribution to our understanding of empathy, and human sociality more broadly, by demonstrating that acute stress has the power to disrupt affiliative smiling and highlights the fact that the effects of acute stress are more nuanced than previously thought.

Taken together, this thesis contributes to our understanding of how acute stress impacts empathy and aspects of human sociality more broadly. Specifically, over two empirical studies I demonstrated that differential effects for two facets of empathy—cognitive and affective empathy—exist. Furthermore, I was able to highlight that for cognitive empathy specifically, gender/sex specific effects should be considered. In the following section I will go beyond individual chapters and discuss the findings from these empirical studies in the broader context of the literature.

4.3 General Discussion

Empathy is a crucial building block for our social life. It is therefore important to understand what contextual factors can influence our ability to successfully connect with others. Acute stress is an omnipresent feature of our daily life and the research presented here suggests that stress will influence how we perceive and interact with our social world, consequently impacting abilities that are grouped under the umbrella term of empathy. Importantly, empathy is a multifaceted construct, and as I have outlined in the previous chapters, it should be treated as

such. Various components of empathy, from the more automatic processes such as mimicry, to more deliberate and controlled processes such as empathic accuracy, have been shown to be differently impacted by acute stress. In this regard, research has repeatedly shown that affective (e.g., a shared emotional "experience') and cognitive empathy (e.g., the cognitive understanding of others' affect and intentions) are not just conceptually different, to some extent these processes rely on different neuro-computational mechanisms (de Waal & Preston, 2017; Lamm et al., 2019; Shamay-Tsoory, 2011; Zaki & Ochsner, 2012). Of note, however, many cognitive empathic abilities draw from a wide-range of sources to accurately infer the mental states of others (Mitchell, 2009), and as such cognitive empathy—and in particular high levels of empathic accuracy—is often associated with a coactivation of both affective and cognitive networks (Schurz et al., 2020; Zaki et al., 2009).

In line with the notion that cognitive and affective empathy represent different, at least partially independent facets, the empirical work in Chapters 2 and 3 finds opposite effects of acute stress on empathy. Whereas acute stress increased cognitive empathic abilities (i.e., social inference making) in men, as seen in Chapter 2; in Chapter 3 I found that stress leads to a reduction in affective empathy (notably, this reduction was only observed for smile-reciprocity, see discussion below) regardless of gender/sex. These findings indicate that acute stress can impact different facets of empathy differently, and it is important to understand how and why this might be the case. One explanation is that, e.g., affiliative mimicry and social inference making are distinct constructs that are only tangentially related. Another explanation is that both constructs rely on different neuronal mechanisms that are differentially affected by acute stress. One question that remains is whether, and to what extent, the facets themselves (i.e., affective and cognitive empathy) are homogenous, and if further distinctions can or should be made (e.g.,

to what extent stress contagion differs from affect sharing, as measured by a facial mimicry task).

The results presented in Chapter 2 are largely consistent with previous findings reported on the effects of acute stress on cognitive empathy. While the literature is still limited, research seems to indicate gender/sex specific effects of stress on complex cognitive inference making (cf. Smeets et al., 2009) (also see the following section). Moreover, research on emotion recognition abilities seem to support stress induced increases in cognitive empathy, to some extent.

The finding of stress-induced reduction in affiliative mimicry in Chapter 3 somewhat diverges from other research on the effects of acute stress on affect sharing (either through first-hand stress or second-hand stress). Broadly, previous research suggests that stress leads to an increase in affect sharing in the perceiver; specifically, that observing others in distress leads to a stress response in the perceiver. However, most of these studies have looked at emotion contagion of a stressed target in an (initially) unstressed perceiver; by design, these studies confound emotion contagion with the experience of stress. The few studies that have induced stress to measure how acute stress affects a perceivers ability to share emotions of a target (e.g., Martin et al., 2015 and Tomova et al., 2017) have found a more complicated picture for emotion contagion, here there is evidence that stress in a perceiver could actually disrupt emotion contagion. Even more difficult, previous studies have relied on negative emotions (e.g., pain, stress) to test this contagion effect. Chapter 3 partly addresses this limitation, by also displaying positive (and thus incongruent, in the stress condition) emotions in the form of smiles. However, we notably measured frowns and smiles, and not pain (as in previous research). How these divergent methodologies to measure affective empathy are affected differently by stress is not yet clear. Furthermore, as mimicry has also been associated with affiliative behaviours (Chartrand &

Lakin, 2013), a reduction in smiles might be more indicative of changes in motivations due to stress, rather than pure emotion contagion, see discussion below. These limitations notwithstanding Chapter 3 makes an important first contribution by better delineating that under certain circumstances different emotions will be appraised differently.

Gender/sex differences in Empathy and Stress

Some of the effects of acute stress will depend on contextual and person dependent factors. In particular, it is important to consider the gender/sex of participants. This is due to several factors: for one, it has been proposed that men and women differ in their aptitudes for empathy, with women generally believed to be more empathic. However, differences between men and women appear to be less pronounced than originally assumed, and when observed, these differences are likely due to self-presentation biases and motivations, rather than differences in abilities. (Baez et al., 2017; Christov-Moore et al., 2014; Ickes et al., 2000; Klein & Hodges, 2001). Secondly, these presumed gender/sex differences extend beyond "baseline" abilities, and it has been suggested that men and women might differ in affiliative and empathic abilities during acutely stressful situations (Taylor et al., 2000) (however, c.f., Geary & Flinn, 2001; Taylor, 2006). Specifically, Taylor and colleagues (2000) propose in their "tend-and befriend" hypothesis that behaviourally, females' response to stress involves seeking out others as a means to cope with the stressor, in contrast to a more *confrontational* or *avoidant* male response. As such, since Taylor et al.'s seminal paper from 2000, a great deal of effort has been made to frame changes, differences, or stability in social abilities due to acute stress through the lens of "tend-and-befriend", and thus hypothesized gender/sex differences. However, most studies investigating these effects have not found many gender/sex differences, with the exception of differences for higher level inferential social cognitions (Smeets et al., 2009). Notably, the

gender/sex specific effects for empathic abilities in relation to stress that have been reported are at odds with the idea that acute stress should specifically enhance women's social abilities. For cognitive empathy findings suggest that men benefit from the experience of acute stress, while for women the findings point to detrimental effects of stress on cognitive abilities, or to no changes at all. Of note, Taylor et al., argue for increased *affiliative efforts*, and not specifically about empathy and related constructs. In addition, most previous studies have commonly used "stranger" stimuli, while the "tend-and-befriend" hypothesis is largely concerned with behaviours towards familiar others, see discussion below. As such, the effects of stress on empathy appear to be more nuanced compared to what has been proposed. Thirdly, when considering the effects of acute stress on empathic abilities, it is important to consider gender/sex differences in stress reactivity. As Kudielka and colleagues (2004) have shown, women typically show an attenuated cortisol response, compared to men. This difference in stress reactivity could have important implications for cognition in general, and for empathic accuracy in particular. Taken together, theoretical considerations and research findings suggest that gender/sex is an important factor to consider when looking at the effects of acute stress on empathy.

Findings from the studies presented in this thesis provide further evidence for this. In Chapter 2, I demonstrate that the effect of stress on cognitive components of empathy is gender/sex dependent. Specifically, I find that acute stress improved cognitive empathic abilities in male participants, while it did not impact female participants' abilities. Moreover, I found that stress induced cortisol levels enhanced social inference making in men but not women. Importantly, this finding was replicated across both the within-subject and between-subject study designs, in two independent samples, thus demonstrating the robustness of these effects. Similar results have

previously been reported by Smeets and colleagues (2009) who found gender/sex specific effects of acute stress on social cognitive abilities. However, where Smeets et al. report that for men in the stress condition, cortisol led to increased performance on the RMET, there were no differences compared to the control condition. For women cortisol had the opposite effect, with high levels of cortisol in the stress condition having detrimental effects, compared to low levels of cortisol. In Chapter 2, I found that acute stress induced cortisol led to increases in empathic accuracy in men, and an overall increase in performance, compared to the control condition. For women, I did not find differences between the control and the stress conditions. The finding that cortisol is associated with an increased empathic accuracy in men offers a potential explanation for the reported gender/sex differences. As mentioned, the male and female stress response differs, with men typically displaying a robust cortisol response, compared to women (Kudielka & Kirschbaum, 2005). Accounts suggest that acute stress triggers a phasic shift in two large-scale neural networks, prioritizing the salience network over the executive control network, at least immediately following the stressor (Hermans et al., 2014). As such, if acute stress facilitates vigilance to contextual cues, especially threat, then one would expect enhanced attention towards, and processing of, the negative emotional experiences conveyed by our empathic accuracy targets. Notably, the original empirical paper by Hermans and colleagues (2011) included mostly male subjects in their two samples (~ 80%). How these stress induced shifts in attention might be applicable for both male and female participants is unclear.

That we did not find gender/sex differences for our measure of affective empathy (mimicry; Chapter 3) is less surprising given that similar effects have been observed previously for mixed gender/sex samples. Further, our finding that increases in stress-induced glucocorticoids is associated with reduced affiliative mimicry is a bit more peculiar, especially

since this effect was observed in both men and women. However, previous research that has looked at mixed gender samples and emotion contagion (cf. Martin et al., 2015) has observed similar, or comparable effects—a cortisol associated reduction in emotion contagion. Of note, past research has used negative emotions, whereas the study described in Chapter 3 only found a reduction for positively valenced emotions, and no effect on negative emotions.

Overall, these findings suggest that the biological stress system influences affective and cognitive abilities differently. With respect to stress, for the affective domain more research is needed to understand the link between affect and biology, for both men and women (Ali et al., 2017; Ali, Nitschke, et al., 2020; Goldfarb et al., 2020).

Other Hormones

One of the reasons for gender/sex differences in the acute stress response is the presence of varying levels of sex-steroids, such as estrogens and progesterone, which fluctuate throughout the different stages of the female menstrual cycle (see section above). However, even in the absence of acute stress the presence of sex-steroid hormones have been associated with differences in empathic abilities. Overall, the research on menstrual cycle specific differences in empathic abilities is limited. There is some indication that emotion recognition skills vary between cycle phases. The two cycle phases of interest are the follicular phase (following menstruation)—characterized by increasing levels of estrogen and low levels of progesterone, and the luteal phase (following ovulation)—characterized by high levels of progesterone and estrogen (Richards, 2018). Research findings on the influence of cycle phases on empathic abilities have been mixed and inconclusive. For example, elevated levels of progesterone (luteal phase) have been associated with both decreased emotion recognition (Derntl et al., 2013; Derntl, Kryspin-Exner, et al., 2008; Derntl, Windischberger, et al., 2008) and increased emotion

recognition (Conway et al., 2007; Kamboj et al., 2015; Wang & Chen, 2020). Additionally, research on the influence of oral contraceptive use—i.e., exogenously manipulated levels of hormones (notably, synthetic sex-steroids), and as such suppressed levels of endogenous sex-steroids—on empathic abilities is similarly inconclusive. In general, the use of oral contraceptives has been linked to decreased social-emotional abilities, particularly emotion recognition abilities (for a review: Montoya & Bos, 2017). However, some inconsistencies exist in the literature. For example, Hamstra and colleagues (2014) compared naturally cycling women to women using oral contraceptives and found that oral contraceptive users recognized fewer facial expressions in an emotion recognition task. Similarly, Pahnke and colleagues (2018) found that the use of oral contraceptives resulted in reduced accuracy for recognizing emotions in the RMET. However, other studies have found no effects of oral contraceptive use on emotion recognition abilities. For example, Shirazi and colleagues (2020) also used the RMET to test emotion recognition abilities for regularly cycling women and women on oral contraceptives, and found no differences between the two groups (cf. Radke & Derntl, 2016). Similarly, a study by Kimmig and colleagues (2021) found no difference in emotion recognition abilities between naturally cycling women and oral contraceptive users but found differences for empathic concern (here labelled affective empathy). Thus, from previous research it is unclear if, or how, oral contraceptives impact empathic abilities, particularly given that the tasks used in these studies suffer from the same range restrictions as the tasks discussed in the section on cognitive empathy and stress (as they are often the same).

In this regard research presented in Chapter 2 might be more elucidating. Using a more complex social inference making task (empathic accuracy), I found that women using hormonal oral contraceptives performed worse on the empathic accuracy task, compared to regularly

cycling women (of any phase), regardless of condition (stress or control). Importantly, I included an equal number of women in the follicular and the luteal phase in Study-2 of Chapter 2 to test possible differences between cycle phases. Statistical analyses including cycle phase as a predictor did not show differences, either at baseline or post-stress (see Chapter 2, Study 2, Supplemental Materials). As such, evidence from Chapter 2 suggests that the effects of sex-steroids on empathy are more apparent for the difference between regularly cycling women and women using oral contraceptives, than for cyclical hormonal variations in regularly cycling women.

Endogenous levels of testosterone—another sex-steroid—have also been linked to changes in empathic abilities, with higher levels of testosterone resulting in poorer performance on the empathic accuracy task, in both men and women (Nitschke & Bartz, 2020; Ronay & Carney, 2013). In a recent study that is not part of this thesis, I found that higher endogenous (naturally occurring) levels of salivary testosterone were negatively associated with empathic accuracy, in both men and women (Nitschke & Bartz, 2020). Similarly, Ronay and Carney (2013) measured endogenous testosterone, and then had participants engage in an economic role-playing task in which they had to make sales-pitches to another participant. Afterwards, participants rated their own thoughts and feelings, and the performance of their interaction partner. These participant-partner ratings were then correlated to create an index of accurate empathic understanding, or "empathic accuracy". Here, the authors found that higher levels of endogenous testosterone were associated with lower empathic accuracy.

Taken together, the literature on the effects of endogenous levels of sex-steroids on empathic abilities is mixed. There is a limited number of studies on this topic and as such it is too early to draw concrete conclusions (Montoya & Bos, 2017). More studies are needed to

understand the effects of sex-steroids on empathic abilities, and notably, studies that utilize more naturalistic tasks.

Overall, the findings in Chapter 2 are in line with previous literature and demonstrate that cognitive empathic abilities are susceptible to fluctuations in both stress and sex hormones. Moreover, stress-induced cortisol seems to play a specific role for men resulting in beneficial effects for empathic accuracy.

Theories of Stress and Affiliation

Acute stress is an adaptive response to a challenging situation (Selye, 1956). It is adaptive in the sense that acute stress mobilises resources and alters information processing to cope with an aversive situation. Changes in empathy—such as affect sharing and social cognitive abilities—due to acute stress should be considered within the framework of adaptiveness, or how these changes might benefit an individual in an immediately challenging situation.

Traditionally, these reactions to stress have often been attributed to a *freeze* or a *fight-or-flight* response (Cannon, 1939). As such, the adaptive function of acute stress is to highlight strategies that first-and-foremost help the stressed individual overcome that particular situation. In the context of experiencing distress this would likely result in withdrawal (trying to distance—physically and/or psychologically) oneself from the aversive experience, or by focusing on the egocentric experience (i.e., what am I feeling?). The literature reviewed in this thesis, as well as the findings from Chapter 3, suggest that this might be the case during self-experienced stress (i.e., *first-hand* stress). Specifically, stressed individuals appear to focus more strongly on their own experience and are less likely to disentangle their own emotions or

stress from that of another person. Importantly, these strategies of behaviour modification due to stress have been described in animal models of social behaviours under stress (Sandi & Haller, 2015), as well as in emotion regulation strategies in humans (Gross, 1998).

Given that humans are a highly social species, and often have to deal with challenges that require interpersonal-problem solving—for example being confronted by one's boss at work—social strategies on how to deal with stressors are necessary (Chrousos & Gold, 1992). Furthermore, as a social species, humans often seek out others to overcome obstacles, or to socially modulate their emotional states (Gross et al., 2000; Zaki, 2020). In this regard, alternatives to the "*fight-or-flight*" hypothesis have been proposed; specifically, it has been suggested that behaviours that emphasize affiliation may increase under stressful circumstances (Depue & Morrone-Strupinsky, 2005; Taylor et al., 2000). As such, research suggests that we more readily share an experience with familiar others, as a shared experience might facilitate these affiliative processes (Echterhoff et al., 2009). Showing affiliative behaviours towards socially close others is likely more rewarding, and less risky, than investing time and effort in strangers (and by extension to abstract computer stimuli). To this end, stress has the power to draw individuals closer together, but it may only do so in situations where the benefits are obvious to the person engaging with the feelings of others. In this regard it has been argued that empathy is not necessarily automatic, but also motivational in nature (Weisz & Cikara, 2020; Zaki, 2014). Individuals can—at least to some degree—up- and down-regulate when to engage in, for example, affect sharing. When a perceiver is actively stressed themselves, a disengagement from their own emotional state is required in order to attend to another person's emotions. To this end, it is beneficial to increase affect sharing when it comes to understanding and supporting a familiar other, while it will be beneficial to lower emotion sharing in situations

where shared affect could be distracting (e.g., negotiations), or where social support provision (or tending and befriending more generally) seems untenable or impractical (e.g., with strangers, or computer stimuli).

Chapter 3 provides first empirical evidence for this social withdrawal, demonstrating that the experience of acute stress can lead to a reduction in affiliative behaviours, in this case a reduction in smile reciprocity. Given that mimicry has also been associated with affiliative intent (Chartrand & Lakin, 2013), I might have been picking up on behavioural motivations more broadly (cf. Weisz & Cikara, 2020). As such, these findings could be seen as evidence for more flight-like behaviours and a disengagement from others' experiences. However, as noted, the experimental set-up did not allow us to directly test approach or avoidance behaviours in a social interaction (and thus, changes in affiliative behaviours), as the stimuli were presented on a computer screen, and affiliative reciprocity would be limited. Future research should test the effect of acute stress on affiliative behaviours more directly using confederates, fellow participants, or close others as targets. In particular the latter would be important as the participant might be motivated to "reach out" and receive social support.

As early as 1959, Schachter proposed that in times of adversity (such as isolation, anxiety, and hunger) individuals might increase their affiliative tendencies, and concluded that "misery doesn't love just any kind of company, it loves only miserable company" (Schachter, 1959, p. 24). In this "emotional similarity hypothesis*"* Schachter proposes that novel threats lead to greater motivation to affiliate with other individuals facing a similar situation. One thing that many laboratory stressors have in common is the elicitation of uncertainty, particularly in a social context (Dickerson & Kemeny, 2004). For example, in the context of the TSST, the

panellists (i.e., the stress elicitors) are instructed to violate the stressed person's expectations by keeping a neutral facial expression, and as such, do not provide any meaningful social feedback (good or bad). As individuals strive to reduce uncertainty, especially by the means of others (FeldmanHall & Shenhav, 2019), the empathy tasks administered post stressor were the first opportunity to do so. It has been proposed that not only does feeling similar emotions as others facilitates that understanding (Preston & de Waal, 2002), it also validates emotions experienced by the stressed individuals and buffers the stress response (Locke & Horowitz, 1990; Townsend et al., 2014). Engaging with others experiencing similar affect might thus be a means of emotion regulation. In this context, there is evidence that the experience of negative emotions can "colour" the perception of stimuli that follow, in particularly faces (cf. Ali, Cooperman, et al., 2020; Ellenbogen et al., 2010; Grupe et al., 2018; Roelofs et al., 2007; Schwarz et al., 2013). For empathy this could mean that following stress induction negative emotions are more easily recognized, or given more weight, compared to positive emotions.

The findings presented in this thesis can be interpreted in this light. In Chapter 2, stressed individuals observed a series of targets recalling negatively valenced autobiographical memories. As such, one way to interpret the increase in empathic accuracy in stressed men is through a matched or congruent emotional state (i.e., negative arousal). In this case, since both the perceiver and the target showed negative arousal and emotions, this could have increased the participants' attention to the target. In order to test this more systematically, future studies should include positive emotions as well. I would expect that acute stress would selectively impact emotion processing, with enhancing effects for congruent emotions (i.e., negative), and none or detrimental effects for incongruent emotions (i.e., positive).

For Chapter 3, I find a decrease in smile reciprocity—an incongruent emotion to the stressed individuals. This decrease could also be explained by the "emotional similarity hypothesis*",* that is stressed individuals do not affiliate with individuals experiencing different emotions from them (i.e., smiles). Although limited, there is indeed research that has examined these effects. Notably, Gump and Kulik (1997) had participants face a threatening situation (a painful experimental task in the future) either with a fellow participant in a similar or a dissimilar situation. Here, stressed participants increased gaze time to the individual believed to be in a similar situation, compared to both participants in a low threat situation (no painful task), and individuals in a dissimilar situation. This could suggest that the observed effect in Chapter 3—a reduction in smile mimicry—is particular for the stimuli and targets used, in that they reflect dis-similarity in the emotional states of the perceiver and a target (i.e., stressed perceiver and smiling target). Future studies should use more naturalistic targets, ideally participants that similarly just experienced a stress task to further elucidate this mechanism. In this case increased smile reciprocity would indicate greater affiliative intention.

Lastly, it has been proposed that acute stress leads to a shift in information processing, with increased attention towards salient features in the environment (Hermans et al., 2014). As such, there is the notion that information conveyed by others carries special weight. It is therefore pertinent for individuals to track others, including their emotions, carefully as it might inform the perceiver about possible dangers, threats, and opportunities in the environment (Oliveira & Faustino, 2017; Olsson et al., 2020). As such social information serves to reduce uncertainties in the environment. In particular for emotion recognition and social cognitive abilities, increases due to stress might be best explained by this. For example, an increase in attention to faces, or

the recognition of emotions in others can be explained by increased vigilance towards contextually salient information. In the context of the TSST, the identification of angry or neutral faces (emotions displayed by the confederates in order to elicit psychosocial stress) would therefore serve the function of understanding potential stressors in the environment, rather than being indicative of increased social motivation. As such, information others convey might be important clues for how to deal with a particular situation, and whether or not threats (or coping opportunities) are present (Ali, Cooperman, et al., 2020; FeldmanHall & Shenhav, 2019; Olsson et al., 2020; Zaki, 2020). Similarly, shared emotions help individuals to better understand threats and opportunities in their environment (and often in a "tangible" way). Sharing a stressful experience with a target prepares the individual to deal with the potential stressor themselves. These responses are adaptive and extend beyond the recruitment of social support or allies in general.

The effects found in Chapter 2 add to this. At least for men, acute stress facilitated empathic accuracy, an effect that was directly tied to the stress induced cortisol response. This is in line with the findings by Hermans and colleagues' (2014) and their observation that stress triggers a large-scale shift in information processing, away from deliberate control networks towards information processing that is more reliant on implicit attention and salience (cf. Schwabe, 2017). As such, stress might have increased vigilance to social information (notably, all negative emotions). Given that male participants typically display a more robust glucocorticoid response, compared to female participants (Kudielka et al., 2004), that we only observed these changes in cognitive empathy in men might speak to these gender/sex specific effects. However, in order to test these effects more directly, it would be necessary to include positive stimuli (and as such contextually less relevant information) as well.

Conclusions

Social connections play an important part in our health and well-being (Nitschke, Forbes, et al., 2020; Holt-Lunstad, 2018; Snyder-Mackler et al., 2020), it is therefore important to understand how empathy—a mechanism believed to facilitate and maintain social relationships—is impacted by contextual factors. One such factor is the experience of acute stress—a common daily occurrence in our lives. Stress and its accompanying psychological and physiological changes can thus potentially impact how we connect with one another through effects on our empathic abilities.

The overarching aim of this thesis was therefore to understand the association between acute stress and empathy. In Chapter 1, I reviewed the literature on stress and empathy and found that the overall findings for cognitive empathy are inconclusive, chiefly because research has relied on tasks that are prone to range restrictions. Intriguingly, research that has used more complex tasks has reported gender/sex specific effects of stress on cognitive empathy. However, there is a need for more systematic research investigating these effects, using more naturalistic tasks and adequately sized samples. In contrast, for affective empathy, the results indicated increased emotion contagion for close others who are stressed, particularly when the perceiver is unstressed at the onset. There are, however, indications that affect sharing, or affective empathy, might be negatively impacted when the perceivers are stressed themselves, potentially leading to a disruption in social behaviours—especially towards strangers. It is important to note that research on the effects of acute stress on affective empathy needs to extend beyond *empathy for pain,* and examine behaviours related to other negative emotions, and crucially to positive emotions as well.

In chapters 2 and 3, I aimed to address these gaps in the literature, chiefly by using more naturalistic tasks. In Chapter 2, I demonstrated that acute stress affects cognitive empathic abilities in a gender/sex specific manner, such that men benefitted from the experience of acute stress, showing improvements in empathic accuracy abilities, while for women no effects of stress on empathic accuracy were observed. Furthermore, the increase in empathic accuracy for men was associated with stress-induced levels of cortisol. Overall, the results of Chapter 2 highlight the importance of gender/sex considerations in the study of cognitive empathic abilities. In Chapter 3, I showed that stress was selectively associated with facial mimicry. While stress did not show an association with negative emotions, it reduced facial mimicry for smile reciprocity (affiliative mimicry). Notably, this effect was present in both men and women, further underscoring the importance of including both gender/sexes in stress and empathy research. Together, the findings from Chapter 2 and Chapter 3 highlight that acute stress is differentially associated with different facets of empathy.

Overall, the body of work presented in this thesis highlights the need for a differentiative view of empathy and its subcomponents. The results of the empirical research represent an important step towards enhancing our understanding of how acute stress impacts empathy. Given that humans are a social species, understanding how stress impacts our social togetherness has important consequences for our social life and well-being.

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