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This dissertation is dedicated to my sister, Marion. We did it.

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Abstract

Humans are a fundamentally social species that are strongly motivated to form and maintain connections with other members of their group. The formation of social connections is facilitated by the ability to perceive, understand, and respond to the emotions and actions of others. Social interaction also increases the risk of passing pathogens between individuals, and the motivation to avoid diseases may interfere with the motivation to connect. This dissertation describes three studies that explore individual differences in social motivation and behavior. Chapter 2 explores psychophysiological reactions to viewing others in distress. Emotional states can be correlated with a variety of psychophysiological responses and an emotion shared between individuals will not necessarily be accompanied by the same patterns of activity. This study demonstrated that individuals experience a strong cardiac response to viewing distress, and that this response may not occur in the same direction as the cardiac response of the person they are observing. Additionally, individual differences in interoceptive accuracy predicted emotional contagion and perceptions of anxiety in the speaker. This suggests that interoception may affect aspects of empathy for distress in others, which can then influence social motivation. Chapter 3 explores the perception of pain in others following exposure to disease cues. In previous research, exposure to disease cues has largely been shown to decrease social. However, in certain contexts, disease cues may also indicate that a member of one's group is in need of care and thus motivate an individual towards social connection. This study found that participants perceived the pain that others were experiencing as more intense after viewing disease-related images. In a separate task, participants also showed reduced attentional bias towards affective content after viewing disease-related images. These results imply that disease cues can cause both a disgust response and increase sensitivity to affective cues that could inform social behavior. Chapter 4

explores the association between the behavioral immune system and social motivation through the lens of loneliness. Loneliness is associated with the motivation to protect and maintain social connections, which requires social interaction. In this context, when social motivation is high, the behavioral immune system may not be able to use social avoidance as a means to prevent infection. The results from this study showed that as loneliness increases, perception of vulnerability to disease also increases, suggesting that the behavioral immune system may heighten sensitivity to possible threats of disease without decreasing social motivation.

Chapter 1: General introduction

1.1 Social species and the need to belong

For social species, group membership provides access to vital benefits that increase the likelihood of survival and increase quality of life. Social living allows for easier procurement and sharing of resources, greater access to potential mates, and group defense against the threat of predators (Alexander, 1974). Gaining access to these benefits requires forming and maintaining social connections with other group members. To that end, humans (and other social species) experience a strong social motivation towards cooperation and behavior that will strengthen their relationships (Axelrod & Hamilton, 1981; Baumeister & Leary, 1995). In part, the motivation toward social behavior is reinforced by an association with pleasant experiences. Cooperation and group decision-making have been shown to increase self-reported positive affect (Tabibnia & Lieberman, 2007). Additionally, social interaction and connection are associated with increased brain activity in reward areas (Insel, 2003; Trezza, Baarendse, & Vanderschuren, 2010). Past the acute pleasant experience, maintenance of social connections contributes to physical and emotional well-being. Social support from close relationships can act as a buffer against the negative impact of stressful life events on health (Cacioppo et al., 2002). Supportive relationships can facilitate healthy behaviors like physical activity and decrease the likelihood that individuals will turn to unhealthy coping mechanisms like drug use (Kiecolt-Glaser, Gouin, & Hantsoo, 2010).

Conversely, perceived threats to group membership and objective loss of social connection can be harmful. Acute instances of social rejection, which indicate loss of connection, produce negative affective and visceral experiences comparable to that of physical pain (Eisenberger, Lieberman, & Williams, 2003; MacDonald & Leary, 2005). In one study,

individuals who reported repeated instances of social rejection were more likely to report the onset of depression (Slavich, Thornton, Torres, Monroe, & Gotlib, 2009). Over time, the consequences of lack of social connection can compound and impact health. Research from several longitudinal studies assessed individuals' degree of social connectedness to their community, including marriage, family, and platonic relationships (Berkman & Syme, 1979; House, Robbins, & Metzner, 1982; Kaplan et al., 1988). They found that individuals with the lowest levels of connection were more likely to have died during the follow-up period, and that low social connection predicted mortality independent of health behaviors like smoking and exercise (House, Landis, & Umberson, 1988).

While these studies largely considered quantity of social connections, it has since been demonstrated that the perception of low quality in social relationships can lead one to feel isolated, and thus impact well-being. Perception of social isolation acts as a chronic source of stress for individuals, leading to increased cortisol levels (Adam, Hawkley, Kudielka, & Cacioppo, 2006; Cacioppo et al., 2000) and the experience of everyday life events as more stressful (Cacioppo & Hawkley, 2003). Chronic perceived social isolation, or loneliness, represents the threat of loss of group membership and impacts an individual whether or not that threat comes to fruition. Loneliness is associated with strong aversive feelings, including depression and pain (Cacioppo, Hughes, Waite, Hawkley, & Thisted, 2006; Jaremka, Fagundes, Glaser, et al., 2013), that typically motivate individuals to alleviate the source of the feeling. Consequently, lonely individuals experience strong motivation towards forming new social connections and maintaining existing ones (Baumeister & Leary, 1995; Maner, Dewart, Baumeister, & Schaller, 2007). If individuals are not able to repair their social connections, they risk losing out on the benefits of the group.

It is worth noting that social living also comes with two automatic costs: increased competition for resources with other group members and the increased risk of disease transmission between individuals (Alexander, 1974; Shakhar, 2019). Mitigating these costs can sometimes produce motivations that compete with social motivation. For example, the possibility of infection from a sick group member may lead to avoidance of that person until the pathogen threat has passed (Schaller & Park, 2011). In this instance, social avoidance takes precedence over maintenance of the social connection. However, if the group member is a close friend, social motivation may win out and one will nurture the relationship by providing care to the friend even at the risk of getting sick (Delton & Robertson, 2016). While living in a social group, individuals must take into account a range of group- and self-oriented motivations to inform social behavior.

1.2 Empathy and emotional communication

Operating as a member of the group requires the tracking of complex and shifting information about other individuals and social context (Dunbar, 2009). The perception, integration, and communication of social information between humans is facilitated by emotions (Rolls, 2013; Van Kleef, 2009). Communication through emotional expressions provides information about individual needs, shared resources, and threats in the environment (Alexander, 1974; Decety, Norman, Berntson, & Cacioppo, 2012). These expressions can be comprised of facial (Frith, 2009), verbal (Bänziger & Scherer, 2005; Eckland, Leyro, Mendes, & Thompson, 2019), and gestural cues (Bänziger, Grandjean, & Scherer, 2009). For example, a human expression of fear may involve a grimace, a shout, and an arm gesture towards the source of threat. The information communicated by this expression would then inform group motivation

and help coordinate the appropriate response – in this case fleeing from the threat (Van Kleef, 2009). Although expressions are not always a reliable reflection of an individual's true emotional state (Gunnery & Ruben, 2015; Mclellan, Johnston, Dalrymple-Alford, & Porter, 2010), they still communicate information that can influence social behavior. Insight into the emotional state of others allows individuals better act on their own motivations and to avoid social blunders that would harm their connections. As such, the perception and understanding of emotions has been proposed as a necessary precursor to social success (Leiberg & Anders, 2006).

Empathy is a complex psychological phenomenon that encompasses that ability to perceive, understand, and respond to another person's emotions and actions (Decety & Jackson, 2016). Often, empathy as a construct is discussed in terms of its affective and cognitive components (Cuff, Brown, Taylor, & Howat, 2014). Affective empathy involves elements such as emotional contagion, which refers to the spread and sharing of emotional states between individuals (Hatfield, Bensman, Thornton, & Rapson, 2014; Hatfield, Cacioppo, & Rapson, 1994), whereas cognitive empathy involves elements like perspective taking, which refers to the recognition and understanding of another's mental state (Leiberg & Anders, 2006). The ability to empathize has some trait-like elements (Reniers, Corcoran, Drake, Shryane, & Völlm, 2011), but is also sensitive to context, including the social relationship between individuals (Decety & Cowell, 2014). In general, one will be more motivated to understand and empathize with close members of one's group than with strangers (Goetz, Keltner, & Simon-Thomas, 2010). The proximate reasons that one can empathize more easily with family and friends may seem intuitive – it is easier to understand and care about those one is close to. However, it has been proposed that the ultimate explanation for the ease of empathizing with group members lies in the provision of care to offspring. To ensure the survival of one's children, parents need to be

able to understand and respond to the needs being communicated, in part, through the expression of emotion (Decety, 2011; Decety, Bartal, Uzevovsky, & Knafo-Noam, 2016). Expressions of distress, pain, and disease signal that an individual needs care and motivate others, be they parents or other group members, towards helping behavior (Steinkopf, 2015, 2016a).

While empathy is less easily produced for those with whom one is unfamiliar than family and friends, it is still possible to understand and respond to the emotional state of strangers (Chakrabarti & Baron-Cohen, 2006). The dispositional, or trait-like, elements of empathy predict an individual's tendency to exhibit compassion and show helping behavior towards strangers (Eisenberg & Miller, 1987; Reniers et al., 2011; Trobst, Collins, & Embree, 1994). This may in part be due to highly empathic individuals showing a greater sensitivity to signals that care is needed. In two studies, individuals with higher empathy perceived expressions of pain in strangers as more intense than those with lower empathy (Moriguchi et al., 2007; Singer et al., 2004). However, this sensitivity to the emotions of others can be a double-edged sword. If an individual is more sensitive to expressions of distress during an interaction, emotional contagion may lead them to strongly take on that distress themselves, with two possible outcomes. The distress may lead to empathic concern and feelings of compassion for the other person, motivating helping behavior as described (Batson et al., 1997). Or, an individual may be overwhelmed by feelings of personal distress, losing focus on the other person and being motivated only to alleviate their own aversive emotional state (Decety et al., 2016; Leiberg & Anders, 2006). The outcome of emotional contagion may depend on an individual's ability to regulate their own emotions in the context of the social interaction. Thus, the inclusion of individual differences in emotional processing in addition to differences in empathy can inform research into social motivation and behavior.

1.3 The behavioral immune system

The elevated risk of transmissible disease is an automatic cost incurred by social species (Shakhar, 2019), as close contact between members of the group makes it more likely that pathogens will pass between individuals. To avoid infection and increase the likelihood of surviving pathogen threats individuals may utilize psychophysiological mechanisms that coordinate shifts in perception, cognition, and behavior (Hart, 1990; Schaller & Park, 2011). Such mechanisms are categorized under the umbrella of the behavioral immune system, which coordinates with the classical immune system. When coming into contact with a pathogen, the classical or “biological” immune system responds through the energetically expensive production of lymphocytes and antibodies that seek out and eliminate the pathogen (Miller & Maner, 2011). The classical immune response is associated with motivational shifts that can result in an array of “sickness behaviors” including loss of appetite, fatigue, and social withdrawal (Dantzer & Kelley, 2007). Sickness behaviors mitigate the metabolic expense of the immune response by encouraging the conservation of energy and avoidance of possible sources of reinfection (Ackerman, Hill, & Murray, 2018; Schaller & Park, 2011). While the behavioral immune system can coordinate these reactive responses to pathogen threat, it may also motivate behaviors that proactively prevent infection from occurring in the first place. Many of these preventative behaviors occur on an individual level, such as maintenance of personal hygiene and hand washing, to prevent pathogens from entering the body (Schaller, Murray, & Bangerter, 2015). Avoidance of potential sources of pathogens altogether is the most preventative measure the behavioral immune system may utilize.

In order to avoid potential sources of pathogens, individuals rely on the ability to perceive pathogen cues in the environment. Humans are able to identify infected individuals as

pathogen sources through the perception of cues associated with disease (Miller & Maner, 2012). These cues can include aversive odors generated by illness (Moshkin et al., 2012; Olsson et al., 2014), expressions of pain or distress (Steinkopf, 2015), changes in body posture and movement (Sundelin et al., 2015), and other visual symptoms of disease (van Leeuwen & Petersen, 2018). Research demonstrating that exposure to pathogen imagery, as compared to non-pathogen related threat (e.g. guns), results in higher levels of proinflammatory cytokines suggests that perception of disease cues helps prepare the body to fight off infection (Schaller, Miller, Gervais, Yager, & Chen, 2010). To minimize risk of becoming infected, the sensory perception of disease cues operates with a fairly low threshold (Miller & Maner, 2012). In their study, Miller & Maner demonstrated that individuals who perceived themselves to be more vulnerable to disease were more likely to categorize images of others as showing disease cues. Because the classical immune response is metabolically expensive, the cost of reacting to benign cues is small compared to the risk of overlooking a serious pathogen threat.

Pathogen cues motivate avoidance of their source in part through the elicitation of disgust, an emotion associated strongly with aversive experiences (Tybur & Lieberman, 2016). Disgust aids in the integration of relevant information about the pathogen cues to inform behavior (Tybur, Lieberman, Kurzban, & Descioli, 2012). The threat of disease can alter social motivation away from behaviors like mating and reproduction in an effort to conserve energy. One study found that when the risk of disease was perceived to be high, men described less willingness to have sex with potential partners (Oaten, Stevenson, Tapp, Case, & Cousins, 2019). Another study demonstrated that increasing concerns about disease, through exposure to a slide show about infections, was sufficient to decrease judgements of attractiveness in strangers (Sawada, Auger, & Lydon, 2018). Exposure to disease cues may also decrease prosocial

behavior in an effort to reduce encounters with potentially infected individuals. Some research has shown that individuals will rate images of people who are sick as less likeable than those who are healthy, ostensibly because they were able to pick up on visual cues to their immune state (Regenbogen et al., 2017). Similarly, following exposure to images of disease cues (e.g. skin rash), individuals show behavioral avoidance (through pulling a lever) in response to images of faces (Miller & Maner, 2011) and report overall decreased interest in making social connections (Sawada et al., 2018).

Social research into the behavioral immune system has largely focused on the ways in which concerns about disease compete with social motivation. However, as previously described, humans experience a strong motivation towards forming social connections, including cooperation and exhibition of helping behavior. In certain circumstances, the motivation to connect may include providing help to a sick group member in response to the perception of disease cues (Hart, 1990; Steinkopf, 2016b). The decision to help or avoid the potential risk of infection depends upon the consideration of individual welfare, as well as the importance of the social connection. If an individual is generally healthy, then the social benefit of providing care may outweigh the cost of a minor illness (Delton & Robertson, 2016). Only recently has research into the behavioral immune system made a distinction between the social impact of reacting to pathogen threats and proactive shifts in social motivation. A number of questions remain open, particularly regarding the activity of the behavioral immune system when social motivation is high and pathogen avoidance is not possible.

1.4 The current work

The fundamental nature of social relationships, along with the affective and cognitive mechanisms that facilitate them, has been an object of focus for psychological research for over a century. The formation and maintenance of social connections is aided by the ability to understand and respond to the emotional state of group members, which is facilitated in part by empathy. However, motivation towards social behavior may also be impacted by other concerns, such as the risk of transmitting infectious disease between individuals. This dissertation describes three studies that explore individual differences in social motivation and behavior. Chapter 2 examines psychophysiological responses to viewing others in distress, emotional contagion, and emotional appraisal of the distress. Chapter 3 examines how exposure to disease cues impacts empathic judgements of pain in others, compassion, and perception of affective content. Finally, Chapter 4 explores the connection between loneliness and perceived vulnerability to disease, as well as potential mediating factors. Together these studies speak to the complex considerations that are at play for social species, and how individual differences in affective and physiological processes may influence social motivation.

Chapter 2: Emotional contagion and responses to distress in others

2.1 Introduction

Humans face an abundance of physical and social stressors over the course of their lives. Stress is a natural consequence of moving through the world, and acute instances of stress exert pressure on an individual to adapt and overcome their circumstances (Mcewen & Gianaros, 2010). However, over time, repeated and/or chronic exposure to stress will have deleterious effects on one's health and well-being (Chrousos, 2009; Mcewen & Gianaros, 2010). In addition to experiencing stress in their individual lives, humans are sensitive to stressors in the lives of their close friends and family members. For example, having a romantic partner who is experiencing significant job stress can affect an individual's long-term well-being, even after controlling for shared environmental stressors (Westman, 2001). This transmissible impact of stress is an extreme consequence of affect sharing, a key component of empathy and the ability to understand the emotions of others. Referred to as emotional contagion, this sharing phenomenon can occur rapidly during social interaction and has a significant influence on the recognition and interpretation of social cues (Hatfield et al., 1994).

Emotional contagion, as it relates to empathy and affect sharing, can be assessed on a basic level through self-reported emotional state (Hatfield et al., 2014). If an individual reports experiencing the same emotion as someone they are observing, then contagion can be said to have occurred. However, this method of assessment may provide an incomplete view of emotional contagion. Though both individuals may report the same emotional state, the psychophysiological experience of that emotion may differ and depend on their perception of the greater context of the observation (Hatfield et al., 2014). Utilization of psychophysiological measures underlying emotion can allow for a more nuanced exploration of the contagion

phenomenon. Buchanan et al. (2012) demonstrated that the observation of distress in another person produced negative affect and a physiological stress response in the observer. In their study, participants observed a stranger completing an acute psychological stressor and salivary cortisol was collected from both individuals. They found that cortisol levels in the participant were predicted by those of the stranger, demonstrating that emotional contagion can be observed at a physiological level. Buchanan et al. equated emotional contagion to physiological resonance, proposing that the response in the observer and the observed must be in the same direction and of a similar magnitude. However, it has been well established that emotions can be correlated with varied psychophysiological responses (Norman, Necka, & Berntson, 2016). Thus it is possible that a transmission of emotional state may occur between individuals but result in differing patterns of behavior and physiological activity (Hatfield et al., 2014). Leiberg & Anders (2006) suggested that observing fear in someone being chased by a lion as compared to fear in someone experiencing a haunted house could by no means require the same response, though the feeling of fear may be contagious in both instances.

Autonomic nervous system activity presents a compelling method for the assessment of stress contagion, as it can easily be measured continuously and is less subject to volitional control than self-reports. Additionally, it is well established that responses to the same stressor may individually differ depending on one's perception of the event (Mendes, Blascovich, Hunter, Lickel, & Jost, 2007), and so the use of autonomic measures can reveal underlying mechanisms that would not be clear from reported emotional state alone. The psychophysiological correlates of stress contagion have been previously observed using various autonomic measures, including electrodermal activity (Guastello, Pincus, & Gunderson, 2006), heart rate (Dimitroff et al., 2017); and parasympathetic (Coutinho et al., 2021) and sympathetic

cardiac control (Waters, West, & Mendes, 2014). As emotional responses are not consistently associated with a single pattern of autonomic activity (Norman et al., 2016), a more robust understanding of the mechanisms underlying emotional contagion can be gathered through the use of diverse measures.

Social communication and interaction are supported by internal emotional processing and external expression (Van Kleef, 2009). Emotional expressions convey salient information to others, ranging from a potential threat in the environment to a desire for cooperation (Decety et al., 2012). These expressions are comprised of facial expression, verbal intonation, and gestural cues (Bänziger et al., 2009). In a dynamic and complex social environment, the ability to generate appropriate responses to the emotional cues of others has been proposed as a prerequisite to success (Leiberg & Anders, 2006). Preston and de Waal (2002) suggested that empathy functions partially through a simulation process in which individuals who observe the emotional state of another come to activate the representation of that emotional state in their own mind. In this way the individual may then experience psychophysiological correlates of that emotional state (though the correlates may not be the same as those experienced by the other person). Through the contagious effect on their own emotional state an individual can then better understand the emotional state of the other (Leiberg & Anders, 2006).

While emotional contagion is not necessarily sufficient to produce full understanding of another's emotions, it is a key component of empathy (Decety & Jackson, 2004). Dispositional empathy consists of multiple affective and cognitive components that individually differ and influence one's ability to comprehend the emotional state of others (Reniers et al., 2011). Empathy aids in navigating the complex social environment and is one of the primary means by which individuals become motivated to act prosocially (Batson et al., 1997). While dispositional

empathy has previously been considered a relatively stable personality trait, empathic processes may be influenced by social context. For example, emotional contagion is more likely to occur between intimate individuals than between strangers (Engert, Plessow, Miller, Kirschbaum, & Singer, 2014). The aforementioned study by Buchanan et al. (2012) demonstrated that individuals who reported greater empathic concern and perspective-taking ability experienced a greater stress response to viewing distress in others.

There has been limited work that connects empathy (and emotional contagion specifically) to representations of the self-other boundary, which help to determine the origins of contagious emotional states (Decety & Sommerville, 2003). Maintaining the self-other boundary and keeping track of what signals originate from one's own body depend in part on afferent neural signaling. The perception and integration of afferent information from the periphery occurs through interoception (Quigley, Kanoski, Grill, Barrett, & Tsakiris, 2021). The moment-to-moment representation of internal bodily state (e.g. energy, stress level, disposition) provides a foundation for feeling states associated with a particular emotion (Craig, 2002). Interoceptive accuracy, the most commonly measured dimension of interoception, represents the ability to accurately perceive a specific afferent signal such as the heartbeat (Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). Interoceptive accuracy has been linked to several aspects of individual emotional experience. High interoceptive accuracy is associated with both a greater intensity of felt emotions (Pollatos, Gramann, & Schandry, 2007) and more effective cognitive reappraisal and down regulation of negative emotions (Füstös, Gramann, Herbert, & Pollatos, 2013; Pinna & Edwards, 2020). One suggested explanation for the role of interoception in emotion regulation is that perception of afferent physiological signals allows for the close monitoring of one's emotional state on that moment-to-moment level, and thus the greater ability

to regulate it (Füstös et al., 2013). This supposition is further supported by the negative association between interoceptive accuracy and the trait-level difficulty in identifying and describing one's emotions, a construct called alexithymia (Murphy, Catmur, & Bird, 2018).

While empathy can account for the experience of shared emotional states, it relies on the ability to keep track of which feelings belong to oneself or another (Decety & Jackson, 2004). In other words, successful utilization of empathy requires maintenance of self-other distinction. This distinction is aided by interoception, which helps assign sensory signals to their internal and external sources (Tajadura-Jiménez & Tsakiris, 2014). In fact, the referenced study demonstrated that low interoceptive accuracy was associated with a malleability to the self-other boundary. These shared associations between aspects of emotional experience and the self-other boundary suggest a connection between interoceptive and empathic ability. However, this connection has yet to be consistently demonstrated. One study found that there were no associations between interoceptive accuracy and any self-report or behavioral measure of empathy (Ainley, Maister, & Tsakiris, 2015). Conversely, greater feelings of compassion and intensity of feeling during an empathy for pain task were predicted by high interoceptive accuracy (Grynberg & Pollatos, 2015). Thus, there remains an explanatory gap in the connections between one's own and another's emotional experience, interoception, and empathy.

Past studies of emotional contagion have largely assessed transmission of stress between individuals within a single interaction, making it difficult to make statements about the individual's susceptibility to emotional contagion outside that specific context. The current study examined emotional contagion in participants when exposed to multiple speakers experiencing varying degrees of stress. The assessment of emotional contagion in multiple instances can aid in addressing the interrelated processes implicated in empathy and interoception within a single

participant. Finally, it is of interest whether the psychophysiological changes that occur while viewing another's distress inform appraisal of their subjective emotional state, or if that judgement reflects a separate component of emotional contagion.

2.1.1 The current work

The present study examines the psychophysiological impact of viewing others' distress and the emotional appraisal of that distress. This study expands the current literature on the psychophysiological evidence of emotional contagion by examining physiological reactivity to viewing multiple instances of distress in others at varying intensity and through the use of multiple autonomic measures. Additionally, this study considered both the participant's physiological reactivity, indexed by the change in autonomic cardiac function while viewing distress, and degree of emotional contagion, indexed by the correlation between the participant's physiological function and that of the speaker. In other words, individual physiological reactivity and its similarity to the physiological activity of the speaker being observed are both explored. It is possible that an individual would experience a reaction that is uncorrelated with that of the speaker, or that a lack of reactivity in the participant would be correlated with a lack of change in the speaker. It was predicted that participants would show greater physiological reactivity and a greater degree of contagion when observing videos of others' distress, in comparison to control videos. Furthermore, it was predicted that participants would rate the anxiety of speakers in distress more highly than speakers in control videos. This study also explored whether dispositional empathy would impact responses to viewing others' distress. It was predicted that individuals higher in empathy would show greater physiological reactivity and that their physiological changes will be more related to the physiological change of the speaker, reflecting

a greater degree of contagion. Finally, this study explores whether knowledge of one's own physiological functioning (interoceptive accuracy) impacts emotional appraisal of other's distress. It was predicted that individuals high in interoceptive accuracy would also give higher anxiety ratings.

2.2 Methods

2.2.1 Participants

99 participants were recruited to participate through the University of Chicago online psychology research participation system (Sona Systems) and received either \$10 or course credit for their participation. Five participants were excluded due to repeated movement artifacts in their ECG signal or for not following directions during the study tasks. Two participants were removed as extreme outliers for their scores in the interoceptive accuracy task. 92 participants (59 women, 34 Asian, 28 Caucasian, $M_{\text{age}} = 21.58$ years, $SD_{\text{age}} = 4.10$ years) were included in the analyses below. A further nine participants were missing impedance cardiography data and so were excluded from any analysis of pre-ejection period, meaning any model with that outcome included 83 participants. Participants were fluent in English and reported no clinical history of neurological or psychiatric disorders. This study was approved by the University of Chicago Institutional Review Board.

2.2.2 Procedure

Participants first completed a demographic survey and battery of psychological questionnaires, including the Questionnaire of Cognitive and Affective Empathy (Reniers et al., 2011). Participants were then fitted with surface electrodes for the recording of

electrocardiography and a five-minute physiological baseline was collected (see 2.2.4. Autonomic measures). After this rest period, participants completed a measure of cardiac interoceptive accuracy. Interoceptive accuracy was assessed utilizing the mental tracking method of heartbeat perception (Schandry, 1981). This paradigm asks participants to count their heartbeats for a certain time interval without taking their pulse. Participants completed six intervals of different lengths (25s, 30s, 35s, 40s, 45s, 50s) in a randomized order. In each interval, participants counted their heart beats from the display of a green “count” cue until a red “stop” cue appeared. Directly after the stop cue participants entered the number of heartbeats they counted and then rated their confidence in their count on a visual analog scale from “Total guess” to “Complete confidence.” Accuracy for each interval was calculated by comparing participant count to the actual number of heartbeats experienced during each interval (taken from the physiological recording) using the formula: $1 - |nbeats_{real} - nbeats_{reported}| / ((nbeats_{real} + nbeats_{reported}) / 2)$ ¹. Values were averaged across the six intervals to obtain interoceptive accuracy for each participant.

Finally, participants viewed 21 stimulus videos in three blocks; a ten-second fixation cross appeared before each video and a two-minute rest period occurred between blocks. Videos were displayed in a randomized order. Following each video participants were asked to rate how anxious the speaker in the video seemed on a visual analog scale. The autonomic cardiac responses to watching each video were used to quantify physiological reactivity and degree of emotional contagion between participants and speakers (see 2.2.5 Data analysis plan).

Task instructions were displayed, and behavioral responses were collected using E-Prime 2.0 (Psychological Software Tools, Pittsburgh, PA).

¹ The inclusion of $nbeats_{reported}$ in the denominator minimizes overestimation of accuracy for participants that show high variance (Garfinkel et al., 2015).

2.2.3 Stimulus set

This stimulus set was created for use in a previous study (see Dimitroff et al., 2017). 21 speakers (11 females, 18 Caucasian, $M_{\text{age}} = 19.65$ years, $SD_{\text{age}} = 1.18$ years) were chosen from a larger group of participants to be included in the set. All participants provided informed consent for their data to be used in future studies. Each stimulus was a one-minute clip taken from a video recording of a speaker completing a Trier Social Stress Test (TSST) (Kirschbaum, Pirke, & Hellhammer, 1993) or a neutral speech. The speakers had two minutes to prepare a response to their particular prompt and then were asked to speak continuously for three minutes. Three video conditions were created: “Stress,” “Poststress” and “Control”. In the “Stress” condition speakers completed a TSST in which they were asked to defend themselves against an allegation of cheating on the GRE. In the “Control” condition speakers were asked to give a detailed description of either their morning routine or the layout of their home. In the “Poststress” condition speakers first completed the TSST, rested for ten minutes, and then were recorded responding to one of the neutral prompts. Cardiac activity was collected for each speaker while they completed their prompt. A one-minute segment was identified for each speaker such that the video clip contained clear speech and no audio-visual abnormalities, and the corresponding cardiac data contained no major artifacts. The number of females and male speakers was balanced within each condition.

2.2.4. Autonomic measures

An electrocardiogram (ECG) was obtained from all participants using a standard lead II configuration of surface electrodes and a BioNex eight-slot desktop platform (Mindware

Technologies, Gahanna, OH), and Mindware Technologies' BioLab Acquisition software (version 3.3.1). An impedance cardiogram (ICG) was also obtained using a tetrapolar configuration of surface electrodes. The ECG was collected at a sampling rate of 1000Hz and analyzed with Mindware Technologies' HRV Analysis software (version 3.2.5). The signal was passed through bandpass and notch filters to remove muscle and ambient electrical noise before being visually inspected. R peaks incorrectly identified by the software (e.g. due to movement artifacts) were manually corrected or excluded from the data if the correct peak was not evident (Berntson et al., 1997). Inter-beat intervals were time-sampled and interpolated at 4Hz to ensure equal interval series. The inter-beat interval (IBI) of the heart represents the time between two heartbeats (in milliseconds) and is the inverse of heart rate. The root mean square of successive differences (RMSSD) was calculated to assess variance in the IBI series. RMSSD is the primary time-domain measure used to index vagally-mediated changes in beat-to-beat heart rate variability (Shaffer, McCraty, & Zerr, 2014); higher values generally reflect greater parasympathetic cardiac control. RMSSD has been validated for samples as short as 10 seconds (Salahuddin, Cho, Jeong, & Kim, 2007). The ICG was collected at a sampling rate of 1000Hz and the derivation of the signal was calculated in real time during collection; the resultant dZ/dt waveform was then analyzed with Mindware Technologies' Impedance Cardiography Analysis software (version 3.2.5). The dZ/dt waveform was passed through the same ambient noise filters and ensemble averaged with the ECG waveform to provide a pre-ejection period (PEP) value in milliseconds. PEP is measured as the time between the electrical innervation of the left ventricle and the opening of the aortic valve². PEP indexes sympathetic nervous system influences on cardiac contractility; smaller PEP values reflect greater sympathetic cardiac control.

² For procedures for calculating these points see: (Berntson, Lozano, Chen, & Cacioppo, 2004; Lozano et al., 2007)

2.2.5 Data analysis plan

Initial one-way ANOVAs were run to determine whether video condition (Stress/Poststress/Control) had an effect on the main outcome variables for this study: physiological reactivity, degree of emotional contagion, and anxiety ratings. Results were then further analyzed with hierarchical linear models (HLM) (Raudenbush & Bryk, 2002) including video condition as a fixed factor and subject as a random factor. This technique allows for missing data without resorting to complete case analysis. Additionally, this technique allows for the assessment of random variability at the subject level, which was of interest given the heterogeneity in physiological patterns between individual speakers, even within the same video condition. Subject baseline for the relevant physiological measure was included as a predictor to control for baseline variability. Affective and cognitive empathy and interoceptive accuracy were added individually to the model as predictors to examine their effects on physiological reactivity.

This same analytic procedure was also used to examine influence of these factors on degree of contagion experienced by participants while watching each video. To quantify emotional contagion between participants and the speakers in the video stimuli, the cardiac signals collected during video recording and viewing were divided into 15-second segments before average IBI, RMSSD, and PEP were calculated. Thus, a series of four values of each autonomic measure were obtained for the participants while viewing each video and for the speaker in that video. Previous studies on emotional contagion have used linear coefficients to establish the relationship between two individuals' physiological function (Buchanan et al., 2012; Dimitroff et al., 2017; Waters et al., 2014). In line with this work, Spearman rank-order

correlations³ between participant and speaker values for each autonomic measure were calculated and each correlation coefficients were saved as a contagion score. In all, each participant was left with 21 contagion values for IBI, RMSSD, and PEP. This allowed for a robust analysis of the possible emotional contagion effects, as the magnitude and direction of change in physiological reactivity of the participant in relation to that of the speaker are represented within the correlation. These contagion scores were then put into HLMs as an outcome variable. Finally, a third set of HLMs were run to examine the effects of video condition and the previously mentioned individual difference variables on anxiety ratings each video made by the participants.

A boundary of 3SD above or below the mean was used to check for extreme outliers in major predictor and outcome variables. Two participants were identified as extreme outliers for interoceptive accuracy and removed from analyses. All analyses were run with and without age and gender as covariates, and their inclusion had no impact on the significance of the models. HLMs were run using the *lme4* package (Bates, Mächler, Bolker, & Walker, 2015) and figures were created using the *ggplot2* (Wickham, 2016) and *sjPlot* (Lüdtke, 2021) packages.

2.3 Results

2.3.1 Cardiac reactivity

Three ANOVAs examined whether there was a significant main effect of video condition on physiological reactivity. The results show that participants' IBI did significantly differ by video condition when controlling for baseline IBI ($F_{2, 88} = 48.65, p < 0.001$). As expected, post-hoc comparisons showed that the increase in IBI while viewing Stress videos was significantly

³ Spearman correlations were used to account for the time-dependent nature of the values

greater than both Poststress and Control conditions ($p < 0.01$; see Figure 1). Participants' RMSSD also significantly differed by condition when controlling for baseline RMSSD ($F_{2, 88} = 4.98, p < 0.01$). Post-hoc comparisons showed that once again reactivity while viewing the Stress videos differed from that Control and Poststress conditions (all $p < 0.05$). However, in this case there was a lack of change in RMSSD in the Stress condition and a significant decrease in RMSSD while viewing Control and Poststress videos. Across conditions, change in RMSSD was significantly correlated with changes in IBI ($r = 0.65, p < 0.001$). In general, PEP increased while during video observation, but there was no significant difference in participants' PEP between video conditions ($F_{2, 80} = 0.86, p = 0.42$). Changes in PEP were also significantly correlated with changes in IBI across conditions ($r = 0.05, p < 0.05$) though to a much lesser degree than RMSSD. Changes in RMSSD and PEP were not correlated ($r = 0.01, p = 0.57$).

HLM analyses were then performed to examine whether individual differences in empathy or interoceptive accuracy impacted physiological reactivity across video conditions. Again, baseline autonomic values were controlled for in the models. All β s reported below are unstandardized. Contrary to what was predicted, affective empathy did not significantly predict physiological response to the video observation in any autonomic measure: IBI ($\beta = -1.08, SE = 0.91, p = 0.23$), RMSSD ($\beta = -0.25, SE = 0.20, p = 0.19$), or PEP ($\beta = 0.01, SE = 0.15, p = 0.97$). Cognitive empathy also did not significantly predict physiological responses to video observation in any autonomic measure: IBI ($\beta = -0.10, SE = 0.51, p = 0.85$), RMSSD ($\beta = 0.03, SE = 0.11, p = 0.75$), or PEP ($\beta = -0.05, SE = 0.08, p = 0.53$). Finally, interoceptive accuracy did not significantly predict physiological responses to video observation in any autonomic measure: IBI ($\beta = 2.00, SE = 20.90, p = 0.92$), RMSSD ($\beta = 5.22, SE = 4.48, p = 0.24$), PEP ($\beta = -1.56, SE = 3.29, p = 0.64$). No interactions with video condition reached significance (all $p > 0.05$).

2.3.2 Emotional contagion

Three ANOVAs examined whether there was a significant effect of video condition on degree of contagion experienced during video observation. As described above, degree of contagion is described by correlation values, thus the sign of the correlation values indicates the direction of the relationship between participant and speaker values while the magnitude indicates degree of similarity. There was a marginal effect of video condition on contagion indexed by IBI ($F_{2,88} = 2.53$, $p = 0.08$) and as indexed by RMSSD ($F_{2,88} = 2.74$, $p = 0.07$). There was a significant effect of video condition on contagion indexed by PEP ($F_{2,80} = 4.12$, $p < 0.05$). Post-hoc comparisons show that contagion values were significantly more positive (indicating participant and speaker values trending in the same direction) for Poststress videos compared to Stress ($p < 0.05$; see Figure 2) but no other comparisons were significant.

HLM analyses were then performed to examine whether individual differences in empathy or interoceptive accuracy impacted degree of contagion experienced across video conditions. For IBI-indexed contagion scores, affective empathy showed a marginal effect ($\beta = -0.01$, $SE = 0.00$, $p = 0.07$), while neither cognitive empathy ($\beta = -0.10$, $SE = 0.51$, $p = 0.25$) nor interoceptive accuracy ($\beta = -0.04$, $SE = 0.09$, $p = 0.67$) had a significant effect. For RMSSD-indexed contagion, no individual difference factors had a significant effect on degree of contagion: affective empathy ($\beta = -0.00$, $SE = 0.00$, $p = 0.92$), cognitive empathy ($\beta = 0.00$, $SE = 0.00$, $p = 0.61$), or interoceptive accuracy ($\beta = 0.06$, $SE = 0.09$, $p = 0.52$). For PEP-indexed contagion scores, affective empathy showed a marginal effect ($\beta = 0.01$, $SE = 0.00$, $p = 0.08$) and cognitive empathy had no significant effect ($\beta = -0.00$, $SE = 0.00$, $p = 0.98$). However, interoceptive accuracy did significantly predict degree of contagion experienced in PEP ($\beta =$

0.24, SE = 0.10, $p < 0.05$) such that lower interoceptive accuracy values showed more negative contagion scores (see Figure 3). Negative scores indicate a negative correlation, meaning that participant and speaker PEP trended in opposite directions. No interactions with video condition reached significance (all $ps > 0.05$)

2.3.3 Anxiety ratings

A one-way ANOVA examined whether there was a significant effect of video condition on ratings of speaker anxiety. Anxiety ratings did significantly differ by condition ($F_{2,91} = 132.70$, $p < 0.001$) in the manner expected such that participants rated greater anxiety for speakers in Stress videos than Poststress, and in turn greater anxiety for Poststress than Control (see Figure 4). Post-hoc pairwise comparisons revealed that, contrary to what was predicted, anxiety ratings were not significantly predicted by either affective ($\beta = -0.14$, SE = 0.20, $p = 0.48$) or cognitive empathy ($\beta = -0.03$, SE = 0.11, $p = 0.77$). Interoceptive accuracy had a marginally significant effect on anxiety ratings ($\beta = 7.64$, SE = 4.18, $p = 0.07$) such that higher interoceptive accuracy corresponded to higher anxiety ratings across conditions (see Figure 5). No interactions with video condition reached significance (all $ps > 0.05$).

2.4 Discussion

Emotional contagion is a key component of empathy that contributes to emotional understanding and appropriate responses during social interaction (Hatfield et al., 1994; Leiberg & Anders, 2006). Past research has established that emotional contagion can be observed on a psychophysiological level (Buchanan et al., 2012; Engert et al., 2014). However, the ways in which different psychophysiological factors contribute to understanding of others' emotions is

not fully understood. The supposition that individual differences in empathy depend both on the ability to understand one's own emotions and to maintain the self-other distinction (Tajadura-Jiménez & Tsakiris, 2014) indicates a role for interoception to contribute to emotional understanding. Through the measure of autonomic nervous system activity, dispositional empathy, and interoceptive accuracy, this study assessed individual differences in the response to distress in others.

When examining physiological reactivity to the observation of others' distress, participants experienced the greatest increase in IBI while viewing Stress videos, as predicted. This increase in IBI indicates cardiac deceleration and is consistent with a passive stress or orienting response, as previous work has shown (Dimitroff et al., 2017; Graham & Clifton, 1966). When looking at RMSSD data, observers experienced the lowest reactivity while viewing Stress videos. Participants experienced a significant decrease in RMSSD while viewing Poststress and Control videos, which reflects a decrease in parasympathetic cardiac control. Though this result was not predicted, the changes in RMSSD were correlated with the changes observed for IBI. Finally, PEP increased in general during video viewing, suggesting a drop in sympathetic cardiac control, but this increase was not different between conditions. Thus, while viewing Stress videos participants experienced a decrease in sympathetic cardiac control and no change in parasympathetic cardiac control; the interaction of these effects would suggest a resulting cardiac deceleration, just as was observed. Conversely in the Poststress and Control conditions, participants showed a decrease in cardiac control and a decrease in parasympathetic cardiac control; as there was no significant change in IBI for these conditions, the co-inhibition of both autonomic branches makes sense.

In addition to the participants' individual physiological reactivity, this study examined the correlation between their responses and those of the speakers in each video. The degree of emotional contagion experienced during video observation was not significantly impacted by video condition when contagion was indexed with either IBI or RMSSD. However, there was a significant difference in degree of contagion indexed with PEP, where participants had positive contagion scores for Poststress videos and negative contagion scores for Stress and Control videos. This suggests that while viewing Poststress videos, participants experienced a change in PEP in the same direction as that of the speaker, while for the Stress and Control videos any shift in PEP was in the opposite direction from the speaker. When further exploring contagion scores indexed with PEP, it was shown that individual differences in interoceptive accuracy predicted emotional contagion across conditions such that lower interoceptive accuracy was associated with more negative contagion scores, again indicating that the participant and speaker PEP values trended in opposite directions. The interpretability of this finding is somewhat limited, but one possible explanation could be that individuals who have higher interoceptive accuracy and thus a greater awareness of their own physiological function will be less susceptible to shifts in physiology associated with emotional contagion. Contrary to our predictions, degree of emotional contagion was not associated significantly with cognitive empathy, and only marginally with affective empathy.

Finally, emotional appraisal of speaker anxiety differed significantly by video condition. As predicted, participants rated speakers in Stress videos as significantly more anxious than those in Poststress videos, who in turn were rated as more anxious than those in Control videos. Contrary to what was predicted, anxiety ratings were not significantly predicted by either affective or cognitive empathy. However, there was a marginal effect of interoceptive accuracy

on emotional appraisal of anxiety for the speakers in the videos. Across all conditions, participants with higher interoceptive accuracy gave higher anxiety ratings. While this is a marginal effect, it is in line with what was predicted. Because interoceptive accuracy was measured using perception of heart rate, this result could reflect the fact that individuals with high interoceptive accuracy were more aware of the changes in IBI resulting from video observation, and therefore more able to make use of that information when rating anxiety.

The primary limitation of this study was the use of video stimuli. Emotional contagion is more likely during in-person interaction than remote observation (Engert et al., 2014). Video stimuli may not implicate the aspects of empathy that are concerned with potential helping behavior since there no opportunity to engage. Additionally, the use of short video stimuli means that these results may not be generalizable for longer social interactions that are likely to occur between friends or intimate partners. However, the benefit of measuring emotional contagion in multiple contexts for each participant must somewhat offset that drawback. It was intended that adding the Poststress condition, in which speakers would be recovering from a stress response, as an intermediary tier between viewing others in distress and no stress at all. The utility of this condition was only partially born out in the results (seen for anxiety ratings but not consistently with autonomic measures). A secondary limitation is the use of the mental tracking method to assess cardiac interoceptive accuracy (Garfinkel et al., 2015), which has been criticized as too susceptible to preconceptions about one's heart rate (Ring, Brener, Knapp, & Mailloux, 2015). However, it has been a commonly used paradigm historically and utilized in several studies of emotion referenced above. These results do add to the existing research on emotional contagion and empathy. Future work concerning these topics may benefit from a participant dyad structure, where these constructs may be observed in a more interactive environment.

2.5 Appendix A: Figures for Chapter 2

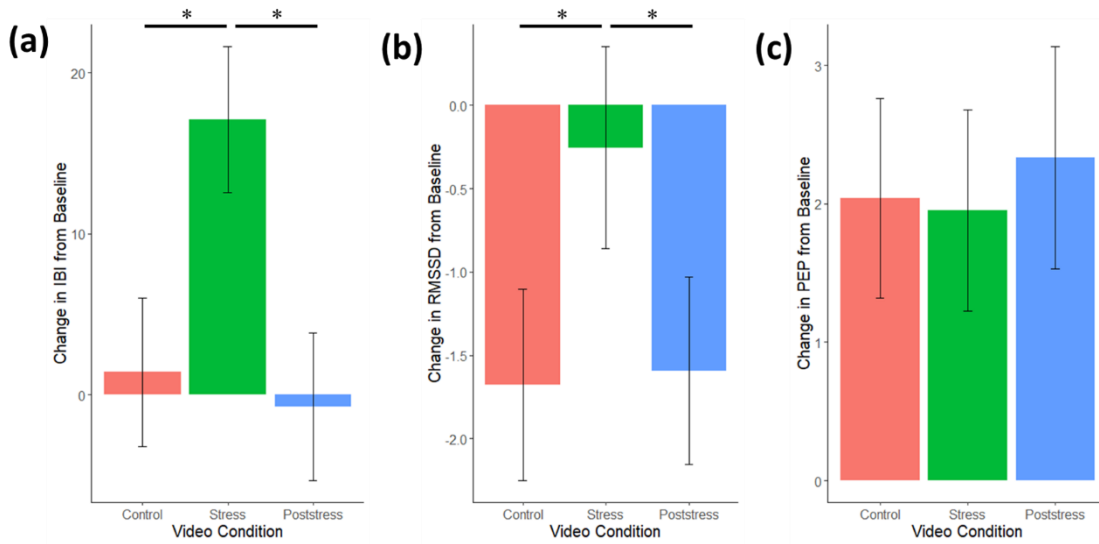


Figure 1. Effect of video condition on physiological reactivity to video observation. This effect was seen for (a) IBI and (b) RMSSD but not for (c) PEP. For IBI, watching the Stress videos produced a larger increase than Control or Poststress videos (*: $p < 0.05$). For RMSSD, watching the Stress videos produced a lesser decrease than Control or Poststress videos. Error bars show standard errors.

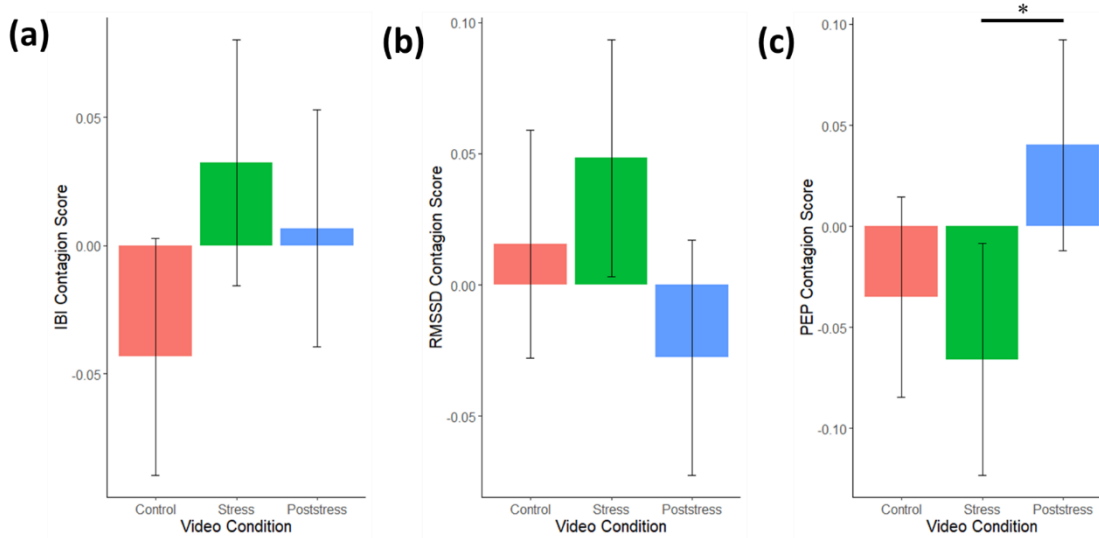


Figure 2. Effect of video condition on degree of contagion experienced during video observation. There was no effect of video condition seen for contagion scores in (a) IBI or (b) RMSSD, but there was a significant effect for (c) PEP. Contagion scores for Poststress videos were more positive than Stress videos (*: $p < 0.05$) but did not differ from Control. Error bars show standard errors.

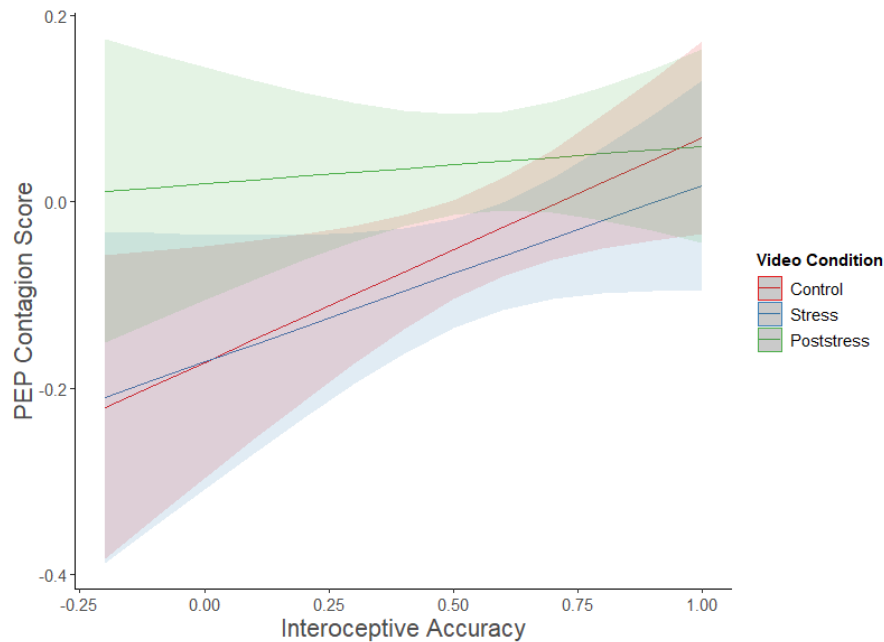


Figure 3. Effect of interoceptive accuracy on contagion scores indexed by PEP. interoceptive accuracy significantly predicted PEP contagion scores ($p < 0.05$) such that lower interoceptive accuracy corresponded to more negative contagion scores. As contagion scores are correlation values, negative scores indicate a reciprocal relationship between participant and speaker PEP. 95% confidence intervals are shown.

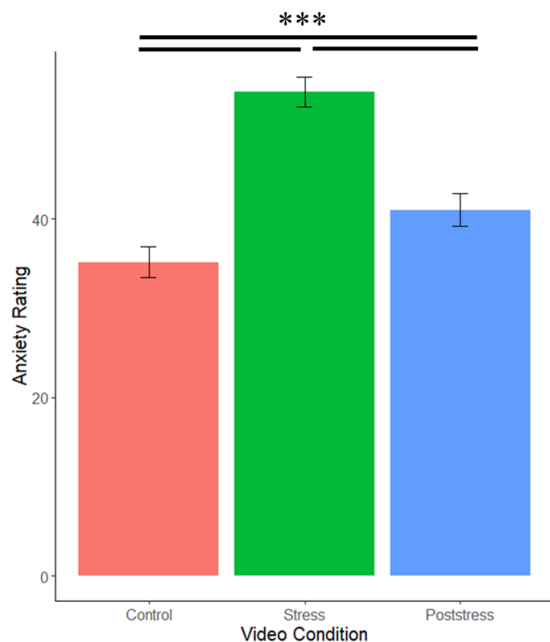


Figure 4. Effect of video condition on ratings of speaker anxiety. There was a significant main effect of video condition on anxiety ratings. All conditions significantly differed from one another (**: $p < 0.01$). As expected, anxiety ratings were greatest for Stress videos and lowest for Control videos. Error bars show standard errors.

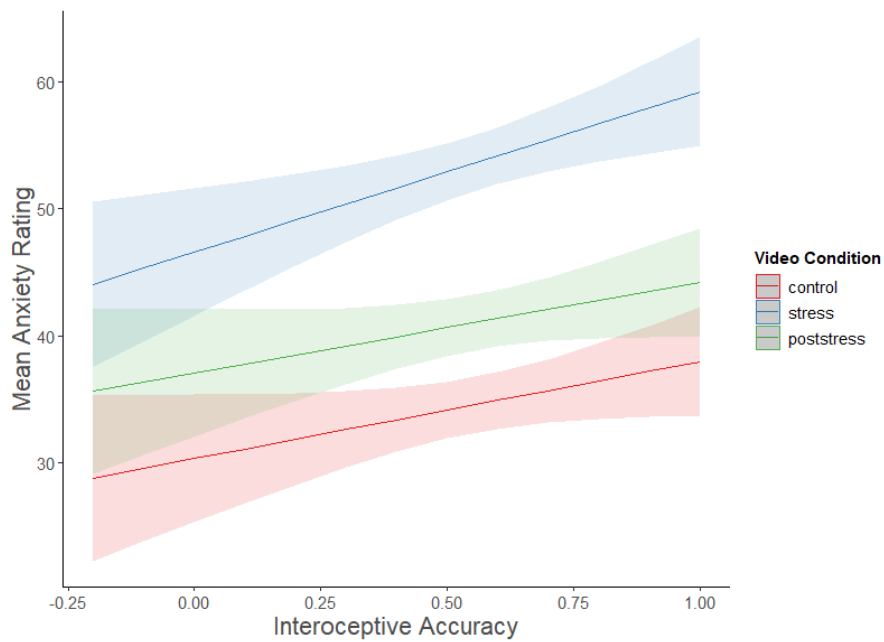


Figure 5. Effect of interoceptive accuracy on ratings of speaker anxiety by video condition. There was a marginal effect of interoceptive accuracy on anxiety ratings ($p = 0.07$) such that higher interoceptive accuracy corresponded to higher anxiety ratings across conditions. 95% confidence intervals are shown.

Chapter 3: Exposure to disease imagery and empathy for pain

3.1 Introduction

Empathy is a complex psychological phenomenon that encompasses the ability to share and understand the emotions and behavior of others (Cuff et al., 2014; Decety & Cowell, 2014; Leiberg & Anders, 2006). Individual emotional responses depend upon one's perception of events and environmental stimuli (Norman et al., 2016). During social interaction, individuals can empathize with another's emotional state even though they may not be exposed to the same event (Lamm, Meltzoff, & Decety, 2010). Understanding of how another person feels can be facilitated by one's own experience with similar events. It has been shown that viewing others in painful scenarios activates mechanisms in the brain similar to the visceral experience of pain (Lamm, Nausbaum, Meltzoff, & Decety, 2007). This suggests that individuals can empathize with another's pain due to their own understanding of what being in pain feels like. The degree to which individuals take on facets of the observed experience are related to differences in empathy. When viewing others experiencing pain, brain activity in areas implicated in the affective experience of pain (e.g. anterior cingulate cortex) was predicted by individual differences in empathy (Jackson, Meltzoff, & Decety, 2005; Singer et al., 2004).

In addition to the simulation of others' emotions based on one's own, empathy requires the representation of their subjective experience as separate from the self (Decety & Jackson, 2004) and the ability to attribute the shared emotion to its source may help determine whether empathy leads to personal distress or empathic concern (Decety & Meyer, 2008). Empathic concern specifically, as a component of empathy, helps to drive prosocial behavior (Preston & de Waal, 2002). This is supported by an evolutionary view of empathy – that it arose to aid in the caring for offspring and facilitation of cohesion within close social groups (Decety et al., 2016;

Decety & Cowell, 2014). Dispositional empathy has been shown to predict intention to help another in distress (Batson et al., 1997; Trobst et al., 1994). Furthermore, perceiving distress in others produces a pattern of brain activation reflective of aversive experiences that may prompt the motivation to help (Decety, 2011; Panksepp, 2011). Neither empathy nor its prosocial consequences occur automatically but are flexible to social context (Decety et al., 2012). For example, an individual is more likely to respond with empathy toward a close group member than a stranger (Decety & Cowell, 2014). Empathy and the provision of care in any context depends on the ability of an individual to perceive that help is needed. Pain is an effective example indicator for the need for help, because it is often accompanied by reliable cues, such as visible signs of injury (Steinkopf, 2016a). Many visible disease symptoms (e.g. redness, blemishes) may serve a similar purpose of signaling need for care from group members, in addition to the warning of possible contagion (Steinkopf, 2015). Disease and sickness present a major obstacle to survival (Murray, Prokosch, & Airington, 2019); and for social species, the provision of care from close group members presents an adaptive solution to this obstacle. It is the selection pressure from pathogen threats that may have led to the ability signal sick state as a need for help to elicit empathy and compassion (Steinkopf, 2017).

The presence of a sick individual can result in two ostensibly opposing motivations: disgust and avoidance or empathy and approach (Hart, 1990). Social and individual context aid in coordinating and compromising between these motivations, including the familiarity of the sick individual and one's own vulnerability to disease (Delton & Robertson, 2016; Steinkopf, 2016b). In the example of caring for a sick close group member, perception of disease cues may result in compassion, which then motivates helping behavior at the expense of possible infection (Goetz et al., 2010). Although prosocial behavior can be a reasonable response to pathogen cues

in certain contexts, research on the behavioral immune system largely proposes that perception of disease cues should result in a decrease in social motivation to aid pathogen avoidance.

The perception of disease cues through visual (Schaller et al., 2010) or olfactory (Olsson et al., 2014) means is commonly thought to reliably elicit disgust. The aversive feeling of disgust can then motivate avoidance of that source of disease (Leeuwen & Jaeger, 2022; Schaller, 2014). As other people present possible sources of disease, perception of disease cues can turn into social avoidance. A number of studies have shown that beliefs about one's vulnerability to disease also negatively impact social behavior, including willingness to interact (Leeuwen & Jaeger, 2022) and attraction to strangers (Sawada et al., 2018). While these studies rely on trait-like perception of disease vulnerability, a similar reduction in social motivation has been shown to follow perception of disease cues. For example, one study found that showing participants a slideshow about disease symptoms resulted in increased motor avoidance in response to images of faces (as measured by pulling a lever) (Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010). Another study found that exposure to disease relevant images (e.g. skin rashes) resulted in a lower feelings of needing to belong to the group (Sacco, Young, & Hugenberg, 2014).

These studies approach the relationship between the behavioral immune system and social motivation from the side of concerns about disease. However, we know that the need for social interaction can produce as strong a motivation as the need to avoid pathogens (Kramer & Bressan, 2021). Comparatively little work has gone into examining the circumstances in which disease cues do not limit an individual's social motivation. It is possible that with the specific context of empathy and helping behavior, exposure to disease cues may prompt an individual to be empathic and motivated to provide care. In a context that poses little risk of actual infection to

an individual, the benefit of helping and promoting social connection could motivate prosocial behavior over avoidance.

It is also unclear whether the social impact of the behavioral immune system carries over into perception of non-disease-related affective content. For several decades, researchers have utilized a variant of the traditional Stroop task to examine shifts in attention to affective stimuli. Individuals are slower to name the color that affectively-valenced words are written in over neutral words, be they threat-related (McKenna & Sharma, 1995), relevant to the clinical condition of the individual (Cisler et al., 2011; Williams, Mathews, & MacLeod, 1996), or simply of emotional relevance (Arioli, Basso, Poggi, & Canessa, 2021; Ben-Haim et al., 2016; Dresler, Mériaux, Heekeren, & Van Der Meer, 2009). This delay in color-naming, referred to as the emotional Stroop effect, is more prominent in individuals who are highly anxious (de Ruiter & Brosschot, 1994; Dresler et al., 2009; Phaf & Kan, 2007). Research on the emotional Stroop effect has been used to show that attention to affective content is sensitive to context and motivation (S. Cacioppo, Balogh, & Cacioppo, 2015a; Montalan et al., 2011; Segerstrom, 2001). However, it has not been examined whether threat of disease specifically will produce this effect. If exposure to disease cues is perceived as a threat, then attention to affective content should increase and result in an emotional Stroop effect. The emotional Stroop task therefore provides a behavioral means by which to examine the impact of exposure to disease cues on affective perception.

3.1.1 The current work

The present study examines how exposure to disease imagery affects empathic judgements and attention to affective content. This study extends the current literature

surrounding the behavioral immune system and its impact on social motivation by testing whether the exposure to disease cues will influence empathic judgements typically associated with helping behavior. Participants were asked to make empathic judgements about pain in individuals who did not present a risk of infection. In this context, it was predicted that individuals who viewed Disease images (compared to Neutral, non-disease-related images) would perceive the pain of others as more intense and report greater compassion for those in pain. This study also explored whether general attention to affective content is affected by exposure to disease imagery. On the premise that disease cues are associated with pathogen threat, it was predicted that participants exposed to disease imagery would show greater attentional interference in response to social stimuli. Finally, it was predicted that any observed effects would be more prominent in individuals high in affective empathy and less prominent in individuals with high perceived vulnerability to disease or high pathogen disgust sensitivity.

3.2 Methods

3.2.1 Participants

126 adults living in the US were recruited via Amazon Mechanical Turk and received \$5 for their participation. Due to missing data for at least one behavioral task, three participants were excluded. One additional participant was found to be an outlier for age and removed from the analysis. All reported analyses were performed on the remaining 122 participants (51 women, 93 Caucasian, $M_{\text{age}} = 38.75$ years, $SD_{\text{age}} = 10.00$ years). All participants were fluent in English. Colorblind individuals were restricted from participation due to the requirements of the emotional Stroop task. This study was approved by the University of Chicago's Institutional Review Board.

3.2.2 Procedure

Participants were randomly assigned to either the experimental (Disease; $N = 63$) or control (Neutral; $N = 59$) condition. All participants began the study by completing demographics questions and a set of standard psychological questionnaires including the Questionnaire of Cognitive and Affective Empathy (QCAE) (Reniers et al., 2011), the Perceived Vulnerability to Disease Scale (PVD) (Duncan, Schaller, & Park, 2009), the pathogen disgust subscale of the Three Domains of Disgust Scale (Tybur, Lieberman, & Griskevicius, 2009). Participants were then told they would be rating images for use in a future study as a cover for the experimental manipulation.

For the experimental manipulation, participants were shown a series of twelve images. Each image was displayed for six seconds, after which participants rated the image on positivity and negativity simultaneously by selecting a square on a five-by-five bivariate evaluative space grid (see Appendix D) (J. T. Larsen, Norris, McGraw, Hawkley, & Cacioppo, 2009) as well as on emotional arousal and disgust, each on a nine-point Likert-type scale. All images were chosen from the International Affective Picture System (IAPS) (Lang, Bradley, & Cuthbert, 1997). In the Disease condition, images were identified as containing disease-relevant cues (e.g. pus) and had been previously shown to elicit disgust in viewers (Stevenson, Case, & Oaten, 2011; Stevenson et al., 2012). In the Neutral condition, images were identified as having no disease-relevant content and chosen based on the normative valence ratings (scale 1-9) available for IAPS images to have as close to a neutral valence possible ($M = 5.09/9$). See Figure 6 for example images or Appendix E for complete list. Immediately following image exposure and

ratings participants completed an empathy for pain task and an emotional Stroop task in counterbalanced order.

In the empathy for pain task participants shown images of hands either being stabbed with a needle (Pain) or touched with a cotton swab (Control) at various locations. Images were borrowed with permission from (Lamm, Meltzoff, & Decety, 2010; see *Figure 2* for example stimuli). Following each image participants were asked to rate the perceived pain intensity as well as the amount of compassion they felt for the owner of the hand in the image. Pain intensity was rated by answering the question “How much pain is this person experiencing?” on a 9-point scale from 1 = “No pain at all” to 9 = “The worst pain imaginable.” Compassion was rated by answering the question “How sorry do you feel for this person?” on a 9-point scale from 1 = “Not sorry at all” to 9 = “Extremely sorry.” Sixteen Pain and sixteen Control images were displayed in a randomized order.

In the emotional Stroop task, participants were asked to identify the color in which words of various categories were displayed as a measure of attentional interference from affective content (Williams et al., 1996). Positive and Negative words were chosen in both Emotional and Social categories, along with a fifth category of Neutral words as a control. Words in each category were previously validated on Amazon Mechanical Turk (Faig et al., unpublished data; see Appendix) and matched within relevant categories for positivity and negativity, and across categories for arousal and frequency of use as recommended by previous work (Dresler, Mériaux, Heekeren, & Van Der Meer, 2009; Larsen, Mercer, & Balota, 2006). Words originated from previous studies using an emotional Stroop task (S. Cacioppo, Balogh, & Cacioppo, 2015b) as well as the Affective Norms for English Words database (Bradley & Lang, 1999). Each category served as a separate block and blocks were displayed in a fixed order as suggested by Ben-Haim

et al. (2016) so as to control the sustained effects of previous blocks. The color of each word was randomized (red, yellow, green, or blue).

The behavioral task portion of this online protocol were run using the PsyToolkit software (Stoet, 2010, 2017).

3.2.3 Data analysis plan

ANOVAs were run to ensure there were no significant differences between groups assigned to the Disease and Neutral conditions. Results from the empathy for pain task were analyzed with HLMs including experimental condition (Disease/Neutral) and image type (Pain/Control) as fixed factors, subject and image type as random factors, and ratings of pain intensity and compassion as dependent variables to examine whether exposure to disease imagery affects empathic judgements. Planned comparisons were run between experimental conditions within Pain and Control images, as the effects are expected to be seen within the Pain images. HLMs were also run including affective and cognitive empathy, perceived vulnerability to disease (PVD), and pathogen disgust as fixed predictors to examine whether individual difference factors influence empathic judgements of pain. An ANOVA was run as a validity check on the emotional Stroop task to ensure there were no significant differences in hit rate (correct color identification) between blocks. Incorrect trials were removed from subsequent analyses. Reaction time for color identification was log10 transformed for analyses. A second ANOVA was run to determine whether there was a main effect of word category on reaction time scores. Planned comparisons were run between affective categories and Neutral words, as well as between Positive and Negative Words for Social and Emotional categories. Reaction time scores were then further analyzed in an HLM including experimental condition and word

category as a fixed factor and subject as a random factor to examine whether exposure to disease imagery impacts attention to affective content. HLMs were also run including the individual difference factors as fixed predictors of reaction time to determine their effects on attention.

A boundary of 3SD above or below the mean was used to check for outliers in predictor and outcome variables. One participant was found to be an extreme outlier for age and was removed from the analysis. All analyses were run with and without age, gender, and counterbalance order (empathy for pain or emotional Stroop first) as covariates. Inclusion of these covariates had no impact on the significance of the analyses described below. Analyses were run using R (R Core Team, 2019) and RStudio (RStudio Team, 2021). HLMs were run using the *nlme* package (Pinheiro, Bates, & R Core Team, 2022) and figures were created using the *ggplot2* package (Wickham, 2016).

3.3 Results

3.3.1 Experimental manipulation

One-way ANOVAs confirmed there was a significant difference in the ratings of image stimuli for the experimental manipulation between the Disease and Neutral conditions (see Figure 8). Disease images were rated as less positive ($F_{1,120} = 33.56, p < 0.001$), more negative ($F_{1,120} = 277.5, p < 0.001$), more arousing ($F_{1,120} = 109.5, p < 0.001$), and more disgusting ($F_{1,120} = 330.8, p < 0.001$) than Neutral images.

3.3.2 Empathy for pain

3.3.2.1 Pain intensity

A HLM revealed that there was a significant main effect of image type when rating pain intensity ($\beta = -2.66$, $SE = 0.17$, $p < 0.001$). As expected, participants rating significantly higher pain for Pain images than Control images. There was no significant main effect of experimental condition when rating pain intensity across image type ($\beta = -0.32$, $SE = 0.22$, $p = 0.15$). However, the planned comparison between experimental conditions within ratings of Pain images revealed a significant difference ($p < 0.01$) such that participants who were exposed to Disease images gave significantly higher ratings of pain intensity than those exposed to Neutral images (see Figure 9). There was no difference between experimental conditions within ratings of control images ($p = 0.67$). Further HLM analyses were performed to examine whether individual difference factors would predict perception of pain intensity across image type and experimental condition. Neither affective ($\beta = -0.01$, $SE = 0.19$, $p = 0.50$) nor cognitive ($\beta = -0.01$, $SE = 0.01$, $p = 0.34$) empathy had a significant main effect on ratings of pain intensity. PVD also did not have a significant effect on ratings of pain intensity ($\beta = 0.00$, $SE = 0.01$, $p = 0.66$). However, pathogen disgust did significantly predict ratings of pain intensity ($\beta = 0.04$, $SE = 0.02$, $p < 0.05$) such that higher pathogen disgust corresponds to greater ratings of pain intensity. There was also a marginal interaction between pathogen disgust and image type ($\beta = -0.03$, $SE = 0.01$, $p = 0.07$) such that the effect of pathogen disgust was stronger for Pain images than Control (see Figure 10). Pathogen disgust and experimental condition did not significantly interact ($\beta = -0.00$, $SE = 0.02$, $p = 0.91$).

3.3.2.2 Compassion

A HLM revealed that there was a significant main effect of image type when rating compassion ($\beta = -2.20$, $SE = 0.22$, $p < 0.001$). Participants reported feeling greater compassion in

response to Pain images than Control images. There was no significant main effect of experimental condition when rating compassion across image type ($\beta = -0.11$, $SE = 0.26$, $p = 0.65$), and post-hoc comparisons revealed no significant differences between experiment conditions for either Pain or Control images ($ps > 0.05$; see Figure 11). Additional HLM analyses were performed to examine whether individual difference factors impact ratings of compassion across image type and experimental condition. There was a main effect of affective empathy on ratings of compassion ($\beta = 0.03$, $SE = 0.02$, $p < 0.05$) as well as a significant interaction with image type ($\beta = -0.06$, $SE = 0.02$, $p < 0.01$) such that individuals higher in affective empathy reported greater compassion only for Pain images (see Figure 12). There was no significant interaction between affective empathy and experimental condition ($\beta = 0.03$, $SE = 0.03$, $p = 0.30$). In contrast, there was no significant main effect of cognitive empathy on ratings of compassion ($\beta = 0.00$, $SE = 0.01$, $p = 0.86$). Similarly, there was no main effect of PVD on ratings of compassion ($\beta = 0.01$, $SE = 0.01$, $p = 0.15$). Finally, there was a significant main effect of pathogen disgust on ratings of compassion ($\beta = 0.04$, $SE = 0.01$, $p < 0.001$) such that higher pathogen disgust corresponds to greater ratings of compassion (see Figure 13). There was no significant interaction with either image type or experimental condition ($ps > 0.05$).

3.3.3 Emotional Stroop

Hit rate, the proportion of trials in which the correct color was named within the allotted time, was calculated for each block of the emotional Stroop task. A repeated-measures ANOVA was run confirmed that there was no significant effect of word category on hit rate ($F_{4,121} = 1.62$, $p = 0.17$). Incorrect trials were then excluded from the analysis on reaction time scores, which indexed attentional bias such that higher scores indicated greater attention. A second ANOVA

revealed that there was a main effect of word category on reaction time scores ($F_{4,121} = 44.94$, $p < 0.001$). However, pairwise comparisons showed that only reaction time scores for Positive Emotional words significantly differed from Neutral words ($p < 0.001$; see *Figure 14*). Reaction times were slower for Positive Emotional words, indicating greater attentional interference. Reaction times for Positive Emotional words were also significantly greater than for Negative Emotional words ($p < 0.001$). This result was not expected, but it is also not generally inconsistent with the mixed results found in studies of the emotional Stroop effect. Positive and Negative Social words did not significantly differ ($p = 0.34$).

A HLM showed that there was a main effect of experimental condition on reaction time scores ($\beta = 0.03$, $SE = 0.02$, $p < 0.05$) across most word categories (see *Figure 15*). Contrary to what was predicted, reaction times were faster for individuals who had been exposed to Disease images compared to Neutral images. This would seem to indicate that Disease imagery reduced attentional bias. The interaction between experimental conditions and word category was not significant ($\beta = -0.05$, $SE = 0.01$, $p = 0.72$). Additional HLM analyses were performed to examine whether individual difference factors impact reaction times across word categories. There was no main effect of affective or cognitive empathy, PVD, or pathogen disgust on reaction time, and no two-way interactions reached significance (all $ps > 0.05$).

3.4 Discussion

The behavioral immune system and its impact on social behavior have been growing in popularity as a research topic in the past two decades (Ackerman et al., 2018). Much of this research has shown that activation of the behavioral immune system leads to decreased interest in social interaction and avoidance of others as possible sources of pathogens (Kramer &

Bressan, 2021; Schaller et al., 2010). If the behavioral immune system only relied on social avoidance to prevent disease transmission between individuals, one would expect to see a corresponding decrease in prosocial motivation with perception of any disease cues. However, work by Steinkopf (2015, 2016a, 2017) suggests disease cues signal the need for care from conspecifics in addition to serving as a warning of pathogen risk, and that in certain contexts the perception of these cues may motivate helping behavior rather than social avoidance. For example, if a situation poses little risk of infection to the individual, then helping carries a social benefit that outweighs the cost. This study explores whether viewing disease-relevant stimuli impacts empathy as a specific social phenomenon that serves, in part, to coordinate prosocial understanding and helping behavior (Decety & Meyer, 2008). The results from this adult population show that empathic judgements during an empathy for pain task were affected by exposure to disease imagery.

When viewing images of others in painful scenarios, participants who had been exposed to Disease images gave significantly greater appraisals of pain intensity than participants exposed to Neutral Images. In line with what was predicted, exposure to disease imagery increased empathic judgements, but only for Pain images. It is informative that this effect was not observed for Control images. The Control images consisted of non-painful scenarios in which there are no cues to indicate the need for helping behavior. Thus, these results may indicate that exposure to disease cues alters empathic judgements in a prosocial manner only when helping behavior may be needed. In line with this appraisal of context, participants rated significantly greater compassion in response to Pain images over Control images, indicating that Control images are not perceived with the same empathic lens. Furthermore, there was a significant association between individual differences in pathogen disgust and ratings of pain

intensity such that those who reported greater pathogen disgust sensitivity also provided greater ratings. There was also a marginal association between pathogen disgust and ratings of compassion in the same direction. One possible explanation for this relationship is that individuals higher in disgust sensitivity experienced greater arousal in response to pain cues. This arousal may elevate personal distress and empathic concern together resulting in an increase in empathic judgements. Though not predicted, the observed effects of pathogen disgust further support empathy for pain as a context in which the behavioral immune system may motivate prosocial and helping behavior over avoidance. Interestingly, neither affective nor cognitive empathy predicted ratings of pain intensity on the empathy for pain task. However, as predicted, affective empathy did have a significant positive effect on ratings of compassion such that greater affective empathy corresponded to greater compassion ratings. Once again, this relationship was only observed for Pain images, not Control, in line with the model of compassion as an affective response to distress in others (Goetz et al., 2010). In the Control images, there were no distress cues to be perceived and thus nothing for affective empathy to amplify.

A secondary interest of this study was to examine whether disease imagery would impact only appraisal of and compassion towards pain in the context of empathy, or if this the effect would be seen more broadly on perception of affective content. Thus, this study utilized an emotional Stroop task, which has been used to assess attentional bias towards affective content (Ben-Haim et al., 2016; S. Cacioppo et al., 2015b; de Ruiter & Brosschot, 1994). The results from this task revealed a significant main effect of experimental condition on reaction time scores. Across word category participants who were exposed to Disease images showed faster reaction times compared to those exposed to Neutral images, which runs opposite to what was

predicted. It was predicted that exposure to disease imagery would be perceived as a threat, making participants more susceptible to attentional interference from affective content. However, the general decrease in reaction time following exposure to disease imagery indicates a decrease in attention, suggesting that when concerns about disease are salient, attentional interference from affective content is reduced. There is little research on the behavioral immune system and non-disease-related perception. However, one study using event-related potentials to measure attention suggested that compared to anger or fear, disgust diverts attention to aid in avoidance (Zhang, Liu, Wang, Ai, & Luo, 2017). It is possible that the Disease images in the experimental manipulation elicited enough disgust to result in the observed attentional shift during the emotional Stroop. When combined with the effect from the empathy for pain task that indicates Disease images could increase prosocial judgements in specific context, this apparent attentional avoidance towards affective and social content alike paints a complex picture. Together the results from this study call for additional research into the impact of shifting motivations on social and affective perception.

The nonsignificant difference between reaction time scores for affective versus Neutral words in the emotional Stroop task presents a slight concern for the interpretability of those results. However, previous studies have established that the emotional Stroop effect can be variable when measured in an empirical setting (Ben-Haim et al., 2016). Additionally, there is a deficit of studies examining the emotional Stroop task following experimental interventions. This work is also limited by options for behavioral data collection in an online format. The use of Amazon Mechanical Turk allows for recruitment of a wider variety of adult participants, but it also limits the control over participant compliance and attention. Furthermore, in a laboratory-based study it would be possible to provide more robust stimuli to activate disgust and the

behavioral immune system (e.g. odors) or stimulate the classical immune response to examine whether the effects differ from those obtained with disease images. Finally, it should be noted that these data were collected early in 2022 when most US states had returned to in-person activities in the wake of the COVID-19 pandemic. Still, it is possible that the ongoing news of the pandemic would influence the efficacy of the disease-related experimental manipulation so it will be important to replicate these findings in the future.

3.5 Appendix B: Figures for Chapter 3

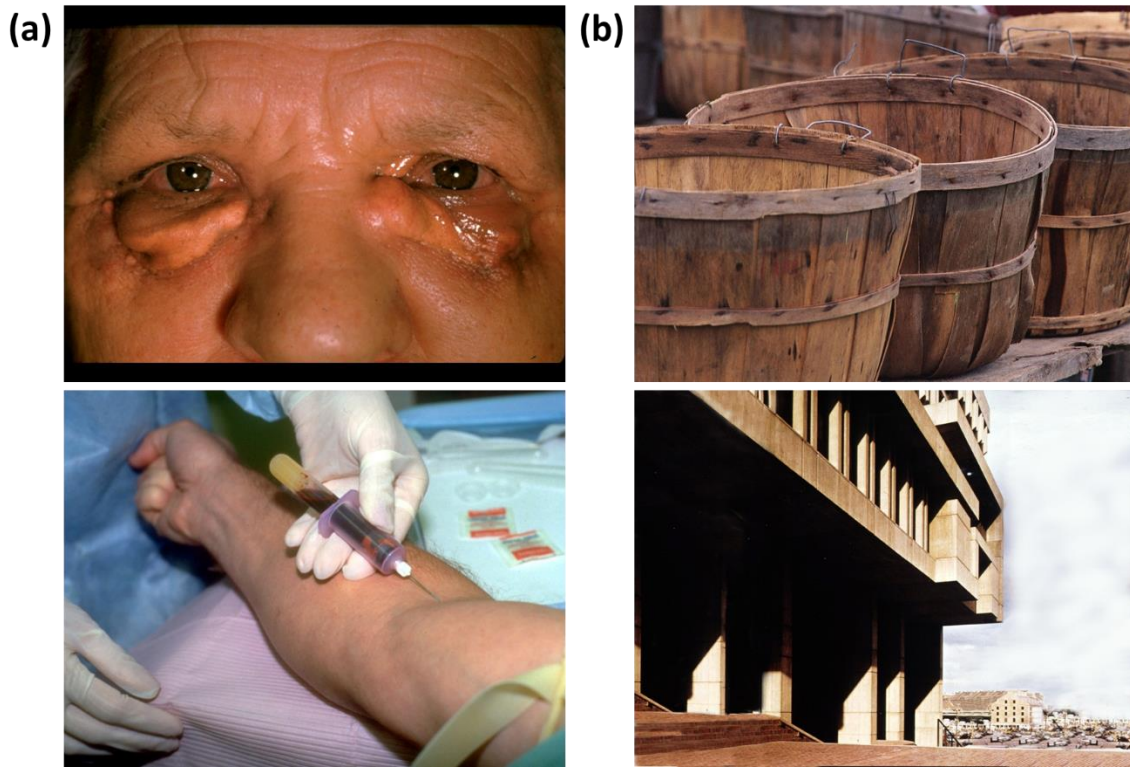


Figure 6. Example images used for the experimental manipulation. (a) The experimental condition (Disease) consisted of twelve IAPS images depicting disease-relevant imagery. (b) The control condition (Neutral) consisted of twelve IAPS images with no disease-relevancy that were chosen for their neutral normative valence ratings.

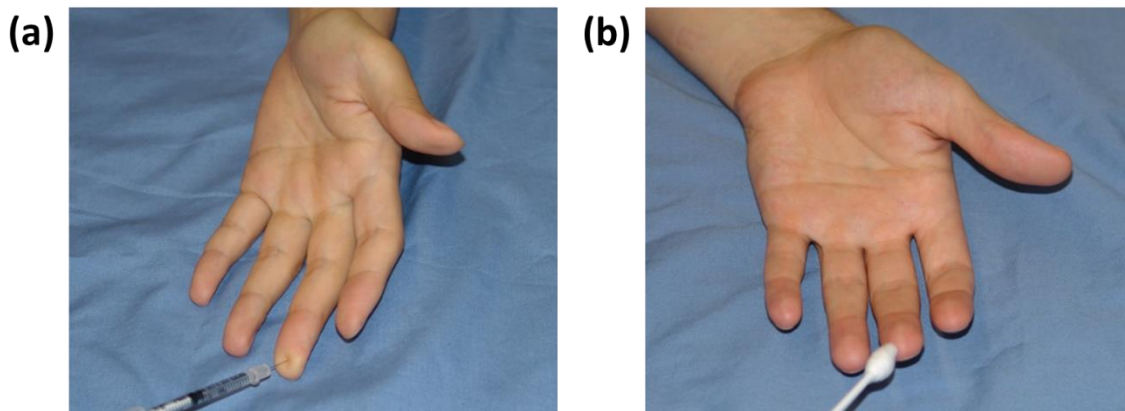


Figure 7. Example image stimuli from the empathy for pain task. (a) Sixteen Pain images depicted a White hand being stabbed with a needle at varying locations. (b) Sixteen Control images depicted a White hand being touched with a soft cotton swab at various locations matched to the Pain images. All participants saw all 32 images in a randomized order. Images reproduced with permission from (Lamm et al., 2010).

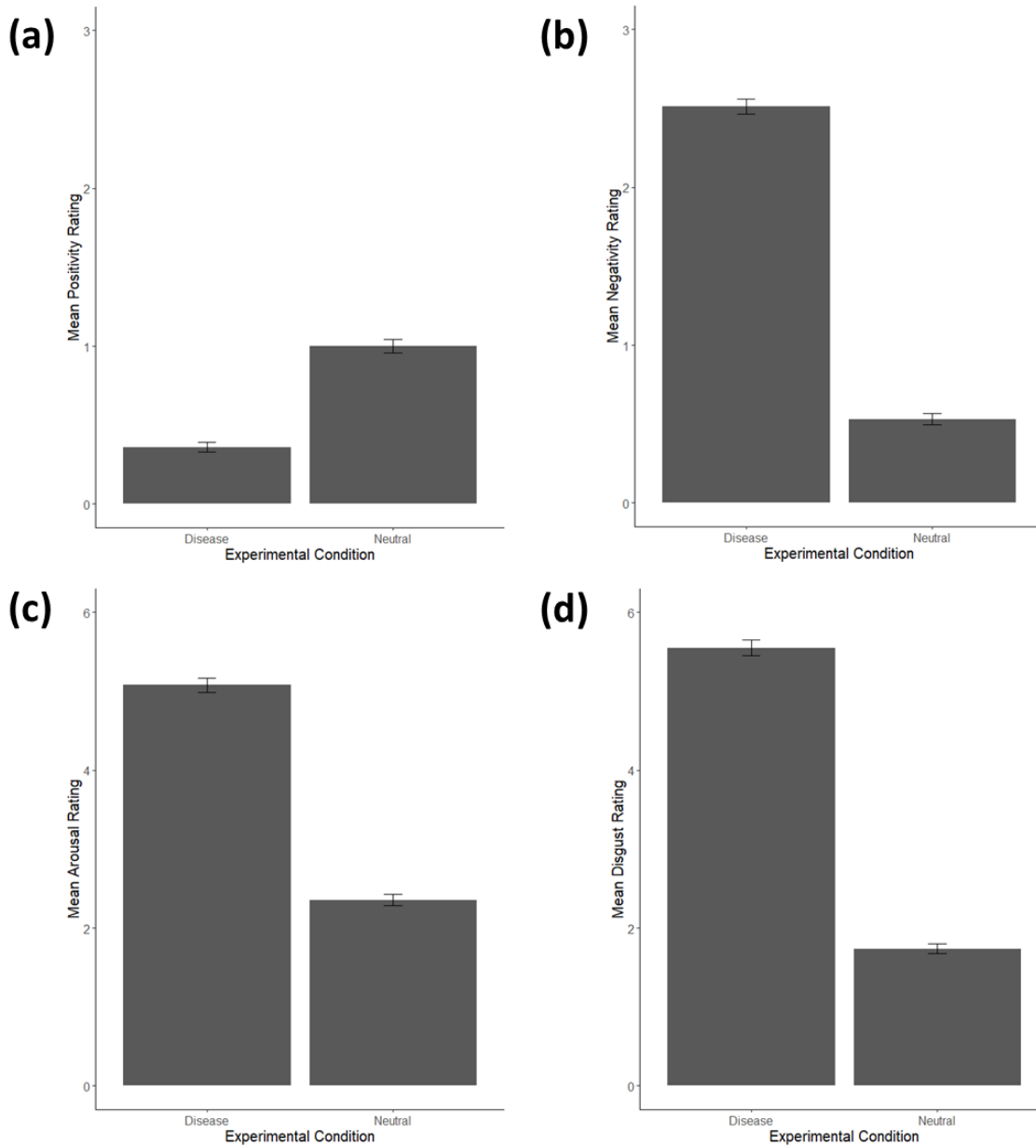


Figure 8. Ratings of (a) positivity, (b) negativity, (c) arousal, and (d) disgust for images shown during the experimental manipulation. For all ratings, the Disease condition was significantly different from the Neutral condition ($p < 0.001$). Error bars show standard errors.

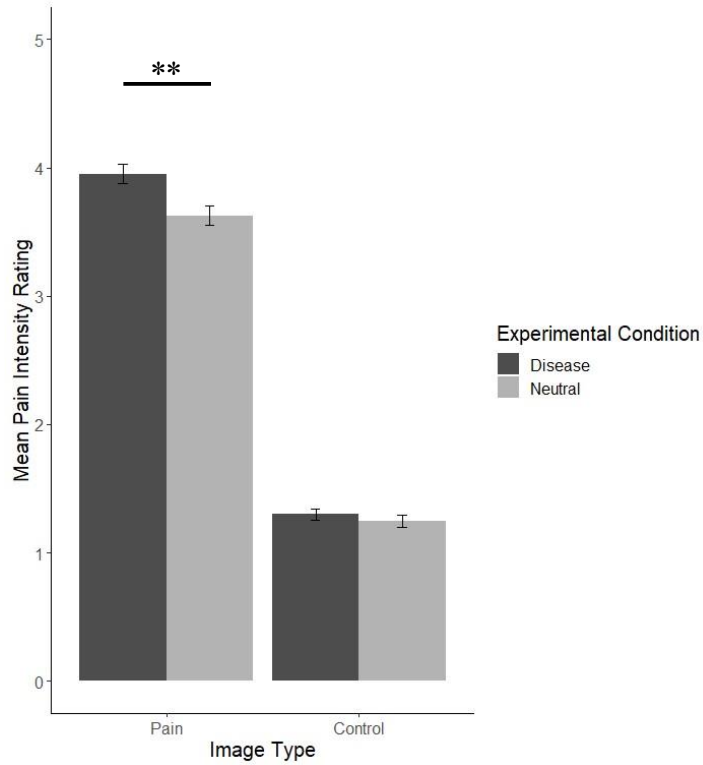


Figure 9. Ratings of pain intensity on the empathy for pain task. As expected, there was a significant main effect of image type when rating pain intensity such that Pain images received higher pain intensity ratings than Control images. When rating Pain images, participants who were exposed to Disease images rated pain intensity significantly higher than participants who were exposed to Neutral images (**: $p < 0.01$). Error bars show standard errors.

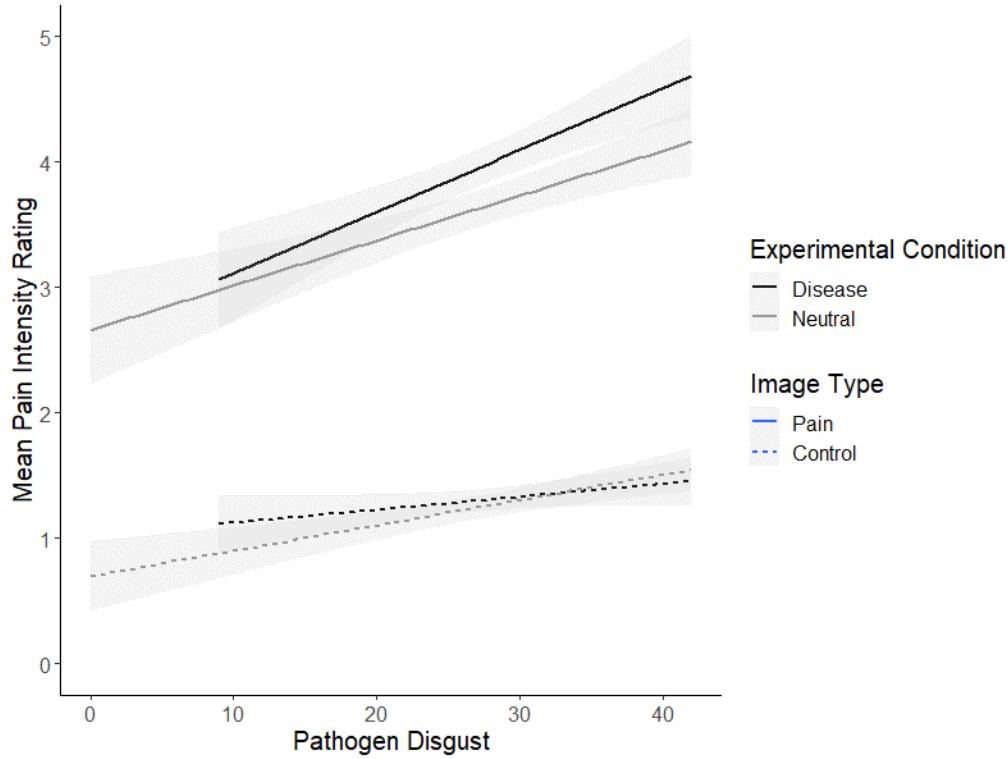


Figure 10. Individual differences in pathogen disgust significantly predicted ratings of pain intensity in the empathy for pain task ($p < 0.05$). There was a marginal interaction with image type ($p = 0.07$) such that the relationship between pathogen disgust and ratings of pain intensity are slightly stronger for Pain images. There was no significant interaction with experimental condition. 95% confidence intervals are shown.

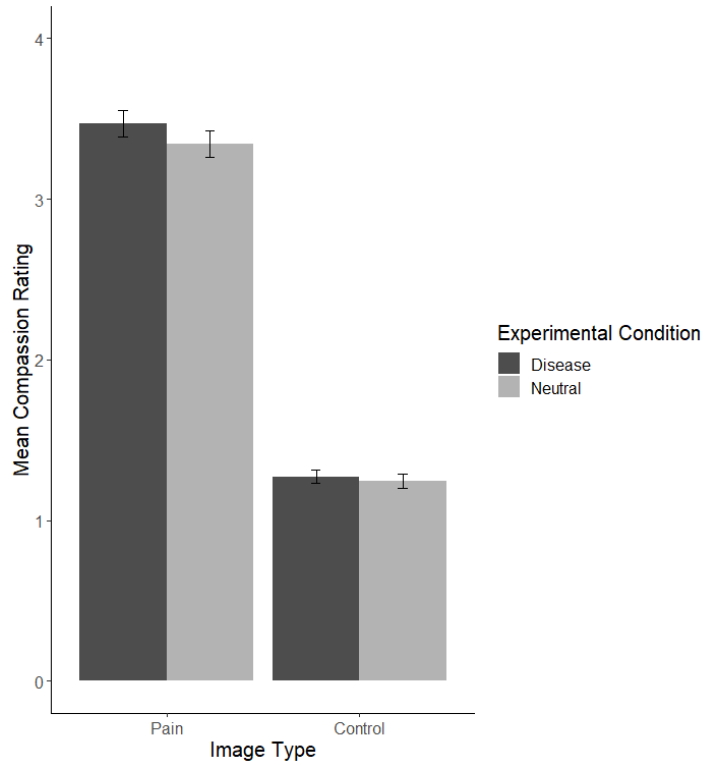


Figure 11. Ratings of compassion on the empathy for pain task. As expected, there was a significant main effect of image type when rating compassion such that Pain images received more compassion than Control images. There was no significant differences in compassion ratings after exposure to Disease images versus Neutral images. Error bars show standard errors.

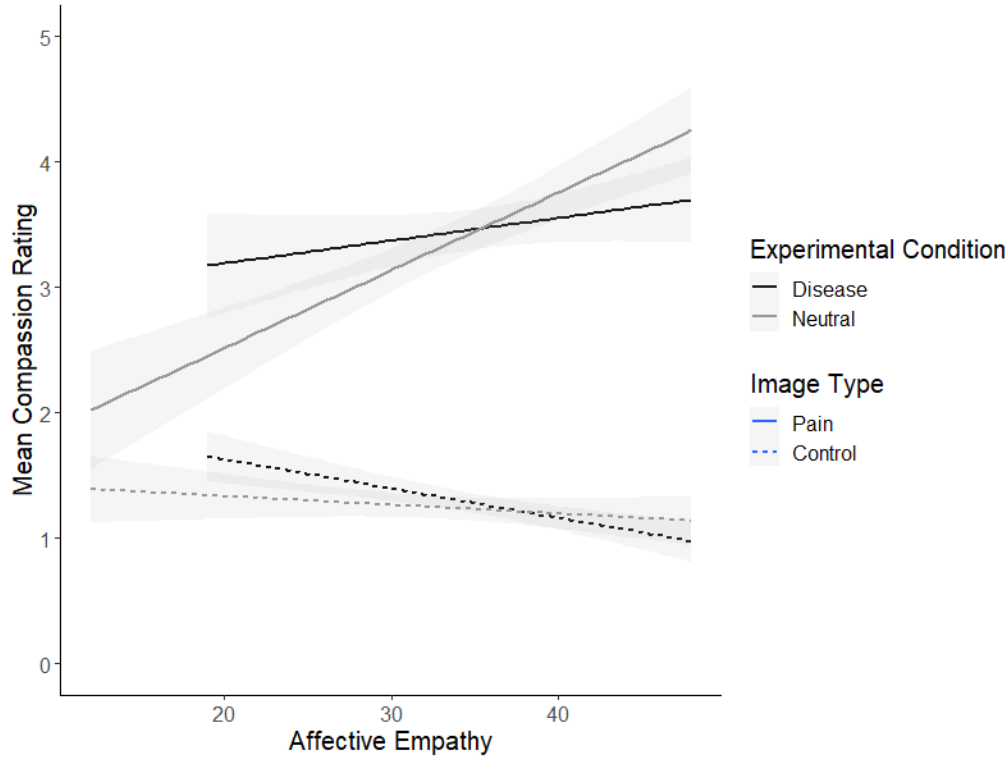


Figure 12. Individual differences in affective empathy significantly predicted ratings of compassion in the empathy for pain task ($p < 0.05$). There was a significant interaction with image type ($p < 0.01$) such that the positive relationship between affective empathy and ratings of compassion is only observed for Pain images. There was no significant interaction with experimental condition. 95% confidence intervals are shown.

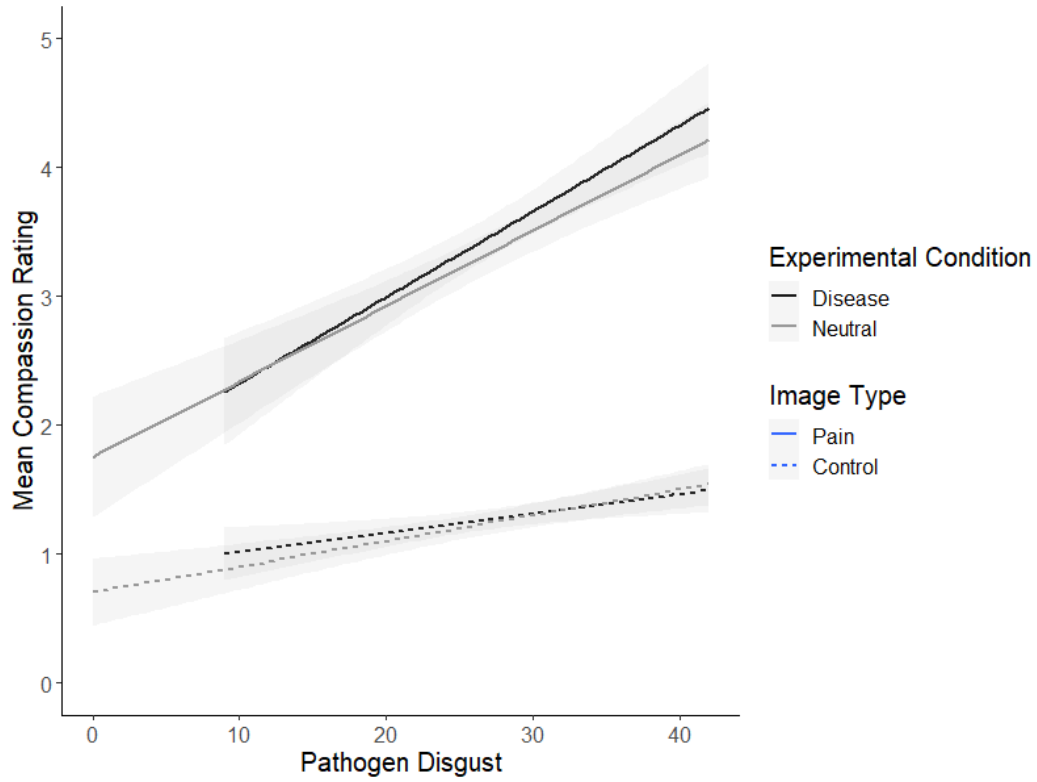


Figure 13. Individual differences in pathogen disgust significantly predicted ratings of compassion in the empathy for pain task ($p < 0.001$). There was no significant interaction with either with image type or experimental condition. 95% confidence intervals are shown.

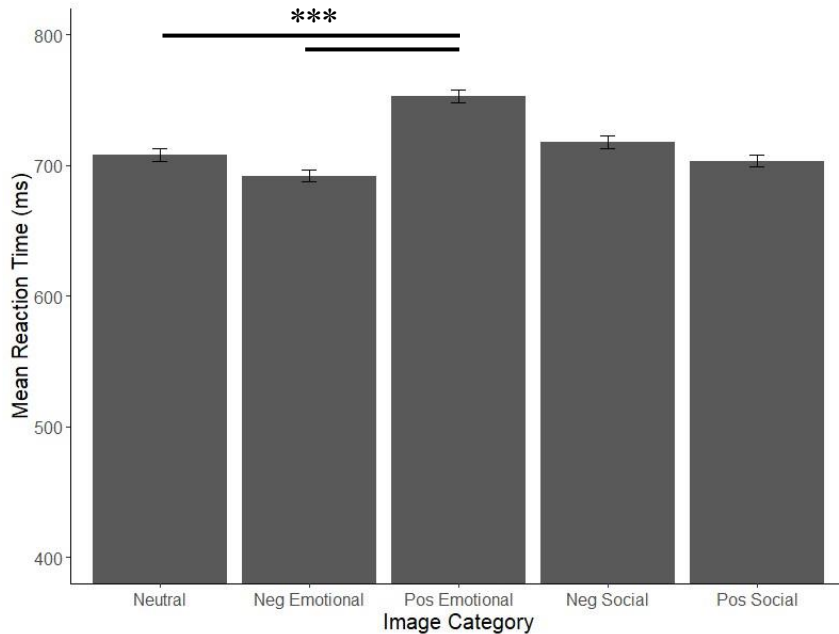


Figure 14. Reaction times on the emotional Stroop task differed significantly by word category. Only Positive Emotional words differed from Neutral words (***: $p < 0.001$). Positive and Negative Emotional words differed from each other and Positive and Negative Social words did not. Tests were performed on log10 transformed reaction times. Error bars show standard errors.

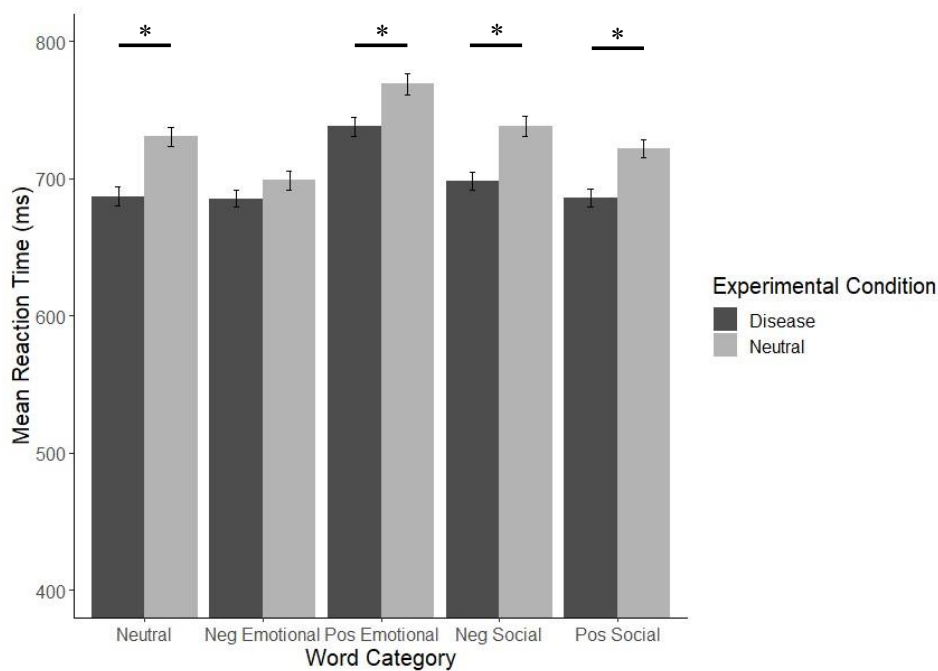


Figure 15. Experimental condition had a significant effect on reaction time in the emotional Stroop task (*: $p < 0.05$). Reaction times decreased across all categories other than Negative Emotional after viewing Disease images compared to Neutral, indicating a reduction in attentional interference counter to what was predicted. Error bars show standard errors.

Chapter 4: Loneliness and perceived vulnerability to disease

4.1 Introduction

Social species incur an elevated risk of infection through transmissible pathogens due to their close physical proximity to other members of the group (Alexander, 1974; Shakhar, 2019). The behavioral immune system helps mitigate this risk through behaviors that decrease the likelihood of both spreading and contracting contagious disease (Ackerman et al., 2018). Shifts in behavior coordinated by the behavioral immune system depend upon the individual ability to perceive and interpret disease cues within conspecifics, such as blemishes and changes in body odor (Miller & Maner, 2011; Schaller & Park, 2011). Many models of the behavioral immune system propose that the perception of disease cues will result in decreased social motivation in an effort to physically avoid infectious individuals (e.g. Park, Faulkner, & Schaller, 2003). However, it is clear that in certain contexts the perception of disease cues may in fact result in prosocial behavior. For example, if an infectious individual is part of one's close social group, one may be motivated to provide care for the individual at the expense of exposure to disease (Delton & Robertson, 2016; Hart, 1990; Kramer & Bressan, 2021). Even for situations involving strangers, individuals may show an increase in social motivation in response to disease cues if help is particularly needed (Steinkopf, 2015). The study described in Chapter 3 examined one such instance, where exposure to disease imagery resulted in increased empathy towards individuals in pain. While such examples indicate that activating the behavioral immune system does not have a one-to-one relationship to social motivation, research on the behavioral immune system has nearly exclusively focused on decreasing risk of infection through social avoidance.

The circumstances in which the behavioral immune system promotes social avoidance to prevent infection are broad and well-established in empirical work. In one study, facial images of

individuals who underwent a potent immune activation via lipopolysaccharide injection were rated as less likeable than images of the same individuals when injected with saline (Regenbogen et al., 2017). In another study, when participants were presented with a slideshow of images of disease symptoms (e.g. skin rash), their interest in social interaction significantly decreased (Sacco et al., 2014). Together these studies provide evidence that perception of disease cues promotes social avoidance. However, the avoidance of other people as possible sources of disease conflicts with the motivation to form social connections that is fundamental to social species (Baumeister & Leary, 1995). Thus, if social motivations, such as the care of a close group member, outweigh an individual's current vulnerability to disease, then it may not be beneficial for the behavioral immune system to promote social avoidance (Delton & Robertson, 2016; Steinkopf, 2016b). The balance between motivations must be flexible to what is most salient at the moment, be that avoidance of disease or maintenance of social connection.

Further evidence for the shifts in social motivation associated with the behavioral immune system comes from both experimental manipulations of disease saliency and the study of individual differences in perceived vulnerability to disease (PVD) (Schaller, 2011). Following activation of the behavioral immune system through exposure to disease-related images and text, individuals showed greater avoidance in response to images of faces, measured by the pulling of a lever away from the stimulus (Miller & Maner, 2011). Furthermore, following similar exposure individuals displayed greater attention towards and memory for images containing disease cues (Miller & Maner, 2011, 2012). A similar pattern of avoidance of faces was seen in individuals with high PVD (Mortensen et al., 2010), suggesting that trait-level concerns about vulnerability to disease are sufficient to alter social motivation, even without exposure to disease cues. In another study of healthy adults, individuals with high PVD showed reduced attraction to

strangers (Sawada et al., 2018). Some limited evidence exists to suggest a bi-directional influence of social motivation and concerns related to the behavioral immune system. When individuals were exposed to a social rejection paradigm, which decreases feelings of connection, they reported lower PVD (Sacco et al., 2014). This would suggest that when individuals recognize that social interactions are unlikely to occur, they perceive the threat of disease to decrease. Yet still, this work does not speak to how the behavioral immune system influences social motivation when the need to form connections is high. If an individual has an acute need for social interaction to bolster their relationships, then the behavioral immune system may not use avoidance as a prevention strategy.

As mentioned above, the motivation to form and maintain group bonds is vital for social species such as humans. Group living provides access to a number of benefits that increase the likelihood of survival and quality of life, including sharing of resources and access to potential mates (Alexander, 1974). Consequently, the lack of feeling of connection produces a motivation to shore up group membership (Baumeister & Leary, 1995; J. T. Cacioppo, Cacioppo, & Boomsma, 2014). In the 1980s, evidence began to mount suggesting a strong relationship between social connectedness and health such that individuals who reported lower social connection to their community suffered considerably higher rates of mortality and morbidity (House et al., 1988, 1982; Kaplan et al., 1988). Subsequent work has clearly demonstrated that individual perceptions social isolation (i.e. loneliness) predict poorer health when controlling for health behavior (Holt-Lunstad, Smith, & Layton, 2010; Luo, Hawkley, Waite, & Cacioppo, 2012). Similarly, there is strong relationship between depression and distress and individual differences in loneliness (Cacioppo et al., 2006; Jaremka, Fagundes, Peng, et al., 2013; Taylor, Taylor, Nguyen, & Chatters, 2018). Just as disgust yields aversion toward sources of pathogens,

loneliness is associated with strong aversive feelings that motivate individuals to protect the social bonds that may be at risk (Cacioppo, Hawkley, Norman, & Berntson, 2011; Eisenberger et al., 2003; MacDonald & Leary, 2005). Thus far, the study of the social impact of the behavioral immune system has focused heavily on a decrease in social motivation when concerns about disease are high. Nevertheless, there are certain contexts that can increase social motivation, in which case the behavioral immune system must decrease risk of disease transmission without utilizing avoidance. It is not well-established what the impact on the behavioral immune system and concerns about disease will be when social considerations are more chronically salient, as when individuals perceive themselves to be socially isolated.

4.1.1 The current work

The present study seeks to explore the association between PVD and loneliness and possible affective mechanisms. This study extends the current literature on affective and social correlates of the behavioral immune system beyond that of a discussion on disgust and pathogen avoidance. It was predicted that there would be a significant association between PVD and loneliness. It was predicted that this relationship would be mediated by additional affective factors, though this analysis was exploratory. Prior to the introduction of the Perceived Vulnerability to Disease Questionnaire (Duncan et al., 2009), disgust sensitivity was used as the primary index of behavioral immune system activation. Disgust aids in the integration of relevant information from one's environment to influence behavioral decision making, which may then play a part in motivational tradeoffs between the behavioral immune system and social motivation (Oaten et al., 2019; Tybur et al., 2012). However, there is not complete overlap between the constructs of disgust and PVD (Díaz, Soriano, & Beleña, 2016). Therefore other

affective mechanisms may be at play, such as perceived stress, which reflects the appraisal of possible threats in one's environment (De Castella et al., 2013; Sheldon, Tom, & Robin, 1983; Snippe, Dziak, Lanza, Nyklíček, & Wichers, 2017). Both perceived stress and pathogen disgust are predicted to be positively associated with PVD. This study also explored whether PVD and loneliness (with their associated motivations) impacted emotional appraisal. It was predicted that PVD would impact the emotional appraisal of affective imagery; specifically, higher PVD would be associated with reduced positivity ratings and greater disgust ratings for social content in images. Finally, it was predicted that loneliness would impact emotional appraisal of affective imagery as well; specifically, higher loneliness would be associated with increased negativity and arousal ratings for social content.

4.2 Methods

4.2.1 Participants

100 participants (40 women, 79 Caucasian, $M_{\text{age}} = 42.27$ years, $SD_{\text{age}} = 13.66$) were recruited via Amazon Mechanical Turk as a part of a larger study on the impact of the COVID-19 pandemic. All participants provided informed consent and were compensated \$4.50 for their time. This study was approved by the University of Chicago's Institutional Review Board.

4.2.2 Procedure

At the beginning of the study, participants were asked to rate a series of images taken from the International Affective Picture System (Lang et al., 1997) to assess emotional appraisal, as these images have been demonstrated to reliably produce affective responses (Lang, Greenwald, Bradley, & Hamm, 1993; Mikels et al., 2005). Based on the normative ratings

available for this stimulus set, images were categorized by affective valence as “Unpleasant” or “Neutral” (Unpleasant mean valence = 2.91/9; Neutral mean valence = 5.06/9). Based on their contents, the images were then further categorized as either “Social” or “Nonsocial” (Berntson, Bechara, Damasio, Tranel, & Cacioppo, 2007). Six images were selected in each category (Unpleasant Social, Unpleasant Nonsocial, Neutral Social, Neutral Nonsocial; see Figure 16 for examples; see Appendix F for complete list). Participants were asked to rate each image for positivity, negativity, arousal, and disgust. Positivity and negativity were rated simultaneously by selecting a square on a five-by-five bivariate evaluative space grid (see Appendix D) (Larsen et al., 2009). Arousal and disgust were rated on a nine-point Likert-type scale.

Following the emotional appraisal task, participants completed a set of questionnaires, including the Perceived Vulnerability to Disease Questionnaire (PVDQ; Duncan, Schaller, & Park, 2009), the revised UCLA Loneliness Scale (UCLA-L(R); Russell, 1996), the pathogen subscale of the Three Domains of Disgust Scale (TDDS; Tybur, Lieberman, & Griskevicius, 2009), and the 10-item Perceived Stress Scale (PSS-10; Sheldon, Tom, & Robin, 1983), in addition to a survey of general demographic information.

4.2.3 Data analysis plan

A series of linear regressions were run using perceived stress, pathogen disgust, and loneliness as predictors of PVD. Then, the possible explanatory power of perceived stress and pathogen disgust for the loneliness-PVD model were explored in mediation analyses using the basic steps suggested by Baron & Kenny (1986). To examine the impact of PVD and the other constructs of interest on emotional appraisal of IAPS images, HLMs were created using valence and social content as within-subjects categorical predictors and the trait-level constructs as

between-subjects continuous predictors of positivity, negativity, arousal, and disgust ratings of the images. Categorical variables were dummy coded to aid in interpretation of results. The models were built systematically to ensure each factor significantly predicted image ratings, beginning with the main and interactive effect of the categorical predictors, then adding a construct of interest.

A boundary of 3SD above and below the mean was used to test for extreme outliers in predictor and outcome variables. No outliers were identified in the constructs of interest. Age and gender were controlled for as covariates in all analyses, and inclusion of these factors did not alter the significance of the models. All analyses were conducted in R (R Core Team, 2019) using RStudio (RStudio Team, 2021) and figures were generated with the *ggplot2* package (Wickham, 2016).

4.3 Results

4.3.1 Perceived vulnerability to disease

Linear regressions revealed individual differences in PVD were related to each construct of interest. All β s reported below are unstandardized. Most notably, there was a significant positive association between loneliness and PVD ($\beta = 0.31$, $SE = 0.09$, $p < 0.001$). Individuals who reported higher loneliness also perceived themselves to be more vulnerable to disease (see Figure 17). As expected, PVD was positively associated with perceived stress ($\beta = 0.63$, $SE = 0.15$, $p < 0.001$) such that higher perceived stress was associated with greater PVD. PVD was also positively associated with scores on the pathogen disgust subscale of the TDDS ($\beta = 0.53$, $SE = 0.15$, $p < 0.001$). To further investigate the association between loneliness and PVD, perceived stress and pathogen disgust were examined as possible mediators of the relationship

(see Figure 18). Perceived stress was found to be a significant mediator of the relationship between loneliness and PVD, rendering the direct effect of loneliness nonsignificant ($\beta = 0.09$, $SE = 0.13$, $p = 0.51$). However, pathogen disgust was not a significant mediator, as the direct effect of loneliness remained significant and of equal weight when controlling for pathogen disgust in the model ($\beta = 0.32$, $SE = 0.08$, $p < 0.001$). All associations hold when controlling for age and gender. Loneliness did not mediate the effect of perceived stress on PVD, nor did PVD mediate the relationship between loneliness and perceived stress when the mediating and outcome variable were rotated.

4.3.2 Emotional appraisal

To examine the effect of PVD, loneliness, and perceived stress on emotional appraisal of IAPS images, an HLM approach was used to look at the different rating dimensions across IAPS image categories. This method was chosen to allow for the addition of categorical within-subjects and continuous between-subjects variables in a systematic fashion. First, a base repeated-measures model was created for each rating dimension taking into account main effects of the categorical image variables (valence and social content). For main effects of categorical image variables, see Appendix G.

PVD was then added to the models for each rating dimension as a predictor to examine the main effect on emotional appraisal of IAPS images (see Figure 19). PVD did show a significant main effect on both positivity ($\beta = 0.01$, $SE = 0.01$, $p < 0.05$) and negativity ratings ($\beta = 0.01$, $SE = 0.01$, $p < 0.01$). Somewhat contrary to our predictions, higher PVD was associated with both higher positivity ratings and higher negativity ratings across all image categories, suggesting a general heightening of sensitivity to affective content. There was also a significant

positive main effect of PVD on ratings of disgust ($\beta = 0.03$, $SE = 0.01$, $p < 0.05$). There was a marginal effect of PVD on ratings of arousal ($\beta = 0.03$, $SE = 0.01$, $p = 0.06$), such that higher PVD was associated with higher arousal ratings. There was no significant interaction of PVD with either image valence or social content for any rating dimension.

Using the same procedure, the main effect of loneliness was tested as a predictor of emotional appraisal but was not significantly associated with ratings of IAPS images on any dimension (all p s > 0.05). This did not meet the prediction that loneliness would affect appraisal of social content in affective images.

The main effect of perceived stress was similarly tested as a predictor (see Figure 20). Surprisingly, perceived stress showed a significant effect on ratings of positivity ($\beta = 0.04$, $SE = 0.02$, $p < 0.05$) but not negativity ($\beta = 0.01$, $SE = 0.01$, $p = 0.33$) for IAPS images. Higher perceived stress was associated with greater ratings of positivity. There was also a significant effect of perceived stress on arousal ratings ($\beta = 0.06$, $SE = 0.02$, $p < 0.01$) such that higher perceived stress was associated with higher arousal ratings, suggesting again some heightened sensitivity to affective content. Finally, there was also a significant main effect of perceived stress on disgust ratings ($\beta = 0.06$, $SE = 0.01$, $p < 0.01$), again such that higher perceived stress was associated with higher ratings. Notably, there was a significant interaction three-way interaction between perceived stress, social content, and image valence for ratings of disgust ($\beta = -0.04$, $SE = 0.02$, $p < 0.05$). The relationship between perceived stress and disgust ratings was stronger for Unpleasant Social images than Unpleasant Nonsocial images, but this distinction was not seen for Neutral images.

4.4 Discussion

Previous research has shown that higher PVD can reduce willingness to affiliate with strangers (Sawada et al., 2018) and that activation of the behavioral immune system can result in decreased feelings of needing to belong (Sacco et al., 2014). In turn, loneliness increases feelings of needing to belong and motivation to form social connections (Cacioppo et al., 2011; DeWall & Richman, 2011). However, the relationship between loneliness and the behavioral immune system has not been empirically established prior to this study. In this sample of healthy adults, there was a positive association between loneliness and PVD, such that higher loneliness was associated with higher PVD. The positive nature of the association was not predicted; however, this finding supports a more dynamic relationship between the behavioral immune system and social motivation. If the well-established reciprocal relationship were to hold true, one might expect that the increase in motivation to form social connections associated with high loneliness would produce a corresponding decrease in PVD, but this is not what was observed. Since social connections are so fundamental to well-being, it may be that lonely individuals (who anticipate needing to increase interaction) experience an increase in concerns about pathogen sources to compensate for close exposure to conspecifics. An additional aim of this research was to investigate the potential affective mechanisms underlying the social impact of the behavioral immune system. Both pathogen disgust and perceived stress were considered as potential mediators of the relationship between loneliness and PVD.

Disgust is commonly discussed as a primary affective mechanism of the behavioral immune system, as it produces aversive feelings that motivate the avoidance of pathogen sources through changes in behavior. Increases in PVD may result in heightened perception of disease cues in others, leading to increased disgust and social avoidance. Both loneliness and PVD are

associated with sensitivity to threats, be it social or pathogen, making overall perceived stress a possible connecting factor. Both perceived stress and pathogen disgust were positively associated with PVD overall, as was expected. However, in the mediation analysis of the loneliness-PVD relationship, only perceived stress served as a significant mediator. While disgust is clearly strongly affiliated with the behavioral immune system, these results suggest that it alone may not be sufficient when considering related shifts in social motivation. As previously discussed, in instances when social motivation is high and interaction is necessary, the behavioral immune system must utilize mechanisms other than avoidance. Perceived stress, which indicates sensitivity to events in one's environment (Snippe et al., 2017) could act as an alarm system in situations when one expects to be put at risk of infection. In other words, if a lonely individual is motivated to increase social interaction, it makes sense that a greater level of perceived stress and sensitivity to pathogen threats would be necessary. This could then be translated to the heightened perception of vulnerability to disease. The pattern of results from this study represents one cross-section in time. However, these mediation analyses were able to be replicated post hoc (see Appendix H) using data from the independent sample described in Chapter 3. In this second sample, loneliness and PVD were also positively associated, and perceived stress, not pathogen disgust, mediated the relationship. With replication it is possible to give credence to the fact that these findings represent more robust underlying relationships.

The interconnections between social and affective correlates of PVD were further investigated through the appraisal of affectively relevant images. Images in four categories (Unpleasant Social, Neutral Social, Unpleasant Nonsocial, and Neutral Nonsocial) were used to examine the interaction between affective and social content. After establishing base models for the effects of categorical image variables on image ratings (see Appendix G), trait-level

constructs were added to the models as continuous predictor variables. Though loneliness showed no main effect on the ratings of any image category, both PVD and perceived stress were positively associated with ratings of IAPS images across all dimensions. Contrary to our prediction, there was no interaction of PVD with either image valence or social content, which indicates the effect of PVD is not specific to social content in this case and that there may be a more general affective mechanism at play. Perceived stress did interact with image valence and social content for ratings of disgust such that the effect was seen strongly for Unpleasant Social, but not Unpleasant Nonsocial images. Unpleasant Nonsocial images were rated as disgusting regardless of individual differences in perceived stress, but for the other categories it seems that higher disgust ratings occurred for individuals higher in perceived stress. The association of both PVD and perceived stress with the emotional appraisal of IAPS images is in line with the positive relationship between the two constructs. These findings further support the proposal that the affective mechanisms implicated in the behavioral immune system may not be specific to disgust alone. Along with the evidence that perceived stress, but not pathogen disgust, mediates the relationship between PVD and loneliness, the pattern of emotional appraisal observed indicates that there is the social impact of the behavioral immune system is complex. There is more research to be done exploring the contexts in which social and immune considerations may amplify each other, rather than trading off saliency.

This work is limited by a relatively small sample size and the online data collection format. While the online format allows for the inclusion of a wider variety of participants than a typical university setting, it also places limitations on the length and complexity of the experimental protocol. Additionally, the associations between PVD and loneliness were established using dispositional self-report measures that would benefit from a larger survey

population. However, this limitation was mitigated by the ability to replicate this pattern of mediation findings using data from an independent study. Future work conducted in a laboratory environment should include the experimental manipulation of the behavioral immune system (e.g. exposure to disease) to see whether loneliness will mitigate the impact of disease concerns on behavior. It is also important to note that this work was conducted at the beginning of the COVID-19 pandemic in May of 2020. The global pandemic has made the vulnerability to infection quite salient and the constant exposure to news of new cases and death rates is likely to make concerns about disease more impactful. Public social distancing ordinances and work-from-home mandates have disrupted the normal social landscape and individuals are isolated in a way that they may have never experienced before. This pairing of social and immune concerns provides a uniquely appropriate environment for the study of both PVD and loneliness. However, further replication of this work should be conducted in the future when universal vigilance to pathogens has fully subsided, and daily social life settles into the new normal.

4.5 Appendix C: Figures for Chapter 4



Figure 16. Example images used for assessment of emotional appraisal. Six IAPS images were chosen to fit into each of four categories: Unpleasant Nonsocial, Unpleasant Social, Neutral Nonsocial, Neutral Social.

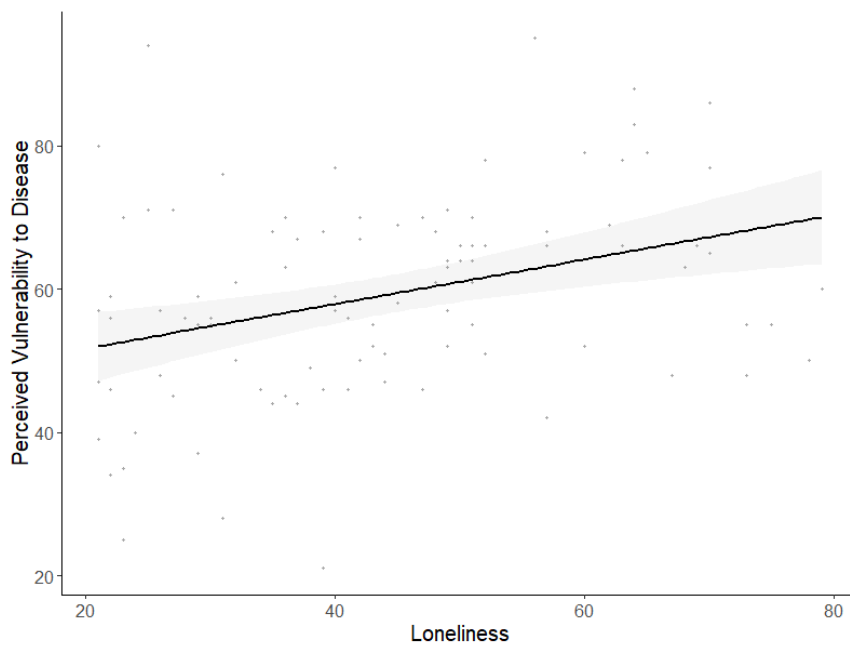


Figure 17. Relationship between loneliness and PVD. There was a significant positive association between loneliness and PVD ($p < 0.001$) such that individuals who reported greater

loneliness also perceived themselves to be more vulnerable to disease. 95% confidence interval is shown.

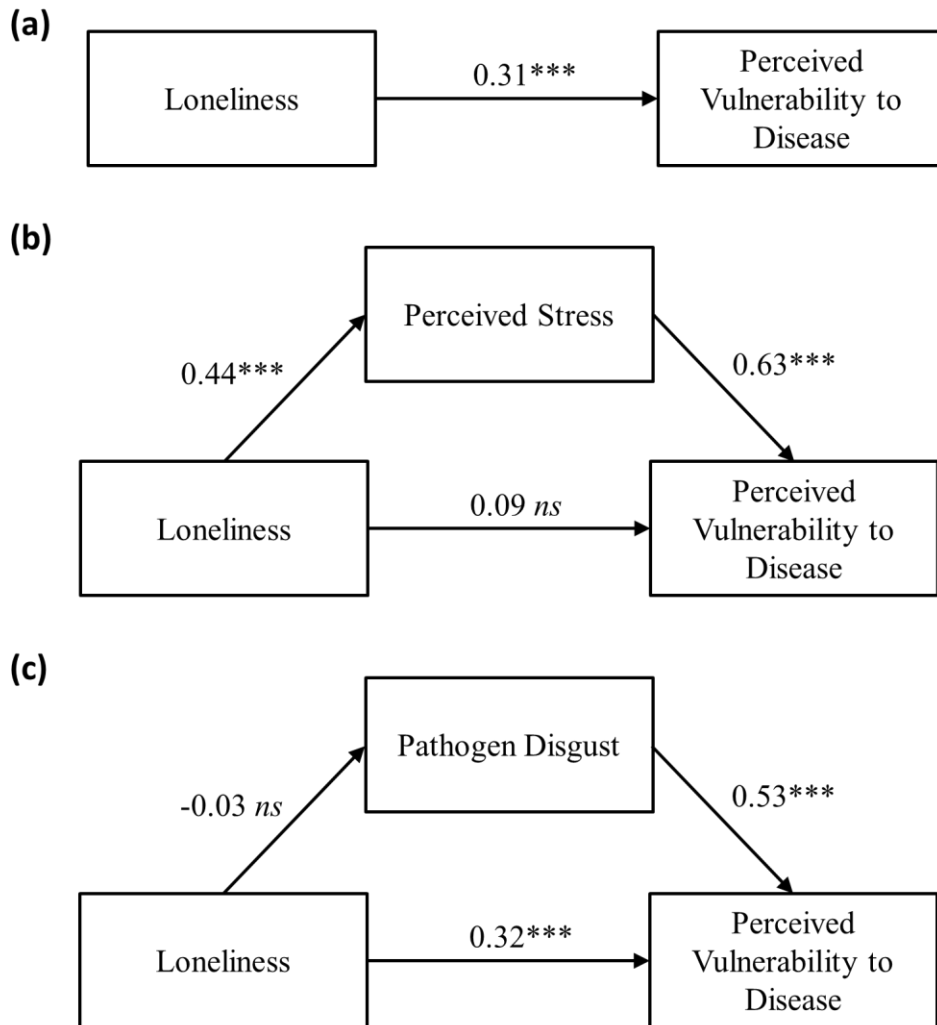


Figure 18. Mediation analyses for the association between loneliness and Perceived Vulnerability to Disease (PVD). Values shown are unstandardized regression coefficients. (a) Significant total effect model for loneliness and PVD. (b) Mediation model showing that perceived stress serves as a significant mediator, rendering the direct effect of loneliness on PVD nonsignificant. (c) Mediation model showing that pathogen disgust does not mediate the relationship between loneliness and PVD. ***: $p < 0.001$, ns: nonsignificant.

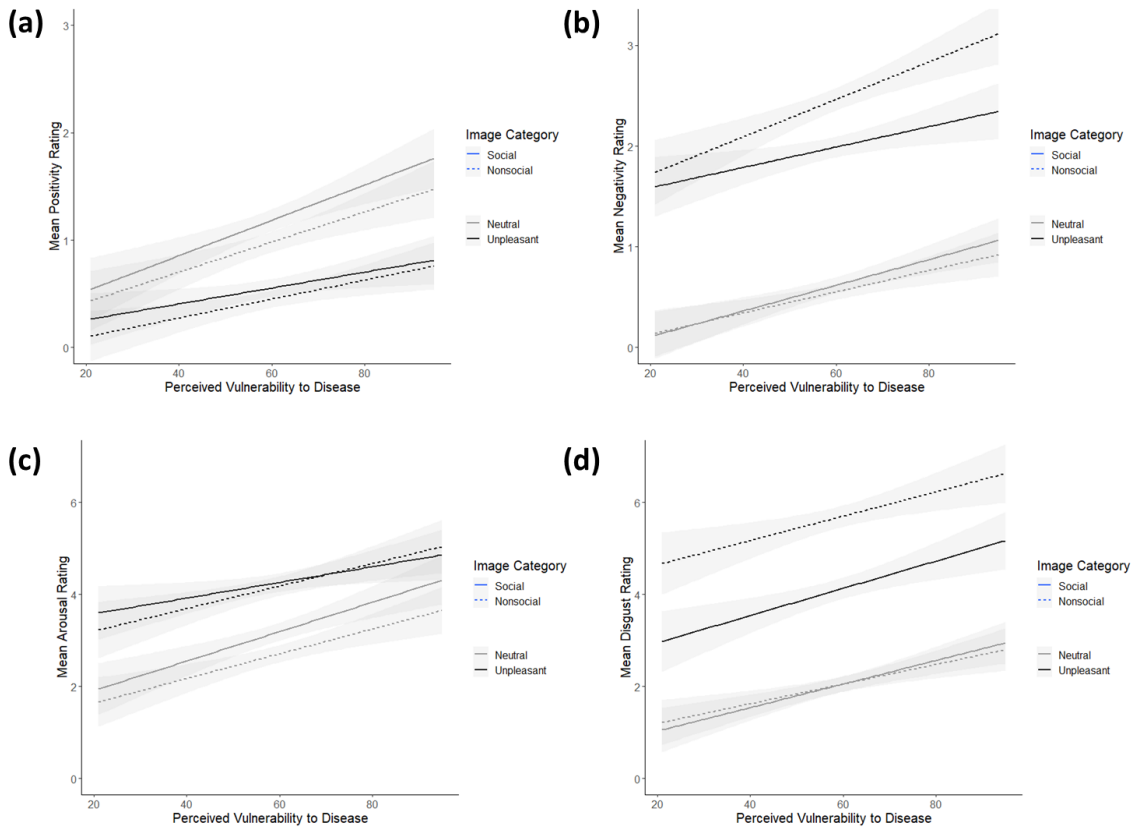


Figure 19. Effect of PVD on mean ratings of IAPS images by image category. There were significant main effects of PVD on ratings of (a) positivity, (b) negativity, and (d) disgust ($p < 0.05$). There was no significant main effect of PVD on ratings of (c) arousal. 95% confidence intervals are shown.

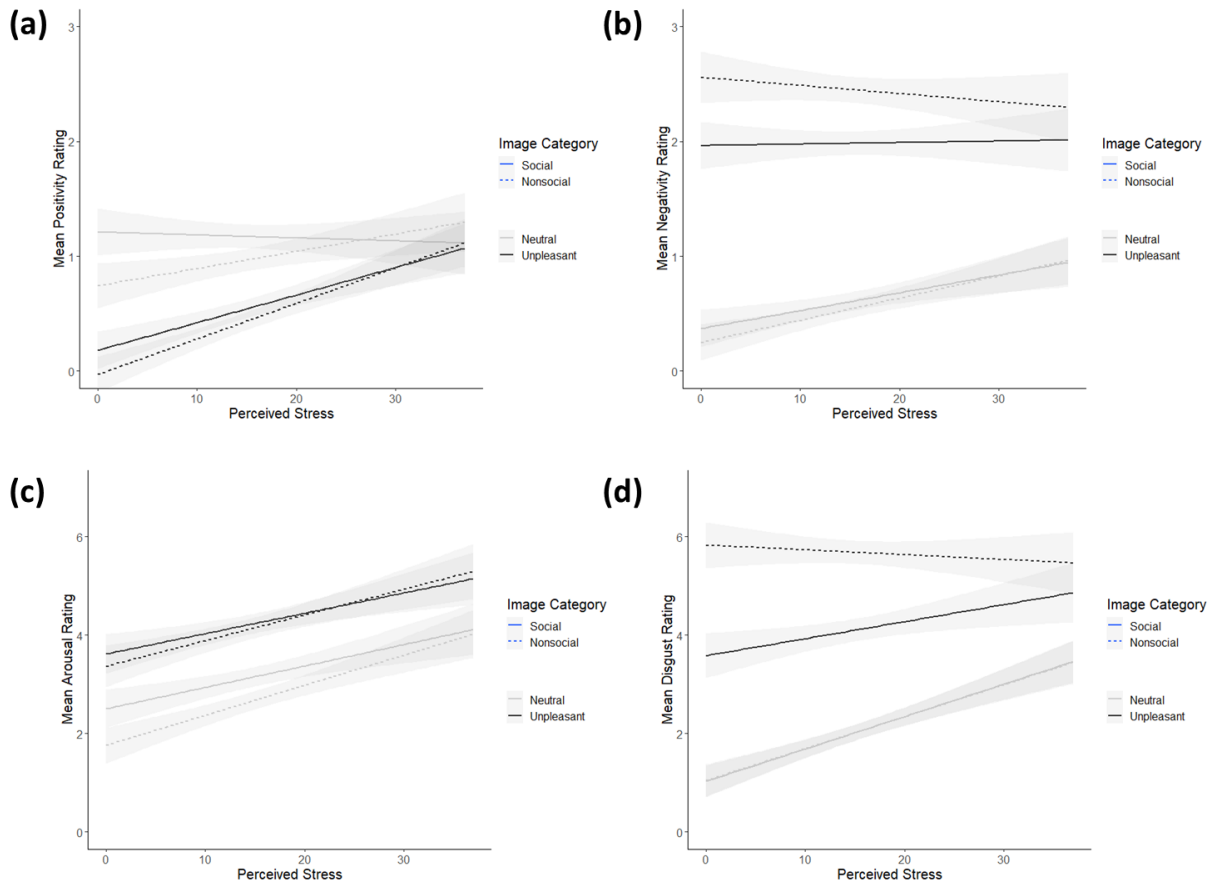


Figure 20. Effect of perceived stress on mean ratings of IAPS images by image category. There were significant main effects of perceived stress on ratings of (a) positivity, (c) arousal, and (d) disgust ($p < 0.05$). There was no significant main effect of perceived stress on ratings of (b) negativity. There was a significant three-way interaction between perceived stress, image valence, and social content for ratings of disgust ($p < 0.05$). 95% confidence intervals are shown.

Chapter 5: General conclusion

The need to belong to a group and maintain social connections motivates humans towards social behavior (Baumeister & Leary, 1995). Forming these connections in a complex social environment relies on the ability to perceive, understand, and respond to the emotions and actions of others (Leiberg & Anders, 2006). By maintaining connection to a social group, an individual gains access to benefits that increase the likelihood of survival, including greater access to resources and protection from predators (Alexander, 1974). Additionally, social behavior is inherently rewarding and can help buffer the negative effects of stressful life events (Cohen & Hoberman, 1983; Insel, 2003). Perceptions of social isolation and lack of connection with the group can conversely lead to depression and poorer physical health (Cacioppo et al., 2006; Steptoe, Owen, Kunz-Ebrecht, & Brydon, 2004). Despite the benefits of group membership, group living also comes with automatic costs such as increased risk of infection (Shakhar, 2019). Individuals can pass harmful pathogens onto others through close contact, and in some cases the risk of being infected will result in decreased social motivation (Ackerman et al., 2018; Hart, 1990). However, if a sick individual is a close member of one's social group, the motivation to provide care and strengthen that social connection may win out over pathogen avoidance (Delton & Robertson, 2016; Steinkopf, 2016b). The context in which perception of pathogen cues may lead to increased social motivation over social avoidance have not been fully explored in the literature. Factors that influence underlying social and affective processes like empathy can also inform the understanding of shifting social motivation.

This dissertation described three studies that explore individual differences in social motivation and behavior in differing contexts. Chapter 2 examined physiological and affective reactions to viewing distress in others. Empathy allows for the understanding and sharing of

emotional states between individuals, in part through emotional contagion (Hatfield et al., 2014). The physiological measurement of emotional contagion has been well-utilized in the literature (e.g. Buchanan et al., 2012; Westman, 2001), but research into individual difference factors that impact emotional contagion and empathy have not shown consistent results. For example, empathy involves distinguishing between emotions that originated in the self and in others (Decety & Cowell, 2014), implicating interoception in the process of sharing emotional states. The study described in this chapter utilized multiple measures of autonomic cardiac control in an effort to explore physiological reactions to others' distress more thoroughly. It was found that participants experienced a significant increase in IBI while viewing Stress videos compared to Control videos. Although this difference in physiological reactivity was observed, there was no difference in emotional contagion experienced while viewing Stress videos compared to Control videos. Though dispositional empathy was not found to be related to physiological responses to others' distress, interoceptive accuracy did have an effect on degree of contagion (indexed with PEP) and subjective anxiety ratings of the speakers in each video.

Previous work has not been able to establish a consistent relationship between interoceptive accuracy and behavioral measures of empathy (Ainley et al., 2015; Heydrich et al., 2021). The results from this study suggest that interoceptive accuracy may be impacting facets of empathic ability, such as emotional contagion and emotional appraisal. To some extent, this implies that perception of one's own physiological functioning is associated with differences in social perception that influence understanding of another's emotional state. Differences in understanding another's emotional state would most likely then lead to differences in the behavioral response, such as the decision to provide help. While these results are limited, they do

support a need for further research into empathic responses in conjunction with other individual difference factors.

Empathy is a complex psychological phenomenon that can motivate helping behavior (Decety et al., 2016; Decety & Cowell, 2014). This motivation is flexible to social context and other salient cues, including pain and sickness (Steinkopf, 2016a). The perception of disease cues in an individual may motivate a close group member to provide care, but this care comes at the cost of risking infection (Goetz et al., 2010). Common models of the behavioral immune system would suggest that perception of disease cues should only lead to decreased social motivation for pathogen avoidance (Leeuwen & Jaeger, 2022; Schaller, 2014). However, this is clearly not always the case. Chapter 3 examines one instance in which exposure to disease cues may increase motivation towards social behavior – empathy for pain. As predicted, the results from this study do show that judgements of pain intensity increased after exposure to Disease images compared to Neutral. Though there was no impact of dispositional empathy on this result, trait pathogen disgust was positively associated with judgements of pain intensity as well. Together these results suggest that saliency of disease and disgust can increase in social motivation for situations in which helping behavior might be needed (e.g. pain). This theory is further supported by the positive association between pathogen disgust and ratings of compassion for pain.

Both Chapters 2 and 3 described different reactions to viewing forms of distress in others and how these reactions may impact social motivation. However, humans experience baseline individual differences in social motivation as well. When individuals perceive themselves to be socially isolated from the group, they experience aversive feelings, visceral and affective, that motivate them to seek out and maintain social connections (Hawkley & Cacioppo, 2010; Maner et al., 2007). The motivation towards social connections may require increased social

interactions, which, as described, can also increase risk of pathogen transmission. However, in this case, when social interaction is necessary, social avoidance cannot be utilized to minimize the risk. Instead, the behavioral immune system may coordinate other shifts in perception and cognition, such as increasing awareness of disease cues. Chapter 4 explores the relationship between loneliness and PVD in a cross-sectional sample taken during the COVID-19 pandemic, when both social and disease concerns are highly salient. The results from the study in this chapter showed that loneliness and PVD were positively associated, suggesting that the behavioral immune system may emphasize awareness of disease threats in anticipation of increasing social interaction. The mediation of the relationship between loneliness and PVD by perceived stress could be interpreted in further support of this theory, in that loneliness may increase general awareness of threats in the environment, and PVD reflects sensitivity to disease-specific threats. This study also showed that individuals with higher PVD were more responsive to affectively salient images, which aligns with an increase in overall sensitivity. Along with the results from Chapter 3, these findings provide evidence for increasing complexity when discussing the behavioral immune system and social motivation.

Looking back to Chapter 2, interoceptive accuracy was associated with certain aspects of the psychophysiological response to viewing distress in others. Interoceptive accuracy may also be implicated in making tradeoffs between the behavioral immune system and social motivation. Tracking of immune status and true vulnerability to disease occurs in part through interoception – afferent signaling from the periphery. Future work should examine whether interoceptive accuracy is associated with perceived vulnerability to disease and responses to disease cues. Additional research is also needed to establish whether lonely and socially motivated individuals show other differences in behavioral immune system activity. The work described in this

dissertation speaks to the complexity of motivation in a fundamentally social species. Humans must communicate and act successfully in a dynamic social environment, accounting for both their own motivations and the behavior of other individuals. Individual differences in affective and physiological processes can have a significant impact on social motivation, and individual differences in social motivation can influence changes in perception and behavior. The factors that determine how humans survive and thrive are numerous and interdependent, and only through the study of their nuances can research lead to a full understanding of social behavior.

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Appendix D: Evaluative space grid

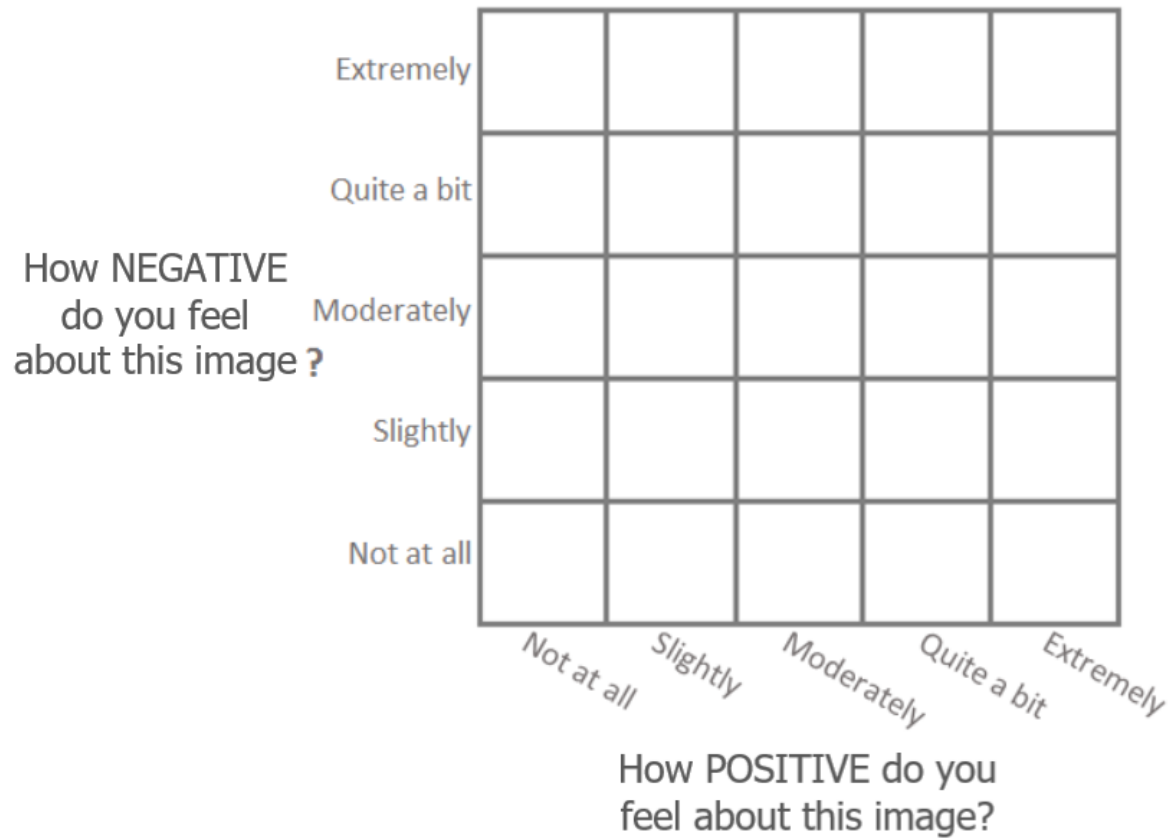


Figure 21. The evaluative space grid used to rate IAPS images on positivity (x-axis) and negativity (y-axis) simultaneously. After an image stimulus was displayed, participants used the mouse to select one of the 25 cells on the grid. This selection then yields both a positivity and negativity score (0-4). Using this grid bivalent rating system captures information that may be lost with a single linear rate of affective valence. Figure is adapted from (J. T. Larsen et al., 2009).

Appendix E: Lists of IAPS images

Chapter 3: Images used in the experimental manipulation

<u>Disease condition</u>	<u>Neutral condition</u>
2750	1908
3160	2514
3400	2594
7380	5120
9181	5130
9301	5390
9320	7009
9322	7041
9342	7050
9432	7242
9584	7249
9592	7500

Chapter 4: Images used in the emotional appraisal of affective images

<u>Unpleasant Social</u>	<u>Unpleasant Nonsocial</u>	<u>Neutral Social</u>	<u>Neutral Nonsocial</u>
2700	5973	2038	7009
2717	9280	2385	7041
3216	9290	2397	7050
3300	9301	2512	7242
9424	9630	2840	7249
9592	9830	9070	7500

Appendix F: Lists of emotional Stroop words

<u>Positive Social</u>	<u>Negative Social</u>	<u>Positive Emotional</u>	<u>Negative Emotional</u>	<u>Neutral</u>
Accepted	Abused	Achieve	Afraid	Barrel
Admired	Assaulted	Bliss	Agony	Board
Affection	Betrayed	Brave	Angry	Bowl
Belong	Deceived	Bright	Anguish	Cabinet
Caring	Defeated	Cheer	Anxious	Chair
Charming	Disliked	Comfort	Brutal	Chin
Desired	Excluded	Delight	Corrupt	Foot
Devoted	Hated	Enjoy	Cruel	Hairpin
Faithful	Hostile	Fun	Depressed	Item
Flirt	Humiliated	Happy	Distress	Kettle
Friendly	Inadequate	Hope	Fear	Locker
Giving	Inferior	Joyful	Frustrated	Nonchalant
Included	Insulted	Laugh	Greed	Paper
Kind	Lonely	Lucky	Insecure	Pencil
Kiss	Pathetic	Pleased	Irritated	Seat
Liked	Rejected	Pleasure	Misery	Square
Loved	Ridiculed	Prize	Pain	Statue
Loyal	Selfish	Success	Panic	Street
Party	Shamed	Terrific	Sad	Table
Thoughtful	Unwanted	Useful	Stress	Taxi

Appendix G: Effect of image category on ratings of IAPS images in Chapter 4

The base regression models for analysis of emotional appraisal of IAPS images take into account the categorical image variables, valence, and social content. The categorical variables were dummy coded (Neutral/Nonsocial = 0, Unpleasant/Social = 1) and reported β s are unstandardized. There was a main effect of image valence on all rating dimensions. As expected, Unpleasant images were rated generally less positively ($\beta = -0.53$, $t(99) = -5.84$, $p < 0.001$) and more negatively ($\beta = 1.91$, $t(99) = 1.10$, $p < 0.001$) than Neutral images. Similarly, Unpleasant images elicited greater arousal ratings ($\beta = 1.47$, $t(99) = 8.06$, $p < 0.001$). Finally, Unpleasant images were rated as significantly more disgusting ($\beta = 3.64$, $t(99) = 19.80$, $p < 0.001$) than Neutral images, though the content of the images were not specifically pathogen- or disease-relevant. Social content also showed a significant main effect on certain ratings. Social images were rated more positively ($\beta = 0.20$, $t(99) = 3.61$, $p < 0.001$) and elicited greater arousal ratings ($\beta = 0.48$, $t(99) = 5.24$, $p < 0.001$) than Nonsocial images. However, there was no significant effect of social content on ratings of negativity ($\beta = 0.06$, $t(99) = 1.09$, $p = 0.28$) or disgust ($\beta = -0.001$, $t(99) = -0.2$, $p = 0.99$). Adding in the interaction between image valence and social content significantly improved the models for all rating factors, and the interaction was significant for ratings of negativity ($\beta = -0.53$, $t(198) = -6.48$, $p < 0.001$), arousal ($\beta = -0.39$, $t(198) = -3.04$, $p < 0.01$), and disgust ($\beta = -1.57$, $t(198) = -10.32$, $p < 0.001$), but not for ratings of positivity ($\beta = -0.10$, $t(198) = -1.21$, $p = 0.23$). The interaction effect differed depending on the rating dimension (see Figure 22).

For ratings of negativity, arousal, and disgust, there was a significant interaction between image valence and social content. Though the distinction between social and nonsocial images has been examined previously (J. T. Cacioppo, Norris, Decety, Monteleone, & Nusbaum, 2009;

Silva et al., 2017), a consistent pattern has not been demonstrated. For Unpleasant images, Social images were rated significantly lower in negativity and disgust than Nonsocial images, while no such distinction was observed for Neutral images. By contrast, there was no difference in ratings of arousal for Unpleasant Social and Nonsocial images, but Neutral Social images were rated higher in arousal to Neutral Nonsocial images. These patterns suggest that overall, the negative affective impact of Unpleasant images may be lower for those with social content, and that for Neutral images, social content produces greater arousal.

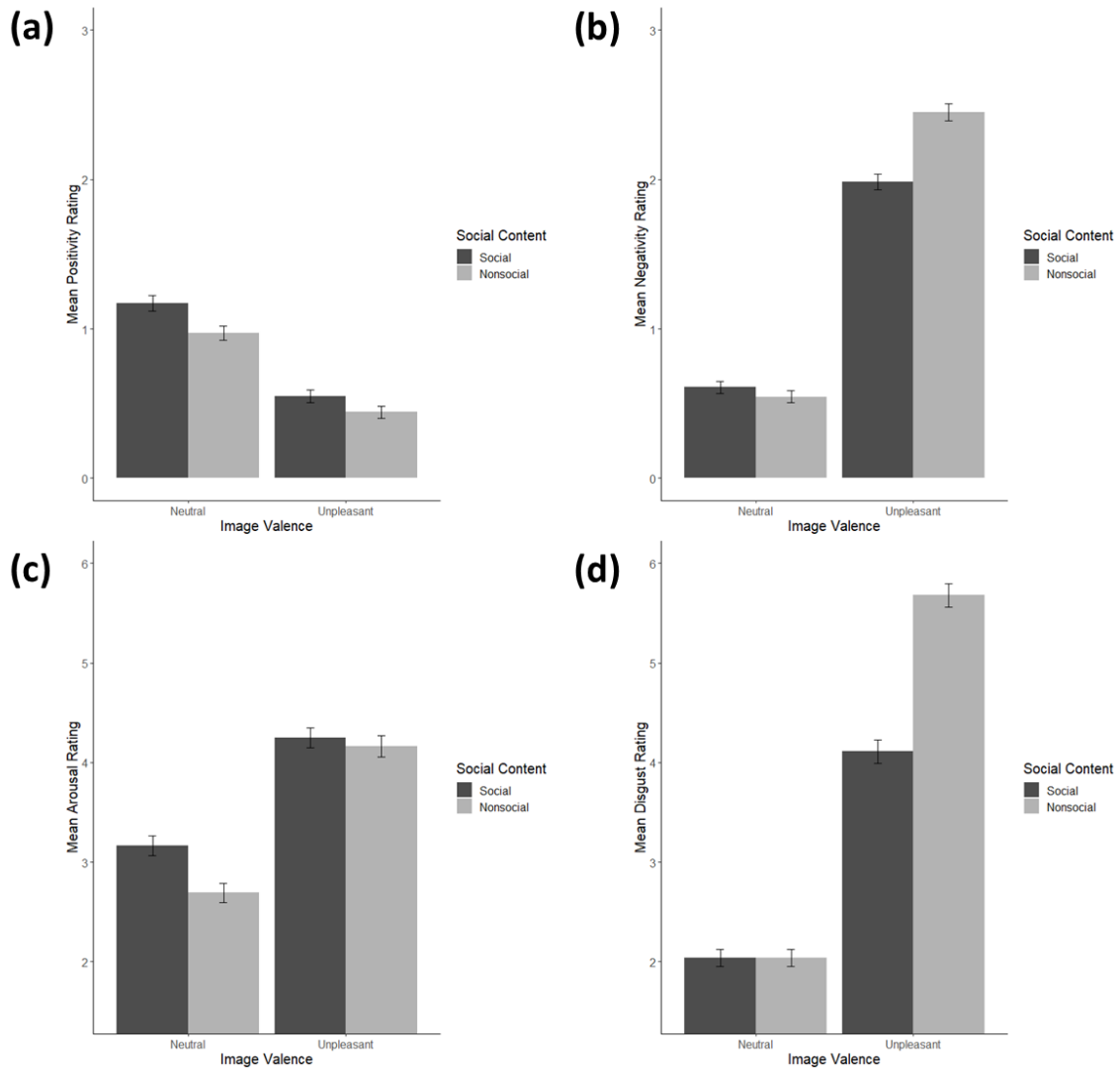


Figure 22. Mean ratings of IAPS images by categorical variables. There were significant main effects of image valence and social content, as well as an interaction effect, on ratings of (a) positivity, (b) negativity, (c) arousal, and (d) disgust (all p s < 0.05). Error bars show standard errors.

Appendix H. Replication of Chapter 4 mediation results

The study described in Chapter 3 (see section 3.2 for description of participants and procedure) administered many of the same self-report assessments as the study described in Chapter 4. Thus, an attempt to replicate the association between loneliness and PVD reported in Chapter 4 was performed using this separate population. The same positive association between loneliness and PVD was observed in this sample ($\beta = 0.37$, $SE = 0.10$, $p < 0.001$) such that higher loneliness was associated with higher PVD. Both perceived stress ($\beta = 0.88$, $SE = 0.17$, $p < 0.001$) and pathogen disgust ($\beta = 0.87$, $SE = 0.16$, $p < 0.001$) were also positively associated with PVD. Using the same procedure for mediation analysis described in section 4.2.3, perceived stress was found to mediate the association between loneliness and PVD while pathogen disgust was not a significant mediator (see *Figure 23*). This replicates the pattern found with this study's data and further supports a relationship between the behavioral immune system and social motivation that is not purely based in pathogen avoidance.

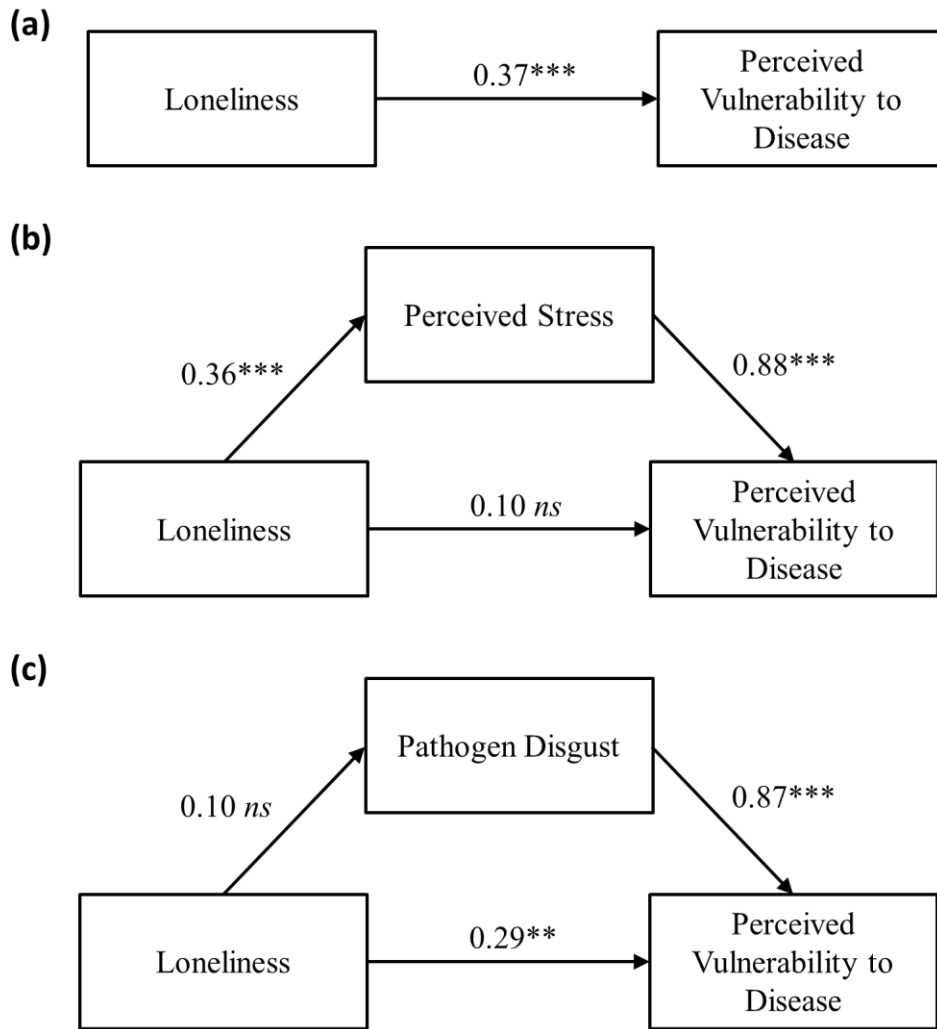


Figure 23. Replication of mediation analyses for the association between loneliness and PVD using data from Chapter 3. Values shown are unstandardized regression coefficients. (a) Significant total effect model for loneliness and PVD. (b) Mediation model showing that perceived stress serves as a significant mediator, rendering the direct effect of loneliness on PVD nonsignificant. (c) Mediation model showing that pathogen disgust does not mediate the relationship between loneliness and PVD. ***: $p < 0.001$, **: $p < 0.01$, ns: nonsignificant.