Sensorimotor representations of emotion: neural pathways and individual differences

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Abstract

Emotions are adaptive physiological responses which enable individuals to respond to threats and react to social stimuli. This response includes both whole-body actions and postures, such as expansive postures which signal dominance, and somatosensory feedback which contributes to the subjective experience of the emotional episode. However, individual differences in emotion are rarely considered at the level of somatomotor processes; moreover, the neural mechanisms of “power posing”, an experimental paradigm which relies on feedback from expansive body postures, have never been examined experimentally. In the present thesis, we address both of these open questions using behavioural and brain imaging methods.

In manuscript 1, we address individual differences in emotional body sensations. Using a behavioural paradigm in which participants paint “bodily sensation maps” of their somatic experiences, we demonstrate that emotional somatosensation from key bodily regions, including the heart and viscera, is associated with pro- and anti-social personality traits such as empathy and psychopathy, in line with embodied simulation accounts of interpersonal understanding. Moreover, we demonstrate that individuals high in empathy report bodily sensation maps more similar to the group average maps, suggesting that such individuals perceive their emotional body sensations more accurately.

In manuscript 2, we consider individual differences in natural, or trait-like body posture. We developed a trait measure of dominant body posture measured from static photos of individuals’ neutral standing posture, quantifying individuals’ postural erectness using a computer vision library. This measure was validated by demonstrating its correlation with relevant muscular physiology and high test-retest reliability. Finally, we showed in three samples that this measure of trait-like dominant posture was robustly associated with Social Dominance Orientation, a personality construct reflecting individuals’ tendencies to endorse social hierarchies.

Finally, in manuscript 3, we use electroencephalography to investigate the neural mechanisms of a “power posing” paradigm. We replicate previous findings showing an effect of expansive body postures on mood, showing that expansive postures increased positive-valenced

and high-arousal affect. We further show that high-frequency neural activity mediates the changes in, but caution that muscle artefacts may play a significant role in these findings.

Overall, the present thesis demonstrates that despite its ancient evolutionary origins, emotion-related somatosensory and motor activity is rich in individual differences which are relevant for key personality traits and aspects of social cognition. It also for the first time provides preliminary data on the neural mechanisms by which expansive and contractive body postures exert influence over mood and behaviour. By working at the intersection of emotion, somatosensory, and motor activity, the present thesis offers a new perspective on individual variation in affect and social cognition.

Résumé en Français

Les émotions sont des réponses physiologiques adaptatives qui permettent aux individus de répondre aux menaces et de réagir aux stimuli sociaux. Cette réponse comprend à la fois des actions et des postures du corps entier, telles que les postures expansives qui signalent la domination, et un retour somatosensoriel qui contribue à l'expérience subjective de l'épisode émotionnel. Cependant, les différences individuelles en matière d'émotion sont rarement prises en compte au niveau des processus somatomoteurs ; aussi, les mécanismes neuronaux de la "pose de pouvoir", un paradigme expérimental qui s'appuie sur le retour d'informations provenant de postures corporelles expansives, n'ont jamais été examinés de manière expérimentale. Dans la présente thèse, nous abordons ces deux questions ouvertes en utilisant des méthodes comportementales et d'imagerie cérébrale.

Dans le manuscrit 1, nous abordons les différences individuelles dans les sensations corporelles émotionnelles. En utilisant un paradigme comportemental dans lequel les participants peignent des "cartes de sensations corporelles" de leurs expériences somatiques, nous démontrons que la somatosensation émotionnelle de régions corporelles clés, y compris le cœur et les viscères, est associée à des traits de personnalité pro- et antisociaux tels que l'empathie et la psychopathie, en accord avec les comptes de simulation incarnée de la compréhension interpersonnelle. De plus, nous démontrons que les individus très empathiques rapportent des cartes de sensations corporelles plus proches des cartes moyennes du groupe, ce qui suggère que ces individus perçoivent leurs sensations corporelles émotionnelles avec plus de précision.

Dans le manuscrit 2, nous examinons les différences individuelles dans la posture corporelle naturelle, ou trait de caractère. Nous avons mis au point une mesure de la posture corporelle dominante mesurée à partir de photos statiques de la position debout neutre d'individus, quantifiant l'érection posturale des individus à l'aide d'une bibliothèque de vision par ordinateur. Cette mesure a été validée en démontrant sa corrélation avec la physiologie musculaire pertinente et une fiabilité test-retest élevée. Enfin, nous avons montré sur trois échantillons que cette mesure de la posture dominante de type trait était solidement associée à l'orientation de dominance sociale, une construction de la personnalité reflétant la tendance des individus à approuver les hiérarchies sociales.

Enfin, dans le manuscrit 3, nous utilisons l'électroencéphalographie pour étudier les mécanismes neuronaux d'un paradigme de "pose de pouvoir". Nous reproduisons les résultats précédents montrant un effet des postures corporelles expansives sur l'humeur, en montrant que les postures expansives augmentent l'affect à valence positive et l'affect à haut niveau d'éveil. Nous montrons en outre que l'activité neuronale à haute fréquence est le médiateur des changements d'humeur, mais nous avertissons que les artefacts musculaires peuvent jouer un rôle important dans ces résultats.

Dans l'ensemble, la présente thèse démontre qu'en dépit de ses origines évolutives anciennes, l'activité somatosensorielle et motrice liée aux émotions est riche en différences individuelles qui sont pertinentes pour des traits de personnalité clés et des aspects de la cognition sociale. Elle fournit également pour la première fois des données préliminaires sur les mécanismes neuronaux par lesquels les postures expansives et contractives du corps exercent une influence sur l'humeur et le comportement. En travaillant à l'intersection de l'émotion, de l'activité somatosensorielle et de l'activité motrice, la présente thèse offre une nouvelle perspective sur la variation individuelle de l'affect et de la cognition sociale.

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Contribution of Authors

Study 1: Antisocial and impulsive personality traits are linked to individual differences in somatosensory maps of emotion

Soren Wainio-Theberge and Jorge L. Armony

Soren Wainio-Theberge: Conceived the study with JLA. Coded the experiment and collected the data. Analyzed the data in consultation with JLA. Wrote the initial draft of the paper and revised it with JLA.

Jorge L. Armony: Contributed to the study design, provided input on the data analysis. Provided multiple rounds of revisions on the paper. Supervised all research.

Study 2: Natural differences in upright body posture are associated with prosociality

Soren Wainio-Theberge and Jorge L. Armony

Soren Wainio-Theberge: Conceived the study with JLA. Coded all three experiments and collected the data. Analyzed the data in consultation with JLA. Wrote the initial draft of the paper and revised it with JLA.

Jorge L. Armony: Contributed to the study design, provided input on the data analysis. Provided multiple rounds of revisions on the paper. Supervised all research.

Study 3: High-frequency brain activity mediates the psychological effects of expansive and contractive postures

Soren Wainio-Theberge and Jorge L. Armony

Soren Wainio-Theberge: Conceived the study with JLA. Coded the experiment and collected the data. Analyzed the data in consultation with JLA. Wrote the initial draft of the paper and revised it with JLA.

Jorge L. Armony: Contributed to the study design, provided input on the data analysis. Provided multiple rounds of revisions on the paper. Supervised all research.

List of tables and figures

List of Abbreviations

AI	Artificial Intelligence
AP	Authentic pride scale
AVI	Affect valuation index
BFI	Big five inventory
BIS-11	Baratt impulsiveness scale
BSM	Bodily sensation map
CERQ	Cognitive emotion regulation questionnaire
COMP-A	Composite arousal
COMP-V	Composite valence
DLPFC	Dorsolateral prefrontal cortex
ECG	Electrocardiography
EEG	Electroencephalography
eLORETA	exact low resolution electromagnetic nomography
EMG	Electromyography
FASTER	Fully automated statistical thresholding for EEG artefact rejection
FDR	False discovery rate
fMRI	Functional magnetic resonance imaging
GABA	Gamma aminobutyric acid
HA	High arousal
HAP	High arousal positive
HAPPE	Harvard automated preprocessing pipeline for electroencephalography
ICA	Independent component analysis
ICC	Intraclass correlation coefficient
IPS	Inferior parietal sulcus
IRI	Interpersonal reactivity index
JATOS	Just Another Tool for Online Studies
LA	Low arousal
LAN	Low arousal negative
LAP	Low arousal positive
LDA	Linear discriminant analysis
LOT-R	Life orientation test - revised
LSRP	Levenson self-report psychopathy scale
MAIA-2	Multidimensional assessment of interoceptive abilities version 2
MARA	Multiple artefact rejection algorithm
MEG	Magnetoencephalography
MEP	Motor evoked potential
mPFC	Medial prefrontal cortex

N	Negative
OFC	Orbitofrontal cortex
P	Positive
PANAS-X	Positive and negative affect schedule - expanded
PCA	Principal component analysis
PNS	Parasympathetic nervous system
PWD	Psychological well-being scale
SD	Standard deviation
SDO	Social dominance orientation
SENIAM	Surface electromyography for the non-invasive assessment of muscles
SNS	Sympathetic nervous system
SSC	Somatosensory cortex
STAXI	State-trait anger expression inventory
STPI	Spielberger state-trait personality inventory
TAS	Toronto alexithymia scale
THAT	Toronto hospital alertness test
TMS	Transcranial magnetic stimulation

Chapter 1: Introduction and review of the relevant literature

The word emotion derives from the Latin “ex-movere”, meaning to move out of or away from. The present thesis describes a program of research dedicated to the study of emotion in the sensorimotor domain. As will be described further, this research relies on an understanding of emotions as adaptive patterns of motor and physiological activity, varying according to contextual factors and individual appraisals. The present review discusses the sensorimotor nature of emotion, beginning with theoretical constructs around emotional somatosensation, discussing physiological changes in emotions and methods for measuring their associated sensations. Next, emotional motor programs are discussed, with a particular focus on dominance and submission behaviours and experimental paradigms designed to investigate their psychological sequelae. In the third section, the neuroscientific basis of these two aspects will be discussed, focusing on neuroimaging studies of emotion-related motor and somatosensory processing in humans whenever available. Next, we will take a brief detour into personality and individual differences, as a key aspect of the thesis is the study of individual differences in somatosensory and motor outputs of emotion. Finally, the aims of the thesis will be described and justified with respect to the above literature.

1: Theoretical background of emotion and sensorimotor processes: Darwin, James, and recent trends

The oldest and most venerable theory of emotion is attributable to Charles Darwin. In his book (Darwin, 1872), Darwin articulates a theory of how emotions evolved as whole-body patterns of coordination which serve adaptive goals for the organism. For example, the widening of the eyes which occurs in surprise serves to improve the detection of threatening stimuli, and the expansion of the body in anger serves to intimidate conspecifics. Darwin’s theory has received considerable empirical support, with neural and behavioural studies highlighting the importance of body language in the perception and experience of emotion. Much like with facial expressions of basic emotions, individuals are able to accurately distinguish bodily expressions of emotion from static photographs and videos (de Gelder & Van den Stock, 2011). Bodily expressions of emotion also operate similarly to emotional stimuli in other modalities, displaying properties such as attention capture (Bannerman et al., 2009) and altered perception in autism and other disorders (Hadjikhani et al., 2009). Following Darwin's theory, emotions also ready individuals for adaptive action, producing the impulse for movement and subtle motor shifts which encourage specific courses of action. For example, approach-related emotions produce subtle forward shifts in center of mass, while avoidance-related emotions produce the opposite (Eerland et al., 2012; Hillman et al., 2004), encouraging approach of appetitive stimuli and avoidance of aversive ones (Harmon-Jones et al., 2011).

Many of the earliest theories of emotion concern the unique somatic sensations evoked by emotional experiences. William James's early model (James, 1890) evokes the image of a man running from a bear. In James' model, somatosensation has a central role. The sight of the bear triggers an automatic, physiological response, including increased heart rate, pupil dilation, and blood vessel dilation; however, the emotional experience of fear emerges from the individual perceiving these somatic changes (James, 1884). While this model was influentially challenged by Walter Cannon, who argued that physiological reactions were too slow and undifferentiated to produce variation in emotional experience (Cannon, 1927), in the midcentury a series of experiments re-emphasized the role of self-perception in emotional experience. Seminal experiments such as Schacter and Singer (1962) established that when exposed to physiological arousal, individuals' emotional experience depended on their interpretation of the cause of this arousal: for example, participants who received an epinephrine injection and then were exposed to an angry confederate felt more angry afterwards, compared with participants who received the same injection but were aware that epinephrine was the cause of their physiological response (Schachter & Singer, 1962).

Modern theories of emotion continue to acknowledge the role of somatosensation in emotion experience; however, the set of cognitive steps involved has grown. Most emotion theories today recognize a cognitive appraisal step prior to physiological activation, in which individuals take into account their resources and action affordances in face of a potentially emotion-evoking stimulus (Scherer, 2022). Moreover, constructivist theories have convincingly argued for a post-hoc categorization step, in which the individual appraises their sensations and identifies an emotion label, which can have feedback effects on the actual experience (Barrett, 2006). Theories differ with respect to their view of the categorical vs continuous nature of emotion. Some researchers argue for a discrete model of emotion, in which emotions reflect unitary, evolutionarily defined systems activated in response to ecological events (see section

2.1; Panksepp, 2004). Others emphasize a “population model” , with an underlying continuum of somatosensory experiences and action tendencies evoked by cognitive appraisals of situations which are perceived and cognitively categorized into discrete emotions in a manner dependent partially on emotion concepts and language (Barrett, 2009). These tensions will be revisited in chapter 2.

2: Emotion in the somatosensory modality

2.1: Emotional physiology: generators of somatosensation and empirical findings

Emotion is often thought on as being composed of two components: valence and arousal (Posner et al., 2005). Valence refers to the cognitive “goodness” or “badness” of an emotion; it reflects a cognitive appraisal of whether a situation or stimulus may be beneficial or harmful to the organism; Arousal, in contrast, reflects the degree of physiological activation associated with the emotion. These two factors are referred to as the “affective circumplex”: a model in which all emotions can be described with reference to their position in a two-dimensional space of valence and arousal. Generally, arousal is thought of in terms of the sympathetic and parasympathetic nervous systems (Jänig, 2006): arousing emotions such as fear, anger, and happiness activate the sympathetic nervous system, which increases levels of stress hormones such as cortisol and epinephrine, increases heart rate and dilates blood vessels, widens the eyes, increases breathing rates, etc (McCorry, 2007). This serves the goal of preparing the organism for action in the environment, such as responding to a threat or seeking out novel stimuli. In contrast, the parasympathetic nervous system, associated with low arousal emotions such as sadness, has the opposite effect, reducing heart rate and calming the organism (the so-called “rest-and-digest” response, in contrast to the well-known “fight-or-flight” of the sympathetic nervous system).

In this classical conception, the sympathetic and parasympathetic nervous systems operate as coherent units: an activation of the SNS or PNS produces all of the effects above concurrently, at roughly the same proportions. However, recent work has suggested that the autonomic nervous system has considerable specificity in its responses, and contains separate neural pathways which can be activated selectively by the brain (Jänig & McLachlan, 1992). Kreibig (2010) reviewed 134 studies examining changes in different physiological variables in emotion, finding that emotions exhibited context-specific effects on heart rate, respiration, and skin conductance (for example, sadness containing crying had opposite effects on heart rate compared with sadness without crying). Even relatively simple physiological processes such as heart rate and respiration have multiple degrees of freedom in their operation which allow for physiological differentiation of emotional responses. For example, respiration can vary in rate (faster vs. slower breathing), but also independently in depth, inspiration/expiration ratio, respiratory pause time, ratio of thoracic to abdominal breathing, and regularity, providing considerable specificity to its modulation in different emotions (Boiten et al., 1994). Similarly, cardiac function can vary in mean rate, but also in heart rate variability (a parameter with widespread relationships with emotional processing; Appelhans & Luecken, 2006), and specific frequency bands of heart rate variability have different functional roles (K. Li et al., 2019). Thus, despite a limited set of effectors (cardiac function, respiration, skin temperature and conductance) which fall broadly under the control of the sympathetic and parasympathetic nervous systems, emotional physiology is rich, complex, and differentiated with respect to emotion categories and different experimental contexts.

2.2: Bodily maps of emotion: a behavioural paradigm to directly measure emotional body sensations

While previous work has identified physiological changes which are doubtless associated with the unique sensations produced by emotion, only recently has a behavioural paradigm designed to directly measure the location, extent, and intensity of emotion-related somatosensation been developed. In the "bodily maps of emotion" paradigm, participants are asked to paint areas of a body silhouette where they feel sensation in different emotions (Nummenmaa et al., 2014). Participants colour two maps, for the broadly-defined categories of "activation" (areas whose activity is increasing or getting stronger) and "deactivation" (activity decreasing or getting weaker). Through these "bodily sensation maps" (BSMs), emotions are reliably distinguishable from one another, as well as from other bodily sensations such as hunger, thirst, or cognitive sensations (Nummenmaa et al., 2014, 2018). BSMs have also been found to be highly consistent between methods of presenting the task (e.g. asking participants to recall how they feel an emotion vs. showing emotional faces or emotion-inducing stimuli; Nummenmaa et al., 2014), as well as across cultures (Volynets et al., 2019).

Bodily sensation maps have also been found to be altered in psychiatric conditions, as well as predictive of some individual differences in psychological traits. BSMs have been found to be less differentiated in conditions such as autism (Palser et al., 2021) and schizophrenia (Torregrossa et al., 2019), indicative of a greater difficulty distinguishing between aspects of emotional experience in these disorders (Henry et al., 2010). Reduced sensations of activation and increased sensations of deactivation have also been found in major depressive disorder (Lyons et al., 2021). Within the healthy population, interoceptive accuracy (Jung et al., 2017) has been found to predict increased activation in the BSM procedure, and empathy has been found to predict greater overlap between self- and other-representations of emotional somatosensation using the paradigm (Sachs et al., 2019). Finally, BSMs tend to converge towards the adult mean across child development, indicating that children learn to associate their bodily sensations with emotion concepts as they develop cognitively (Hietanen et al., 2016). Together, these results suggest that the BSM procedure is sensitive to individual differences in development, psychopathology, and psychological traits.

3: Emotion in body action and posture

3.1: The dominance behavioural system and social communication of hierarchy

Of particular importance in emotional body language is the communication of dominance and submission. Dominance relationships affect the distribution of resources among members of a group, with dominant individuals gaining greater access to resources at the expense of submissive individuals (Johnson et al., 2012). In turn, submission is adaptive because it allows individuals to avoid dangerous and costly conflict with a stronger conspecific. Dominance relationships have been observed across the animal kingdom (Chase & Seitz, 2011). In humans and other animals, dominance relationships are communicated with a variety of signals, including vocalizations and vocal tone, facial expressions, and gestures (Hall et al., 2005). Of particular importance in conveying dominance, particularly among non-human animals for whom vocal communication is more limited, is body posture. Humans and other animals convey dominance through erect, expanded postures which make the animal appear larger and more threatening; in contrast, submission is conveyed using slumped and contracted postures which reduce the appearance of threat (Burgoon & Dunbar, 2006).

In humans, studies of non-verbal behaviour consistently reveal that individuals higher in power or in more dominant positions display more expansive and upright postures in interactions with their peers; for example, supervisors tend to adopt more expansive postures than their employees (Hall & Friedman, 1999), as do teachers in comparison with students (Leffler et al., 1982). In turn, people judge individuals with more expansive and upright postures as being more successful (Weisfeld & Beresford, 1982), more confident, and being higher in social status (Cashdan, 1998). Moreover, the use of nonverbal cues such as dominant body postures is associated with both actual personality traits such as extraversion and neuroticism and their perception (Breil et al., 2021).

3.2: Connecting emotional motor displays and somatosensory information: postural feedback

Recent studies of dominance and submission have focused on experimental manipulations of body posture, demonstrating a causal link between body posture, mood, and behaviour. These studies, under the banner of "power posing", involve placing participants in the expansive and contractive body postures characteristic of dominance and submission and observing the effects on individuals' mood and task performance (Carney et al., 2010). Typically, these manipulations are disguised by a cover story, indicating to participants that they are participating in a separate experiment on body posture and heart rate. In such designs, body posture has been shown to enhance and prolong positive affect (Körner et al., 2019; Veenstra et al., 2017), increase risk-taking (Carney et al., 2010), and encourage higher rates of cheating and immoral behaviour (Yap et al., 2013). We refer to the broad set of studies focusing on the effects of experimental manipulation of body posture on psychological and cognitive outcomes as "postural feedback" paradigms.

Because of its diversity of behaviour effects, contexts, and the small-medium effect size the procedure produces, the power posing literature has been fraught with controversy, as some meta-analyses have called into question its claims (Jonas et al., 2017). However, recent reviews which consider a wider body of literature have found robust effects of expansive postures on the self-report and behavioural outcomes indicated above (Elkjaer et al., 2020), though earlier hormonal effects remain unverified. Part of the inconsistency appears to be attributable to the relationship between the nature of the pose adopted and the output measure: Körner & Schütz (2020) note that the postures associated with the recent "power posing" paradigm are only a specific, exaggerated subset of a broader literature which considers the psychological effects of erect and slumped postures. These postures may be associated with different outputs: the erectness dimension is proposed to be related to actual social rank and authentic pride (also referred to as the "prestige" route to power; Körner & Schütz, 2020), while the exaggerated "power pose" is suggested to be associated with aggressive dominance and hubristic pride.

4: Neuroscience of emotion in the somatosensory and motor systems

4.1: Emotions and somatosensation: imaging studies

Studies of somatosensation in emotion have revealed an important role for somatosensory structures in emotional processing. Early lesion studies by Damasio and colleagues (Adolphs et al., 2000; Damasio et al., 2000) demonstrated that individuals with lesions to primary somatosensory cortex (SSC) showed impaired emotion recognition abilities, and disordered emotion regulation. More recently, a number of studies have replicated these findings using Transcranial Magnetic Stimulation to inhibit somatosensory cortex; these studies demonstrate that inhibiting SSC produces impairments in emotion perception similar to those observed in lesion studies (Paracampo et al., 2017; Pitcher et al., 2008). Moreover, inhibition of SSC using transcranial magnetic stimulation (TMS) impairs affective empathy as indexed by self-reports (Borgomaneri et al., 2015) and somatosensory evoked potentials are modulated by viewing pain and affective touch in others (Bufalari et al., 2007). fMRI studies have also shown that activity in the somatosensory cortex carries predictive power for discriminating between emotion categories (Saarimäki et al., 2016). In addition to somatosensory cortex, the insula, a brain structure which receives sensory information from the viscera and internal organs (Uddin et al., 2017), plays a similar role in emotion experience and empathy, with functional imaging showing activation of the insula in response to emotional stimuli (Pugnaghi et al., 2011), empathy for others' pain (Lamm & Singer, 2010), and lesion studies showing disrupted affective processing in patients with insular lesions (C. L. Jones et al., 2010). Moreover, the amygdala, a subcortical region strongly associated with emotion (Sergerie et al., 2008), receives somatosensory input both from primary sensory cortices and directly from brainstem nuclei, allowing this region to represent the body state and carry out emotion-related computations (Bechara et al., 2003).

The role of somatosensation and visceral sensation is accounted for in an influential theoretical model of empathy, the Embodied Simulation model (Gallese & Goldman, 1998). This theory suggests that empathy, including both its cognitive and emotional aspects, emerges from vicarious experience of others' emotional states. The embodied simulation account hinges on mirror neurons, a general term for neurons which fire in response to both one's own actions and the observation of others' actions; these mirror neurons are thought to allow organisms to represent others' actions, intentions, and affective states by simulating them with one's own motor system (Rizzolatti & Craighero, 2004). Rather than reflecting a single organized area, mirror neurons have been reported in diverse areas, including premotor cortices, the supplementary motor area, the inferior parietal lobule, and, more recently, directly in SI and SII somatosensory areas (Keysers et al., 2010; Molenberghs et al., 2009). In the context of empathy, this mirroring is thought to involve mirror neurons in the somatosensory cortex, supported by the TMS studies described above (e.g. Gazzola et al., 2012). However, it may also involve a more extended loop. Prochazkova & Kret (2017) propose that empathy occurs via automatic motor mimicry via the motor mirror neuron system; somatosensory perception of this automatic mirroring thus triggers the emotional event in the observer, resulting in empathic awareness.

4.2: Emotions and the motor system: perception and action

Emotion-evoked actions and emotional body language in the brain has been most often studied using psychophysiological methods analogous to previous studies of emotion perception in faces. Typically, this has involved presenting individuals with images or videos of bodily expressions of emotion in neuroimaging experiments. Viewing these bodily expressions of emotion activates the fusiform gyrus and the amygdala, similar to other emotional stimuli (De Gelder, 2006; Hadjikhani & de Gelder, 2003); this work has further revealed a "fusiform body area", analogous to the fusiform face area, which appears to represent emotional bodies (De Gelder, 2006). Further similarities have been observed between emotional facial expressions and emotional bodies with respect to the N100 potential, with both types of stimuli modulating this marker of early cortical processing (Stekelenburg & de Gelder, 2004).

Motor and premotor cortices, areas of the brain which facilitate motor actions and movement planning, are also implicated in studies of emotion perception. Bodily expressions of fear and fear-related experimental contexts also appear to activate motor and premotor areas, which is suggested to prepare the organism to flee from danger (Butler et al., 2007; de Gelder et al., 2004). Further supporting the Darwin's view that emotions prime the organism for adaptive actions, studies have shown that emotions modulate motor-evoked potentials, a measure of cortico-spinal excitability (Hajcak et al., 2007): emotional stimuli irrespective of valence increased MEP amplitudes, indicating that an emotional context prepares the organism for action. This finding has been replicated numerous times, even showing that emotions modulate the motor thresholds of facial action units which are specific to the expressions of the particular emotion (e.g. muscles for smiling in happiness; Ginatempo et al., 2020). fMRI studies using multivariate pattern analysis have also shown a role for motor cortex in distinguishing different categories of emotional stimuli (Putkinen et al., 2021).

Imaging studies have further found strong connectivity between the amygdala and the motor cortex. DTI studies reveal a direct structural pathway between the amygdala and motor and premotor regions, particularly from the superficial nucleus (Grèzes et al., 2014). Moreover, the amygdala forms part of a resting-state functional network with motor and somatosensory cortices (Toschi et al., 2017), and this amygdala-motor connectivity is implicated in approach-avoidance behaviour (Leitão et al., 2022). Functional imaging studies have corroborated this role of the amygdala in motor control in emotional contexts, showing that the amygdala can enhance "freezing" responses to fearful stimuli in a stop signal task (Sagaspe et al., 2011).

4.3: Neuroscience of postural feedback

Despite their prominence in the psychological literature, neuroscience studies have rarely investigated postural feedback directly, and never feedback from expansive and contractive postures. In line with embodied accounts of emotion, which suggest that somatosensory perception of the individual's bodily state drive emotional experience, one plausible hypothesis is that postural feedback paradigms operate through somatosensory feedback. A limited body evidence has emerged supporting this notion, showing that somatosensory activity and emotional motor activity are linked. Kragel & LaBar (2016) found a somatotopic correspondence between emotion-related somatosensory activity in an emotion perception experiment and corresponding facial expressions: when viewing expressions such as happiness and surprise, which preferentially involve the lower half of the face, SSC was more active in areas corresponding to the lower half of the face, while for expressions such as fear and anger, which involve the eyes and upper face, SSC was more active in these areas. If, according to embodied simulation theory, emotion perception involves the recruitment of motor areas to simulate the observed emotions, these results suggest a direct correspondence between emotion-related motor programs and somatosensory activity. This, in turn, suggests a role for SSC in mediating postural feedback, whereby the deliberate adoption of emotion-related body postures triggers a somatosensory response which produced the associated emotion. These results are supported by somatosensory-evoked potential findings which show somatotopic responses in SSC corresponding to somatosensation from the bodily maps of emotion paradigm (Sel et al., 2020): Sel et al. found that somatosensory-evoked potentials in the hands discriminated between sadness and anger, where anger shows high activity in the hands (due likely to the anger's association with clenching the fists).

While evidence remains limited on the mechanisms of power posing specifically, previous studies have investigated the neural processing of social rank and hierarchy. Much work has been done in animal models, examining the neural processing of status signals and subordination behaviours (see Dwortz et al., 2022 for a review). This work has generally revealed roles for several prefrontal structures, such as dorsolateral prefrontal cortex (DLPFC), medial prefrontal cortex (mPFC), and orbitofrontal cortex (OFC) in processing status signals (Dwortz et al., 2022; K. K. Watson & Platt, 2012). Additionally, subcortical structures associated with emotion, reward, and conditioning, such as the amygdala, nucleus accumbens, and ventral tegmental area, are implicated, with reward regions responding to viewing subordinate individuals (Korzan et al., 2006) and regions like the amygdala and hippocampus providing neural substrates for fear conditioning of submissive behaviours (Jasnow & Huhman, 2001). Neuroimaging studies in humans have been more limited. Analogously to primate studies, a few fMRI studies have revealed roles for the DLPFC, mPFC, insula, and inferior parietal lobule in social status judgements and when learning social hierarchy-related information (Cloutier &

Gyurovski, 2014; S. Li et al., 2021; Zink et al., 2008); however, evidence is inconsistent, and other studies have found that these regions are associated with social processing in general, rather than specifically with dominance (Mah et al., 2004). Similarly, reward and limbic regions such as the ventral striatum, amygdala, and hippocampus have been shown to be activated in hierarchical interactions and social comparison (S. Li et al., 2021; Luo et al., 2018).

5. Individual differences in emotion processing

5.1: Personality and individual differences in socioemotional processing

While the above discussion has forwarded an evolutionary approach to emotion, in which the response tendencies associated with emotions are preserved across species, individuals vary considerably in their emotional response to the same situation. Such stable individual differences in social cognitive, emotional, and motivational tendencies are often grouped under the banner of personality (McAdams & Pals, 2006). The most popular current model of personality is the big five (Goldberg, 1990). The big five is a factorial model of personality in which individuals are described in terms of five traits: extraversion, agreeableness, conscientiousness, neuroticism, and openness to experience. Developed from factor analyses of person-descriptive adjectives (c.f. the lexical hypothesis, the idea that language already contains the necessary terms to fully describe individual differences in personality; Allport & Odbert, 1936), the big five shows strong test-retest reliability (Gnambs, 2014) and replicates its structure across cultures (McCrae et al., 1998). Big five traits are also predictive of numerous life outcomes, with openness and conscientiousness predicting educational performance (Noftle & Robins, 2007), neuroticism predicting rates of mental health issues (Widiger & Oltmanns, 2017), and agreeableness predicting social competence and career stability (Laursen et al., 2002). Big five traits have also found support in neuroscience studies, showing that traits such as extraversion/openness and neuroticism are related to dopaminergic and serotonergic circuits, respectively (DeYoung & Gray, 2009).

However, the big five does not constitute a complete taxonomy of personality factors. Even within the big five model, traits can be grouped or subdivided into a superordinate two-factor model (Stability and Plasticity; DeYoung, 2006) or subordinate traits called facets

(McCrae & Costa Jr, 1992). Moreover, additional traits exist which explain variance in behaviour over and above the big five (Feher & Vernon, 2021). These include factors such as the dark triad (Machiavellianism, Narcissism, and Psychopathy; Paulhus & Williams, 2002), emotional intelligence/alexithymia (Bagby et al., 1994; Salovey & Mayer, 1990), and trait affect, which refers to stable tendencies to experience positive and negative emotion (D. Watson et al., 1988). While each of these traits have broad analogues in the big five (e.g. dark triad traits correlate with agreeableness, negative affect correlates with neuroticism), they reflect more specific aspects of personality which frequently have greater explanatory power for specific behaviours (Feher & Vernon, 2021). Traits with particular relevance to emotion-related somatosensory and motor processing are outlined in the sections below.

5.2: Interoception, somatosensation, and emotion processing

While studies of personality based on the lexical hypothesis invariably uncover traits much like the big five, other, physiologically motivated individual differences exist which are relevant for emotion perception and experience. One such factor is interoception, which refers to one's ability to perceive changes in one's bodily state (Chen et al., 2021). Interoception is often measured with either tasks such as heartbeat-counting or heartbeat-tracking tasks, which measure an individual's ability to perceive their own heartbeat (Schandry, 1981), or using self-report scales (e.g. Mehling et al., 2012). These estimates can diverge: self-report scales typically measure the *propensity* for perceiving bodily sensations (i.e. the degree of focus on bodily sensations, termed interoceptive awareness), while tasks measure the *ability* to accurately perceive changes in bodily state (termed interoceptive accuracy; Garfinkel et al., 2015). Moreover, connectivity of the insula, which was previously discussed for its role in emotion processing, appears to be a factor guiding individual differences in interoceptive processing (Chong et al., 2017; Ueno et al., 2020).

As a mediating variable between physiological sensations and subjective perception, interoception is robustly associated with traits related to emotion processing. Interoceptive individuals exhibit enhanced emotional memory and more intense emotional experience (Pollatos & Schandry, 2008), including increased neural responses to emotional stimuli (Herbert et al., 2007). Despite this, interoception is also associated with enhanced emotion regulation abilities (Füstös et al., 2013), and is argued to be a crucial foundation of mindfulness interventions, with which it shares neural circuits in the insula (Gibson, 2019). In accordance with the embodied simulation account of empathy described above, trait interoception is associated with empathy (Fukushima et al., 2011), as well as with prosocial behaviour (Piech et al., 2017). Interoception is also correlated with the construct of emotional granularity (Ventura-Bort et al., 2021), which refers to the ability to make fine-grained distinctions between physiological and enactive states and represent them with separate emotion categories (Lindquist & Barrett, 2008). The shared aspect to these relationships is that interoception modulates the somatosensory component of emotion, allowing for more detailed, intense, and thoughtful approaches to emotion.

5.3: Psychological consequences of individual differences in power and rank

Above, we discussed how social status is expressed in dyadic interactions through body posture. However, these differences in social status themselves carry significant consequences for individual variation in affect, cognition, and personality. Individuals higher in social rank, indexed by objective measures of socioeconomic status, typically display less prosocial and more unethical behaviour (Piff & Robinson, 2017): for example, they are less generous in both experimental economic games and in actual donations (Piff et al., 2010), and cheat, lie, and steal more in a variety of experimental contexts (Piff et al., 2012). They also have less accurate perceptions of others' emotions (Kraus et al., 2010), even exhibiting reduced vicarious neural responses to others' pain (Varnum et al., 2015). These features are considered to be a result of the greater access to resources afforded to high-status individuals (Kraus et al., 2012). For such individuals, threats are less relevant and they have the resources to pursue their goals, exerting control and choice over the environment; they thus develop a self-focused cognitive style focused on their own actions, motivations, and goals. In contrast, lower-status individuals, with less access to resources, are constrained by the environment and the needs of their peers; this encourages a cognitive style focused on cooperation and others' needs. In line with this hypothesis, individuals higher in social rank also display greater risk-taking and greater positive affect (Anderson & Galinsky, 2006). In contrast, lower social status is associated with a wide variety of negative health outcomes (Sapolsky, 1982); this effect holds for subjective social status independently of objective measures, suggesting that the experience of low social rank is inherently stressful, irrespective of differences in material resources (Euteneuer, 2014).

Individual differences also exist in attitudes towards social dominance and hierarchy. One measure of these attitudes is the influential Social Dominance Orientation (SDO) construct, which describes individuals' tendencies to endorse or oppose hierarchical social relations (Pratto et al., 1994). Individuals high in SDO endorse statements like "some people are just inferior to others" and "this country would be better off if we cared less about how equal all people are" (Pratto et al., 1994). Much like actual social rank, SDO is negatively associated with empathy (Pratto et al., 1994), and is higher in high-status groups than in low-status ones (Sidanius et al., 2000). It also is predictive of the development of prejudice against a variety of minority groups (Kteily et al., 2011), and predicts individuals' career preferences for occupations which legitimize social hierarchy (e.g. law enforcement; Zubielevitch et al., 2022). SDO even predicts prejudice in the context of "minimal group" experiments, in which participants are arbitrarily assigned to a group and make judgements about their own group vs. others (Sidanius et al., 1994).

6. Open questions in the literature and aims of the thesis

6.1: The role of individual differences in emotion-related somatosensation

While somatosensation in emotion has a rich history, individual differences in emotional somatosensation have been less considered. As discussed above, physiological processes vary contextually with respect to different aspects of emotion; thus, they may vary between individuals as well according to individual variation in context appraisal and cognitive factors. As interoception is associated with differences in emotion processing, it stands to reason that emotional body sensations may also covary with personality and social variables. Moreover, previous work has shown that individuals higher in emotional granularity exhibit more diverse and situationally specific patterns of emotional physiology (Hoemann et al., 2021), suggesting a direct link between emotional somatosensation and individual cognitive differences.

As discussed above, the bodily maps of emotion paradigm is a behavioural method which allows experimenters to collect rich data on the subjective component of emotional somatosensation, without the computation of a large unspecifiable number of physiological features (Kreibig, 2010). As a behavioural measure, it is also appropriate for remote studies, which were necessary during the COVID-19 pandemic, and allows the collection of a large sample size necessary for individual differences research (Gignac & Szodorai, 2016). Operationally, studies using the bodily maps of emotion paradigm have shown that emotional somatosensation is altered in clinical populations, and some limited evidence supports associations with some personality traits, suggesting that the measure is sensitive to individual variation.

Thus, the first aim of this thesis was to use this paradigm to study individual variation in somatosensation. We applied the bodily sensation map (BSM) paradigm in a large online sample, as well as a detailed battery of personality measures. We then applied data science techniques (principal components analysis) to extract key features of the bodily maps, combine the personality measures into a smaller number of major dimensions, and relate these components. We applied a linear discriminant analysis classifier and cosine-distance based analyses to relate personality traits to somatosensory emotion differentiation, an aspect of BSMs considered by previous clinical studies (Torregrossa et al., 2019) and relevant for the emotional granularity construct discussed above. These results are described in chapter 2.

6.2: The role of individual differences in natural body posture

Similarly to emotional somatosensation, dominant and submissive body postures are usually considered as evolutionarily conserved aspects of emotion, consistent across organisms down the evolutionary tree. Expansive and contractive body postures are usually considered in terms of state-dependent modulation in emotional contexts: when an organism expresses dominance, they expand their posture to intimidate their interlocutor, or make themselves smaller to express submission. However, individuals vary in their natural, or habitual body posture as well; despite the existence of relatively temporally stable differences in dominance in humans and animals, the trait aspect of body posture has rarely been considered. Given the known associations between dominance and personality traits discussed in section 5.3, the relationship between stable aspects of dominant body posture and personality is a relevant research question that remains to be addressed.

A few studies have investigated variation in static body posture in relation to stable individual traits. Guimond & Massrieh (2012) set out explicitly to quantify the relationship between trait body posture and personality, using a posture classification scheme derived from physiotherapy; they found a relationship between upright body posture and extraversion, as quantified by the Myers-Briggs Type Inventory (a personality measure which has not received much empirical support; Pittenger, 2005); similarly, Notarnicola et al. (2017) found a relationship between postural asymmetry (scoliosis-like lateral deviations in standing posture) and neuroticism using a physiotherapy measure (the Barré line). Examining aspects of personality judgements from static photos, Naumann et al. (2009) also found a relationship between body posture and big five personality traits, but posture was defined subjectively and idiosyncratically by raters in terms of energetic vs. tired and tense vs. relaxed stances. Thus, the literature on trait posture and personality is small and limited; only a restricted set of personality measures have been applied, and measurements of posture have been idiosyncratic and guided by raters who may use global cues in making their determinations, rather than accurately rating low-level features such as posture (Redies et al., 2020). Moreover, the selection of personality measures and posture operationalizations have been largely unrelated to key theoretical dimensions such as social dominance.

The second aim of this thesis was thus to develop a measure of posture quantification based on social dominance theory and relate it to relevant personality dimensions. Like previous studies, we chose to quantify posture using photogrammetric posture assessment (Furlanetto et al., 2016) because of its ease of use and adaptability for online studies. Unlike previous studies, however, we used a machine learning algorithm to explicitly quantify postural angles, motivated by previous studies on emotional body language (Poyo Solanas et al., 2020) and postural quantification schemes adapted from the physiotherapy literature (Szucs & Brown, 2018). We then related this measure with a battery of personality measures motivated by the research on dominance and submission outlined in section 5.3, including the Social Dominance Orientation scale, measures of empathy, impulsivity, and positive and negative affect, as well as scales related to interoception and alexithymia which may serve as moderators. We validated our posture measure by measuring electromyography from relevant neck musculature and measuring its test-retest reliability. These results are outlined in chapter 3.

6.3: The neural mechanisms of postural feedback

As detailed above, no studies have directly addressed the question of postural feedback from a neuroscience standpoint. As such, it remains unknown which processes may be involved. The involvement of somatosensory cortex is suspected because of the role of somatosensory feedback in generating emotion experience and because of the relationship between emotional somatosensation and emotion-related motor behaviour; brain regions involved in hierarchy processing, such as the DLPFC, mPFC, IPS, and limbic and reward areas may also be implicated.

Electroencephalography (EEG) is a non-invasive brain imaging method which measures post-synaptic currents using electrodes on the scalp. While other neuroimaging methods such as functional Magnetic Resonance Imaging (fMRI) and magnetoencephalography (MEG) require participants to sit or lie immobile in large machines, EEG is an appropriate method to study body posture as it allows participants to be mobile. EEG allows for the measurement of a number of parameters related to somatosensory and motor activity: power in several frequency bands, including the beta band (Barone & Rossiter, 2021), mu rhythm over central sensors (S. R. Jones et al., 2010), and gamma power (Aoki et al., 1999) has been associated with somatomotor activity, and other bands are known to reflect cognitive and attentional factors (Buzsáki, 2006; Klimesch, 2012). Moreover, high-density electrode montages allow for reasonably accurate localization of the cortical sources of electrical activity (Lantz et al., 2003), allowing us to investigate the activity of specific regions such as those listed above (with the exception of subcortical and limbic areas, whose EEG signals are typically small).

The third aim of the thesis was thus to investigate the neural mechanisms of postural feedback paradigms, particularly the “power posing” design. To this end, we randomized participants into expansive and contractive posture conditions, and measured mood and resting-state EEG before, during, and after the posture. We then computed measures of frequency band power in EEG and compared these between posture conditions, and correlated these changes with mood effects. Moreover, we used source localization approaches to examine the regions involved in the effects of power posing, and controlled for muscle activity during the posture. These results are reported in chapter 4.

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Chapter 2: Antisocial and impulsive personality traits are linked to individual differences in somatosensory maps of emotion

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Antisocial and impulsive personality traits are linked to individual differences in somatosensory maps of emotion

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Abstract

Somatosensory experience is an important component of emotion, playing a prominent role in many traditional emotion theories. Nonetheless, and despite the extensive literature on the influence of individual differences in emotional processing, the relation between personality traits and emotion-related somatosensation has received little attention. Here, we addressed this question in a large sample of healthy individuals through the "bodily maps of emotion" behavioural paradigm, in which participants indicated the location and extent of their body sensations for the 6 basic and 4 additional social emotions (contempt, envy, pride, shame). We found that emotional somatosensation in specific body areas, including the heart, the stomach, and the head, was related to specific personality factors, particularly antisocial attitudes and impulsivity. Moreover, the similarity of individual participants' maps to the group-average was likewise negatively correlated with antisocial tendencies. Overall, our results suggest that differences in individuals' sensitivity to somatosensation from different body areas, as well as the typicality of their topographical patterns, may partly underlie variation in higher-order social and affective traits.

Introduction

Emotions are thought to reflect states of whole-body coordination, orchestrated by the brain to achieve evolutionarily salient goals. This physical response involves changes in the autonomic nervous system[1], including changes in heart rate, blood pressure[2,3], skin temperature[4], and respiration[5], as well as predisposing whole-body movements and postures[6]. The somatosensory feedback from these processes has a prominent role in many theories of emotion, including William James' early model[7], which proposed that the emotional experience emerges from the perception of physiological events automatically triggered by biologically-relevant (e.g., threat) stimuli. Other, later models added a cognitive component for the interpretation of these physiological processes in terms of specific emotional experiences[8]. Supporting these theories, recent studies using neuroimaging and brain stimulation techniques have found that somatosensory processes are key to processing emotions in both the self [9] and others[10,11].

Notably, there seems to be a general agreement in (some) characteristic bodily sensations of emotions, as evidenced by their representation in common idioms in many languages, such as the feelings of "butterflies in one's stomach" or the feeling of one's "heart sinking". More recently, a behavioural method has been developed to directly and quantitatively measure individuals' emotion-related bodily sensations. In the "bodily maps of emotion" paradigm employed by Nummenmaa et al.[12], participants "paint" areas of an on-screen manikin in which they feel increases or decreases in somatic sensation in response to particular emotions. This procedure reveals that different emotions have distinct patterns of associated somatosensation. For example, anger features heightened sensation (*activation*) in the chest, arms, and head, while sadness involves activation in the torso and reduced sensation (*deactivation*) in the limbs[12]. Interestingly, the spatial patterns of bodily maps of the different emotions converge throughout development towards those drawn by adults, which could reflect increasing accuracy and awareness of emotion-related bodily sensations with age[13].

Importantly, these *bodily sensation maps* (BSMs) have been shown to be consistent across different methods of emotion induction (e.g., recall, emotional faces and movies[12,14]), as well as concordant across cultures and between men and women [15]. Nonetheless, significant group differences in BSMs have also been reported, especially in clinical populations. For instance, Palser et al. found that BSMs drawn by children with autism spectrum disorders were less differentiated than those drawn by typically-developing children[16], whereas Torregrossa et al. found a similar pattern when comparing patients with schizophrenia to healthy controls[17]. Finally, Lyons et al. reported that BSMs of nonmedicated depressed individuals showed less overall activation compared to those drawn by healthy controls[18]. Taken together, these studies suggest that bodily maps of emotion capture variation in somatosensory processes as a function of disease. Given that disease states often reflect extreme versions of traits that exist in the general population (Cuthbert & Insel, 2013; Hudziak et al., 2007), it could be expected that variability in emotional somatosensation may also be present in healthy individuals, and related to personality factors.

Particularly relevant candidate traits are those that have been shown to modulate emotional sensations. For instance, individuals high in empathy tend to experience emotions as more differentiated[20], as do individuals high in interoceptive sensitivity[21]. This ability to experience fine-grained distinctions between emotional experiences is referred to as emotional granularity[22] and is predictive of resilience to psychiatric disease, as well as serving as a protective factor against aggressive tendencies and alcohol abuse[23]. Similarly, it is known that impulsivity is associated with impaired emotion regulation abilities[24], and that impulsive individuals are more inclined to act on strong positive and negative emotions[25].

Thus, the aim of this study was to employ the bodily maps of emotion paradigm to investigate individual differences in emotion-related somatosensation as a function of personality. Specifically, we conducted a data-driven investigation to determine if and how major personality traits -- such as positive and negative affect, impulsivity, pro- and anti-social attitudes and interoceptive ability -- were related to individual variations in emotional somatosensation. Based on previous research using the BSM paradigm in healthy and clinical populations[12,13,17], we examined two main aspects of emotional somatosensation in relation to personality. First, we considered somatosensation in different body areas, assessed using principal component analyses of participants' maps. Second, inspired by the emotional granularity research[23], we used a linear discriminant analysis classifier as a proxy for the between-emotion and between-subject distinctiveness of somatosensory maps. To further assess the relative contributions of these two factors to the observed relation between certain personality traits and classification confidence, we performed a post-hoc analysis in which we calculated the cosine distance between participants' maps and the group average and correlated it with those personality components. In brief, we found widespread relationships between personality variables and features of emotion-related somatosensation, including several features of BSMs predicting antisocial tendencies, interoception, impulsivity, and negative affect. These results suggest that personality is an embodied phenomenon, with individual differences in somatosensory processes having upstream effects on higher-level cognition and personality.

Methods

Participants

A total of 362 volunteers (mean age = 20.9 years, SD = 2.0; 54 males) were recruited as part of a broader online study on body posture, emotional perception, and personality. Participants were recruited from the general public using social media advertisements (n = 63) and from the McGill University Department of Psychology extra credit participant pool (n = 299). The study was approved by the McGill University Faculty of Medicine Institutional Review Board (IRB# A00-B62-21A) and written informed consent was obtained from all participants. They were either compensated with CAD 15$ for their participation or received course credit. The study procedures were carried out in accordance with the Declaration of Helsinki.

Experimental procedure

The study consisted of four 15-minute experimental modules run on a JATOS server[26], hosted by the International Laboratory for Brain, Music, and Sound Research (BRAMS), using the jsPsych library[27]. One module consisted of an unrelated behavioral task, not reported here. Two other modules consisted of personality questionnaires (described in *Personality measures*, below).

The final module consisted of the bodily maps of emotion task from Nummenmaa et al. [12,14]. Participants were presented with emotion words and two silhouettes of bodies and asked to paint, using a mouse, areas of their body whose activity they felt increasing or getting stronger on one silhouette (referred to as "activation" in the text; coloured in red), and areas whose activity they felt decreasing or getting weaker on the other (referred to as "deactivation"; coloured in blue), when experiencing that emotion. "Paint" was added continuously, such that increasing the time spent over a given region increased the opacity of colour over that region. Further details of the procedure are described in Nummenmaa et al.[12]. Participants created body sensation maps (BSMs) for the six basic emotions (anger, fear, sadness, happiness, disgust, surprise) as well as four social emotions (pride, shame, contempt, and envy) of the 14 reported in Nummenmaa et al., to reduce the duration of the experiment.

Finally, participants answered five questions about their experience of each emotion, drawn from Nummenmaa et al.[14]: i) how much do you feel this emotion in your body, ii) how much do you feel this emotion in your mind, iii) how pleasant does this emotion feel, iv) how much control do you feel you have over this emotion, and v) how frequently do you experience this emotion. Participants answered these questions on 5-point Likert scales immediately following completion of each bodily map.

Personality measures

A battery of personality questionnaires was administered in two modules (personality modules 1 and 2). Personality module 1 included the Barratt Impulsivity Scale (BIS-11; Patton et al., 1995), the Big Five Inventory (BFI; John et al., 1991), the Interpersonal Reactivity Index (IRI; Davis, 1983), the Multidimensional Assessment of Interoceptive Abilities Version 2 (MAIA-2; Mehling et al., 2018), the Levenson Self-Report Psychopathy Scale [32], the Social Dominance Orientation scale (SDO; Pratto et al., 1994), and the Life Orientation Test Revised (LOT-R; Scheier et al., 1994). Personality module 2 consisted of Positive and Negative Affect Schedule – Expanded (PANAS-X; Watson & Clark, 1999), the Spielberger State-Trait Personality Inventory (STPI; Spielberger & Reheiser, 2009), the State-Trait Anger Expression Inventory (STAXI; Spielberger et al., 1999), the Toronto Alexithymia Scale (TAS; Bagby et al., 1994), the Cognitive Emotion Regulation Questionnaire (CERQ; Garnefski & Kraaij, 2006), and the Psychological Well-Being Scale (PWB; Ryff, 1989). These scales were chosen due to their relevance to trait emotionality and emotion processing in healthy populations. Although state emotion in the PANAS-X and STPI was also collected (for the behavioral task), only trait emotionality was considered here, as we were interested in the relation between body sensation and stable personality traits.

Data preprocessing and reduction

We screened the body map and personality data for random responding and non-compliance as follows: For the body map data, we visually inspected each map, removing participants if they had drawn clear symbols (e.g. smiley faces, hearts), marked only single dots rather than colouring in areas, or circled regions instead of colouring them in (these behaviours indicated a lack of understanding of, or willingness to follow, the instructions). Participants were also removed if they failed to colour any area for 3 or more emotions (i.e. more than 25% of body maps). For the personality data, a multivariate outlier detection procedure was used to screen for random responders [41]. Since there were more questions in the personality battery than participants (536 vs. 362), we conducted the Hadi procedure 1000 times on random subsets of 50% of the questions in the personality battery. Participants who were marked as outliers at the 5% significance level in more than 10% of these random splits were removed.

Data reduction of personality and body maps: principal component analyses and correlation

To reduce the personality and BSM data, we performed principal component analyses on each, separately, using the same approach for each data type. For BSM data, pixels within the body silhouette were taken as variables (50,364 pixels total) and individual maps were taken as observations: thus, there were 10 observations per participant, corresponding to that participant's map of each emotion. For the personality data, each personality scale was its own variable, and subjects were observations. The number of components retained in each PCA was determined using a permutation test procedure. In order to account for heterogeneous noise which may be present in both datasets (particularly the body maps), we used the procedure from Hong et al.[42]. Briefly, the eigenvalues obtained from the PCA were compared with the eigenvalues obtained from 1,000 permutations of the data created by applying a matrix of random sign-flips, rather than shuffling the data as in a standard permutation test. For both the personality and body map PCA analyses, components whose eigenvalue exceeded the 95th percentile of this permutation distribution were retained. To improve interpretability, factor rotation was then performed on the retained components using Quartimax rotation. Significant loadings for each retained component were then calculated using bootstrapping[43]: 1,000 bootstrap resamplings of the data were computed, and bootstrapped loading z-scores were created by dividing each loading by its bootstrap standard deviation.

Our first analyses then consisted of correlating the components obtained from the personality and body maps PCAs with each other using Spearman's rank correlation. As over 50 components were obtained for the bodily maps using the permutation test, a smaller number of components (4) was selected for the correlation analyses by visual inspection of the eigenvalue plots. Multiple comparisons were corrected for using False Discovery Rate correction[44].

Emotional granularity: linear discriminant analysis classification and analyses of differentiation and representativeness

We trained a linear discriminant analysis (LDA) classifier to classify emotions from participants' BSMs, and related the confidence of this classification to personality factors. Linear discriminant analysis classifiers are a family of classifiers which attempt to find a linear decision boundary between classes in a multidimensional space. Here, the data used in the LDA classifier consisted of the emotion- and subject-specific scores of the significant BSM principal components obtained in PCA described above. These data were then used to predict the emotion category of each map. The LDA classifier was trained using the default settings of the *fitcdiscr* function in MATLAB R2020a, with the prior distributions for each class taken as the empirical frequencies within each class. Significance of the classifier was assessed using standard parametric statistics (χ^2 test) and a multiple cross-validation procedure: 1000 random splits of the data were created, and for each split the classifier was trained on one half of the data and tested on the other half. A p-value was generated by calculating the percentile of 10% (chance level) within the distribution of test-set accuracies.

As our subjects did not belong to *a priori* different groups (e.g., clinical and healthy, as in Torregrossa et al.[17]), to relate classifier accuracy to personality we used the posterior probabilities generated by the LDA as an index of the confidence of the classifier in classifying any given map [45]. These classifier confidence scores were then correlated with the personality PCA components obtained above. Specifically, we calculated the posterior probability that each map would be correctly classified as the emotion label for which it was drawn; we then averaged these probabilities for each subject to obtain a subject-level classification confidence score. This classification confidence score was then correlated with the personality PCA components using Spearman's rank correlation.

In order to accurately discriminate data from different classes, classifiers such as linear discriminant analysis need not only high inter-class variability, but low within-class variability [46,47]. These properties can be related to the *differentiation* and *representativeness* of participants' maps, respectively. Differentiation refers to how distinguishable participants' maps are between emotions; that is, does a participant paint the same sensation map for every emotion, or are emotions differentiated in the magnitude or location of their sensations? Representativeness, on the other hand, refers to the degree to which an individual BSM resembles the group-average map: that is, does a participant's map of a given emotion resemble the group average, or is it instead idiosyncratic or random?

We sought to assess the extent to which any correlation between personality and classification accuracy was driven by each of these properties. In order to determine to what extent differences in classifier accuracy were driven by differentiation and/or representativeness in BSMs, we operationalized these concepts using cosine-distance-based metrics. Differentiation was operationalized as the within-subject average pairwise cosine distance between emotions in the body-map PCA space (i.e., higher values represented larger differentiation between emotions). Representativeness, on the other hand, was implemented as a participant's average pairwise cosine similarity between their maps and the group average for each emotion (i.e., higher values corresponded more representative BSMs).

We used cosine similarity/distance as we were interested in pattern similarity across emotions/subjects, regardless of the magnitudes (pixel values). This approach, commonly used in machine learning research for evaluating the similarity of images [48], was chosen in order to minimize individual differences in the interpretation of instructions and the amount of painting, and is and equivalent to measures used previously to compute similarities in BSMs across groups[13].

Results

Correlation between personality and bodily sensation maps

After removal of participants based on visual inspection of bodily maps and the multivariate outlier-detection procedure for personality (see *Methods*), the final dataset consisted of 228 participants (mean age 20.49, SD = 1.58; 32 males). The principal components analysis on the personality data, designed to reduce the number of comparisons and yield interpretable findings from our large battery of personality scales, yielded 5 statistically significant components (Figure 2): components loaded mainly on (1) negative components of PANAS, anxiety, and negatively on optimism, environmental mastery and self-acceptance (henceforth named *Negative Affect*); (2) psychopathy and social dominance and negatively on empathy (*Antisocial Attitudes*); (3) positive affect and negatively on anxiety and depression (*Positive Affect*); (4) impulsivity and secondary psychopathy and negatively on conscientiousness and attentiveness (*Impulsivity*); and (5) positive on interoceptive abilities and emotional awareness and negative on difficulty to describe and identify emotions (*Interoception*). Full component loadings with bootstrap confidence intervals are reported in the supplementary materials (Supplementary Figure 1).

For the bodily sensation maps, the parallel analysis yielded 55 components which were significant above the permutation threshold (Figure 3a, top). The first 4 of these components are displayed in Figure 3b. The first component reflected mainly activation in the head and upper chest (referred to as *Head Activation*), and was strongly represented in anger, happiness and pride. The second component reflected activation in the stomach area (*Stomach Activation*), and was mainly present in disgust and, to a lesser degree, in fear and shame. The third component reflected deactivation in the limbs, particularly the legs and feet (*Legs Deactivation*); this component was particularly present in sadness and shame, as well as fear and disgust. Finally, the fourth component represented activation in the heart (*Heart Activation*) and was present in all emotions, but particularly strongly in happiness, pride, and surprise.

To determine if there were significant relationships between specific aspects of emotional body sensations and personality, we correlated subjects' emotion-averaged BSM and personality PCA components. Full results of these correlations are reported in Table 1. Only two correlations survived FDR correction for multiple comparisons, with a third being marginally significant: A negative correlation of *Antisocial Attitudes* with *Stomach Activation* ($\rho = -.21$, $p = 0.002$, $p_{FDR} = .03$) and with *Heart Activation* ($\rho = -.19$, $p = 0.003$, $p_{FDR} = .03$), and an almost-significant negative correlation of *Impulsivity* with *Head Activation* ($\rho = -.17$, $p = 0.01$, $p_{FDR} = .06$; Figure 3c).

Table 1: Correlations of personality and body map principal components. Spearman's rank correlation coefficients are presented with uncorrected p-values in brackets. Significant or marginal results after FDR-correction for multiple comparisons are highlighted in bold.

	Head Activation	Stomach Activation	Legs Deactivation	Heart Activation
Negative Affect	-0.056 (0.40)	-0.080 (0.23)	-0.057 (0.39)	-0.051 (0.44)
Antisocial Attitudes	-0.091 (0.17)	**-0.207 (0.002)**	-0.018 (0.79)	**-0.194 (0.003)**
Positive Affect	0.007 (0.92)	0.027 (0.69)	-0.052 (0.43)	-0.049 (0.46)
Impulsivity	**-0.172 (0.01)**	-0.054 (0.42)	0.005 (0.94)	-0.115 (0.08)
Interoception	0.023 (0.73)	0.096 (0.15)	-0.134 (0.043)	0.105 (0.12)

Table 2- 1: Correlations of personality and body map principal components.

Emotional granularity in bodily maps of emotion: Classifier confidence

Next, we considered whether a BSM-based measure of emotional granularity (i.e., tendency to experience fine-grained distinctions between emotions[23]) might be related to personality features. Following Torregrossa et al.[17], we considered the linear discriminant analysis BSM classifier accuracy as a proxy for emotion sensation differentiation. All 10 emotions were classified well above chance in an all-against-all classification scheme (average classification accuracy = 29%, chance level = 10%; $\chi^2 = 1165.1$, $p < .001$; Figure 4a). The classifier was also significant following cross-validation ($p = .01$). We then correlated each subject's average classification confidence (defined as the posterior probability that a given emotion would be classified as the correct emotion; see Methods) with that subject's personality PCA components. We found that classification confidence was negatively correlated with *Antisocial Attitudes* ($\rho = -.19$, $p = .004$, $p_{FDR} = .02$) and *Negative Affect* ($\rho = -.13$, $p = .04$, $p_{FDR} =$

.09; Figure 4b), as well as marginally positively correlated with *Interoception* ($\rho = .13$, $p = .05$, $p_{FDR} = .09$).

Emotion representativeness and differentiation: Cosine-based distance metrics

To assess the contributions of between-emotion distinctiveness and between-subject consistency to classification accuracy, we computed cosine-based distance scores in BSM PCA space (see Methods for details). Considering the representativeness of participants' BSMs (i.e., similarity to the group mean), there were significant negative correlations with *Antisocial Attitudes* ($\rho = -.18$, $p = .01$, $p_{FDR} = .03$; Figure 5) and *Impulsivity* ($\rho = -.17$, $p = .01$, $p_{FDR} = .03$), respectively, as well as a trend for a positive correlation with *Interoception* ($\rho = .13$, $p = .06$). In contrast, there were no significant correlations between emotion differentiation and personality factors, although there was a trend for a negative correlation with *Interoception* ($\rho = -.14$, $p = .05$).

Antisocial Attitudes also showed a trend towards a positive correlation with emotion differentiation ($\rho = 0.12$, $p = 0.1$); that is, higher *Antisocial Attitudes* scores were associated with lower BSM representativeness but higher emotion differentiation.

Validation analyses: correlations with subjective reports of bodily/mental salience

As a validation of our analyses, we correlated the BSM PCA components with participants' subjective reports of how much they felt each emotion in their body or their mind, respectively. We found that the *Heart Activation and Leg Deactivation* components of the BSMs were positively ($\rho = 0.17$, $p = 0.009$) and negatively ($\rho = -0.16$, $p = 0.01$) correlated with body salience, respectively. Meanwhile, the *Head Activation* BSM component was significantly correlated with mental salience ($\rho = 0.23$, $p = 0.0004$).

Discussion

Using a hypothesis-free, data-driven approach, we investigated the relation between individual differences in personality traits in healthy individuals and their representation of whole-body patterns of somatic sensation using the bodily sensation maps (BSM) paradigm[12]. In agreement with previous findings, we obtained consistent patterns of somatosensation which are stable across individuals. Indeed, the group-level bodily maps of emotions found in our study were highly similar to the ones originally presented by Nummenmaa and colleagues (Figure 1). However, our findings also suggest that inter-individual variability exists in these maps, and that some of this variation is systematically related to personality (although the nature of our analyses does not allow for a determination of the causal direction of this relation). Specifically, we observed that several dimensions of participants' emotion-related somatic sensations, including the amount of "activation" in the heart, viscera, and head, were associated with different personality features, namely antisocial tendencies, interoception and impulsivity. Moreover, we showed that patterns of variability in participants' BSMs (including emotion differentiation and representativeness of the group-average) were also associated with personality. Overall, our results confirm previous work suggesting a role for somatosensation in emotion awareness and understanding, and extend it by providing possible mechanisms for some of the observed inter-individual variability and its relation to particular personality traits.

Dimensions of emotional somatosensation and personality traits

We found that the bodily maps of emotion coloured by participants were well described by a lower-dimensional space composed of localized components representing different body areas. The first component was strongly localized to the upper head, and was implicated in most emotions; as such, it may index the somatic experience of cognition, as it correlated with the mental salience of emotions (see Results – Validation Analyses). Supporting this notion, recent work using the BSM paradigm has shown that "cognitive feelings", such as the feelings associated with imagining, remembering, or being attentive, also have somatic components, and that these are often localized to the head [14]. The second component (*Stomach Activation*) mainly reflected activation in the stomach, and was primarily represented in disgust; this component may thus reflect visceral activity, including sensations from the gut[49]. The third component (*Legs Deactivation)* reflected contributions from negative, distress-related emotions such as sadness, fear and shame, as well as disgust. As this component represented deactivation (i.e., the sensation of the body getting weaker or heavier), this may reflect aspects of the freezing response to stress, which has been suggested to be implicated in disorders such as depression[50].

Interestingly, the *Stomach Activation* component also loaded strongly on these emotions, perhaps reflecting alterations in digestion and gastric signalling which occur during stress[51]. Finally, the fourth component (*Heart Activation*) was present particularly in high-arousal positive emotions such as happiness and pride, as well as surprise. Thus, this component likely represents perceived heart rate changes associated with the physiological reactions elicited by these emotions[2].

The finding that the amount of colouring in the heart and stomach in body maps of emotion was negatively correlated with the *Antisocial Attitudes* personality component suggests that somatosensory representations of emotion, particularly those associated with physiological responses, are reduced in individuals with antisocial tendencies. This finding is consistent with a considerable body of previous work implicating somatosensory processes in social and empathic perception. For instance, TMS studies have found that inhibition of somatosensory cortex reduces participants' skill at judging emotional expressions and performance on an affective go/no-go task[11], and imaging and lesion studies have implicated somatosensory cortex in the perception of emotional facial expressions[10,52,53], as well as in empathy for pain[54].

Our result showing that emotional somatosensation from the heart is important for social perception and prosocial behaviour is also in agreement with a large body of literature on the importance of cardiac interoception in emotion processing. As changes in heart rate accompany changes in arousal and stress, the heart is one of the most commonly implicated structures in emotion experience[2]. Moreover, cortical processing of heartbeat signals has been associated with first vs. third-person perspective taking, a process which underlies theory of mind and thus empathic understanding[55]. For instance, neural processing of heartbeats has been shown to be increased during an empathy task in which participants made affective or physical judgements of facial expressions[56]. Our results support the growing view that cardiac interoception is a key substrate of empathic individuals' ability to understand their own and others' emotions. Similar interpretations apply for somatosensation from the stomach, as digestion and gastric signals are also affected by emotions[57]. Moreover, gastric signals have likewise been proposed to underlie first-person perspective and thus, indirectly, the ability to mentalize and understand the perspectives of others[58].

A number of theories of psychopathy implicate blunted emotional responses in the disorder, providing an interesting context to our findings. For example, the low-fear model of

Lykken[59] proposes that psychopaths have reduced fear responses to aversive stimuli, preventing moral conditioning, while the Violence Inhibition Model and Integrated Emotion Systems models[60,61] propose deficits in amygdala functioning as key to the condition. Our findings showing reduced emotional somatosensation in individuals high in antisocial personality traits support these theories, and point to altered emotional somatosensation as a potential mediating mechanism between neurobiological alterations in psychopathy and the experience of blunted affect. Furthermore, our findings extend these theories and the relevance of altered emotional experience to non-clinical antisocial traits, such as non-clinical psychopathy, low agreeableness, and social dominance.

Interestingly, the *Head* Activation BSM component correlated negatively with *Impulsivity*. As discussed above, this head activation component may be associated with the somatic experience of cognition, following its correlation with mental salience and in accordance with recent work using the BSM paradigm[14]. Physiologically, this may be related to muscle activation: for example, cognitive effort is associated with activation of the frontalis muscle in the forehead, which may be a reflection of the common experience of "furrowing one's brow" when deep in thought about a difficult subject[62]. Thus, despite the common idiomatic expression that impulsive people are "hot-headed", our results suggest that these cognitive feelings are reduced in these individuals, which may contribute to the reduced influence of top-down cognitive control during emotion experience in impulsive individuals[63]. However, the directionality of this effect is unclear – while somatosensory representations of emotion may influence personality development, it is equally possible that reduced top-down control in impulsive individuals extends to the somatosensory experience of emotion as well.

Together, our findings suggest that dimensions of emotional somatosensation, which cut across individual emotions, are relevant for personality. While bodily maps of emotion have been discussed previously as categorically distinct, evolutionarily-determined physiological signatures of basic emotions[12,15], our results here suggest a more dimensional approach. Most of the principal components we observed were represented strongly in multiple emotions, rather than being specific to any given one. Moreover, our findings considering the distance between BSMs (see below), revealed that the group-average maps of emotion are substantially more similar than any individual subject's maps. That is not to say that the BSMs for the different emotions were indistinguishable from each other, as the classifier was able to accurately classify the body sensation maps well above chance. However, instead of the current interpretation that the accurate classification of BSMs reflects emotion-specific, categorically distinct maps, our results point to a circumplex model of emotional somatosensation: in this model, sensations for different emotions are described by the relative weights of underlying components, such as the heart, head, and stomach activation components observed in the present study (see Clark-Polner et al.[64] for a similar argument regarding classifiers and basic emotions).

Emotional granularity and body sensation maps: the importance of representative and accurate somatosensation

Our second major set of findings concerned emotional granularity, as measured by the similarity of bodily maps across emotions and participants. Emotion differentiation was previously assessed by Torregrossa et al.[17] and Palser et al.[16] using the classifier approach described above to argue that BSMs were less differentiated in autism and schizophrenia patients with respect to healthy controls. Following this work, we trained a classifier on our BSM data, taking its classification confidence as a measure of emotion differentiation. We followed up this analysis by calculating participants' emotion differentiation and representativeness (indexed by cosine distance-based metrics), to determine the driving factors underlying accurate classification of emotions. We found that interoception was positively associated with classification confidence, while antisocial attitudes and negative affect were negatively correlated. In the case of antisocial attitudes, the lower classification confidence occurred despite the concomitant positive correlation with intra-individual, inter-emotion distance. These counterintuitive findings can be explained by the fact that BSM representativeness (distance to the group mean) and differentiation (within-subject distance between emotions) were in fact negatively correlated ($r = -.76$). Indeed, the group-average templates exhibited considerably higher similarity between emotions (average cosine similarity = 0.77) than most subjects' individual BSMs (average cosine similarity = 0.17). As mentioned in the Methods section, successful emotion classification requires both high inter-class and low intra-class variability[46,47]. Results from the classification analysis suggest that the higher inter-emotion BSM differentiation in participants with high antisocial traits was not sufficient to confidently categorize them accurately, given their higher dissimilarity to the group averages. Consistent with this, we observed that the correlation between *Antisocial Attitudes* scores and emotion differentiation was in fact mediated by its relation with representativeness (Sobel test; $p = .04$).

Emotional granularity reflects the experience of fine-grained distinctions in emotion [22] and is an important aspect of individual variation in emotion experience. That is, it has a wide variety of associations with personality and life outcomes[65]. Methods of assessing emotional granularity typically involve correlating instances of emotion labels collected over experience sampling, with the rationale that a lower correlation implies a more differentiated experience of emotion[66]. However, the bodily maps of emotion paradigm has the key advantage of producing a multidimensional representation of an individual's actual emotional experience, allowing for the direct and quantitative measurement of emotion differentiation. Indeed, previous studies have used classification accuracy as a proxy for emotion differentiation, showing that emotions are less differentiated in schizophrenia [17]. Likewise, in our data classification confidence was related to several personality factors previously associated with emotional granularity, including negative affect[67], interoception[21], and prosocial tendencies such as empathy[20]. Thus, the BSM paradigm allows for a conceptually different, complementary assessment of emotional granularity, focusing on the similarities and differences between the experience of different emotions, in contrast with traditional methods that instead assess the temporal coherence between the occurrence of different emotions.

Classifiers such as the linear discriminant analysis used in our study attempt to maximize the ratio of between-class variance to within-class variance[46]. Thus, associations such as the ones we found between classification confidence and personality may be driven either by differences in the degree of intra-individual separation between classes, or in the degree of inter-individual homogeneity within classes. In our study, we found that the correlation of empathy with classifier confidence was driven primarily by its strong association with the representativeness of participants' maps; that is, how much any given map resembled the group average. Our results thus suggest that within-category homogeneity across individuals is a key factor in determining associations with personality, with between-category variability less so, at least the personality and granularity measures considered here. This result carries implications for research on emotional granularity, where the aspect of within-category, between-subject homogeneity is rarely considered. Indeed, it suggests that some of the proposed benefits of emotional granularity and observed relationships with personality (such as its relationship with empathy) may stem from the accuracy or representativeness of an emotional experience, and not just (or mainly) from its distinctiveness relative to the experience of other emotions. Interestingly, however, negative affect correlated significantly with emotion differentiation, but not with any of the BSM PCA components or with our measure of representativeness: this suggests that there may be different physiological routes to undifferentiated emotion experience. Further research is needed to investigate this possibility, as well as to apply our design to other factors associated with emotional granularity such as resilience and psychosocial functioning[65].

Interestingly, the finding that antisocial attitudes negatively correlate with BSM representativeness suggests that another key feature of this personality trait may be that it places the individual in the margins of the distribution of emotional somatosensation among the population, thus reducing their ability to recognize and interpret other people's emotions. According to the Perception-Action Model of empathy[68], observation of the emotional state of another activates corresponding emotional states in oneself, including their somatosensory component. If there are individual differences in emotional somatosensation, then the vicarious emotional representation in the self may be more or less similar to the other's. Thus, if antisocial individuals' emotional somatosensation is idiosyncratic, this may reduce the likelihood of affective empathy with other individuals' expressions, by virtue of the reduced overlap between their respective somatosensory representation of emotion. Consistent with this hypothesis, several studies have shown that psychopaths show reduced somatosensory and motor response when viewing expressions of pain or emotion in others [69–71]; but see [72]. Our findings also agree with previous findings by Sachs et al. that empathy was predictive of self-other overlap in BSMs[73]; indeed, if high-empathy individuals are closer to the group-average BSMs, they will likely overlap more with a larger set of others' maps.

Processes underlying BSM generation: somatosensation, appraisal, and categorization

In order for the relationships observed between participants' BSMs and personality to be interpretable, a theoretical model of the processes underlying the BSM task is informative and necessary. Recently, an integrative model of physiological, appraisal, and cognitive factors in emotion has been proposed [74], which can provide a useful framework within which to interpret our findings. Following this model, we propose that there are 4 stages involved in the production of a participant's bodily sensation map where individual variation might have an effect on the BSMs. First, individual differences in the actual emotion-related physiological response: for example, a participant who is more physiologically reactive to threats[75] and has a larger heartrate increase in response to fearful situations may experience greater changes in emotional somatosensation, and thus colour more intensely on the BSM task. Second, variation in an individual's sensitivity to emotional somatosensation: if an individual is more aware of their somatic sensations, they will be more able to report them in the body maps task. Third, variation in an individual's conceptual ability to associate somatosensation with emotion: for example, if an individual experiences sensation from their heart whenever they feel fear, but interpret it as symptoms of a cardiac abnormality (as in somatization: [76]) they will not report sensation from the heart in the fear BSM. Finally, memory retrieval processes may also affect the drawing of the maps: a participant's recollection of their emotional experience may influence the intensity or specificity of the maps.

Existing data suggests that the second variable listed above (variation in sensitivity or attention to emotional somatosensation) produces the largest contribution to inter-individual variation in BSMs. The original study by Nummenmaa et al. found that BSMs were highly similar between different modes of evoking emotion, including emotion labels, emotion-inducing videos, and asking participants to colour BSMs for other individuals based on emotional facial expressions. This suggests that variation at cognitive categorization and memory levels may be small, though BSM similarity between modalities was only assessed at the group level, and not at the individual level (i.e., within-individual similarity of BSMs across the different evoking modes). In contrast, a previous study [77] found that interoceptive accuracy, using a heartbeat detection task, was predictive of magnitude and specificity of BSM colouration, suggesting that there may be significant variation at the level of individual sensitivity to somatosensation; our data support this, finding correlations between BSM factors and interoceptive sensitivity. Nonetheless, future work should confirm the relationships found here using different modes of evoking the emotions for each BSM, and by adding other, more objective measures, for example using physiological recordings or neuroimaging techniques.

Limitations and Future Directions

While the present work addresses the main questions raised in the introduction, there are a number of issues that may limit the generalizability of our findings. The majority of our participants were university students taking psychology courses, thus likely of a medium-high socioeconomic status, and thus not representative of the general population on several psychological dimensions[78]. While corrected for multiple comparisons, our p-values also were fairly high. Thus, the results reported here may be considered somewhat preliminary, and, as with any initial set of findings, there is a need for replication, especially using broader samples[79]. Moreover, our sample was composed mostly of (self-identified) women (as do most studies recruiting volunteer healthy participants), leaving open the question of the generalizability of our findings to men and non-binary individuals. However, we note that previous research using the bodily maps of emotion paradigm has found that BSMs are largely consistent across cultures and sexes[15], suggesting that these factors may not substantially affect our results. Nonetheless, further studies designed to directly test this should be carried out.

The present work demonstrates associations between dimensions of personality and emotional somatosensation. However, given the a cross-sectional and correlational nature of our procedure and analysis, respectively, we are unable to establish causal relationships between personality and somatosensory processes. Future studies are necessary to determine this, as well as which of the different factors underlying emotional somatosensation, as described above, play a role in this relationship.

While the bodily maps of emotion task is useful for determining the location of emotion-related somatosensation, a key limitation of the method is that the quality of emotional somatosensation is not well-specified: the task asks participants simply to paint “activation” or “deactivation”, and typically these labels are treated as two poles of a single activation-deactivation continuum. However, somatosensation for different emotions may have distinct phenomenology – for example, the tightness in the chest felt for anxiety is not the same sensation as the full, brimming sensation felt in happiness or pride, yet both may be coloured as “activation” in the bodily maps procedure. Thus, future work should expand the bodily maps of emotion paradigm by incorporating different qualities of somatosensation.

Conclusion

Patterns of body sensation are crucial for the experience of emotion, but individual differences in these sensations have rarely been studied in the context of personality. Using a behavioural paradigm in which participants "paint" areas of their body where they feel sensation during different emotions, we investigated the relationship between people's bodily sensations of emotion and their personality using data-driven principal components regression. Several aspects of participants' emotion-related body sensations were related to antisocial tendencies and impulsivity, including activation in the heart, viscera, and head. Furthermore, classification accuracy was related to antisocial attitudes and, to a lesser degree, interoception, an effect which was mainly driven by the category-representativeness of BSMs, rather than intra-individual emotional differentiation. These results suggest that while emotions have generally consistent somatosensory fingerprints, individuals may be more or less sensitive to different aspects of these sensations, and that these differing somatosensory representations of emotion may be related to specific aspects of personality.

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Declaration of Competing Interests

The authors declare no competing interests.

Data Availability Statement

The data from the above study is available from the corresponding author upon reasonable request.

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Figures

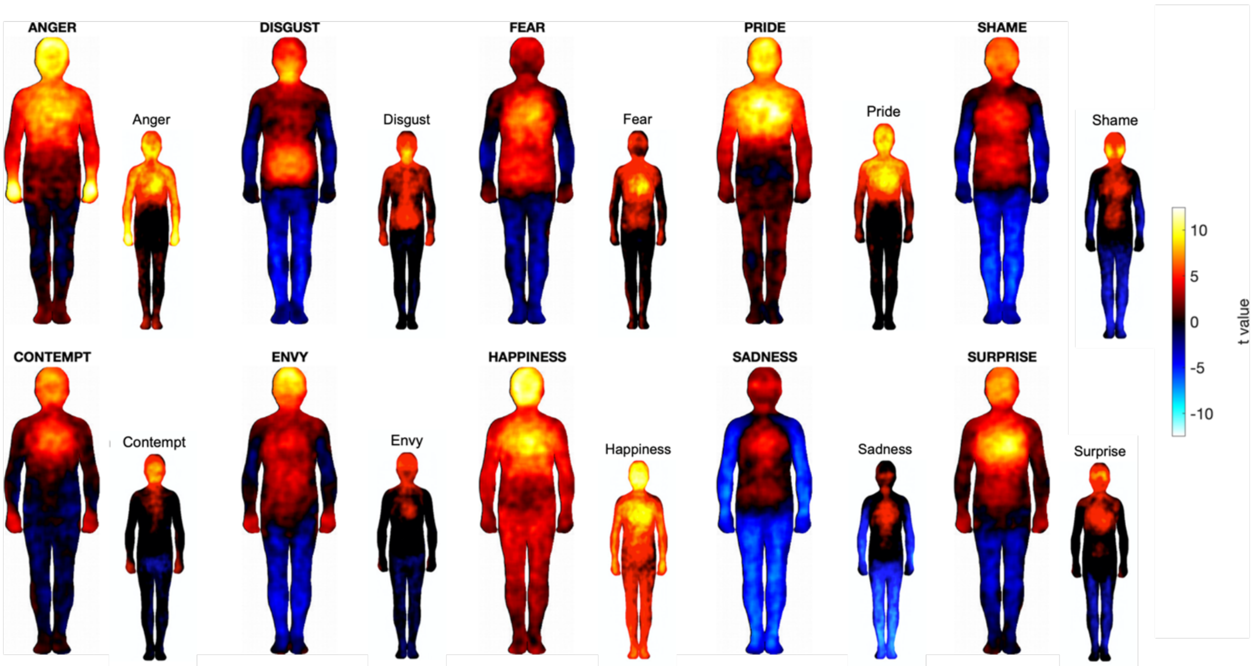

Figure 2- 1: Group-level t maps for the bodily sensation maps analyzed in the present study.

Figure 1. Group-level t maps for the bodily sensation maps analyzed in the present study. Large silhouettes show t-statistics from a t-test against zero calculated at each pixel in the body maps. Small silhouettes show the corresponding maps from Nummenmaa et al. (2014), to indicate correspondence.

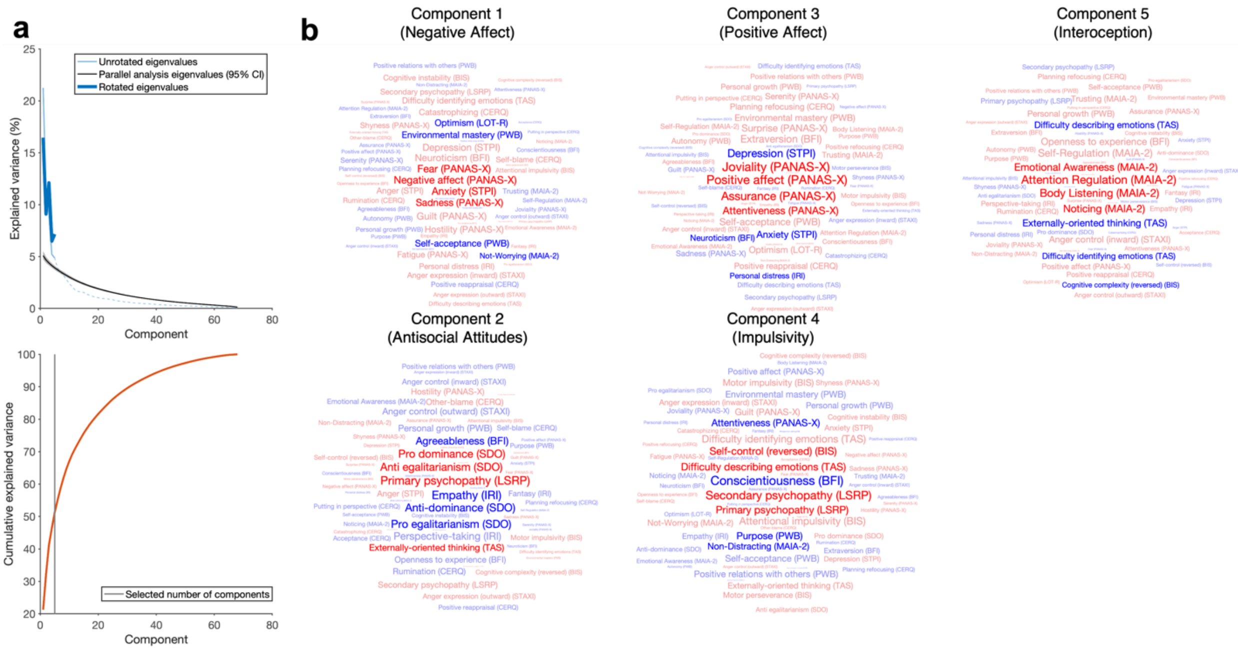

Figure 2- 2: Latent dimensions of personality uncovered using PCA and used in the linear modelling procedure.

Figure 2. Latent dimensions of personality uncovered using PCA and used in the linear modelling procedure. A) Eigenvalue plot showing the distribution of eigenvalues by component. Light blue line shows the unrotated eigenvalues; the dashed part reflects eigenvalues not significant following the permutation test. Black line shows the eigenvalues from the permutation test and the 95% confidence interval of these (grey shading). Dark blue shows the eigenvalues of the components following quartimax rotation. B) Loadings of all significant components (determined by the permutation test). The size of the word corresponds to the magnitude of the loading, and red words reflect positive loadings while blue words reflect negative loadings.

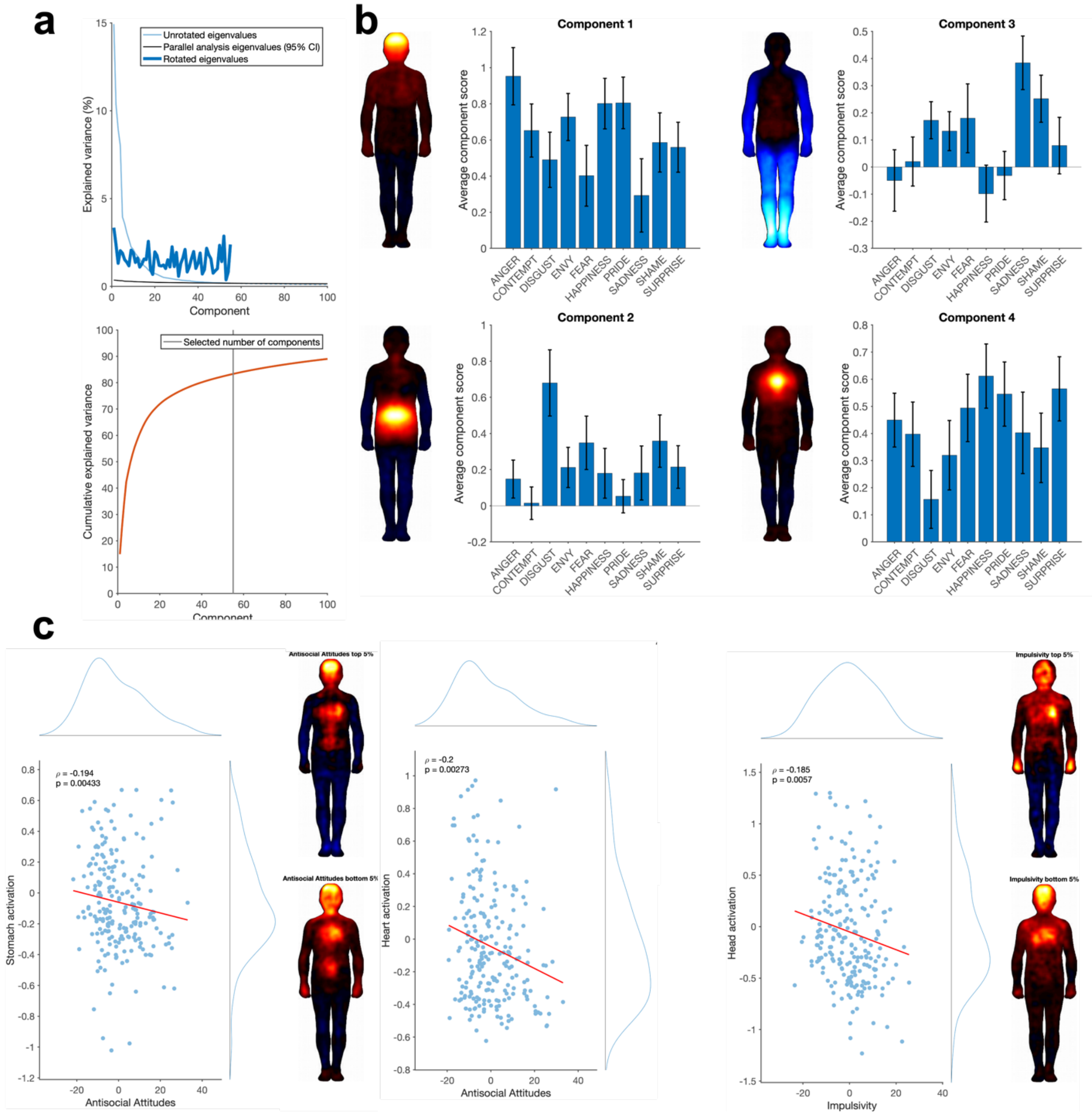

Figure 2- 3: Results of the PCA of the body map data and correlation of BSM and personality PCA components.

Figure 3. Results of the PCA of the body map data and correlation of BSM and personality PCA components. A) Eigenvalue plot for the BSM PCA, as in figure 2A. B) Loadings and averaged component scores for the top 4 components. Silhouette plots show the loadings of the rotated component. Bar plots show the scores of the component, averaged over subjects within each emotion; error bars indicate standard error. These bars indicate the magnitude at which the component is activated in each emotion. C) Correlation analysis of body map and personality PCA components. Spearman's ρ and its corresponding p-value are indicated. Histograms show

the distribution of each variable. Silhouette plots show averaged BSMs from the extremes of the personality distribution (top and bottom 5% of each personality PCA component), averaged across emotions.

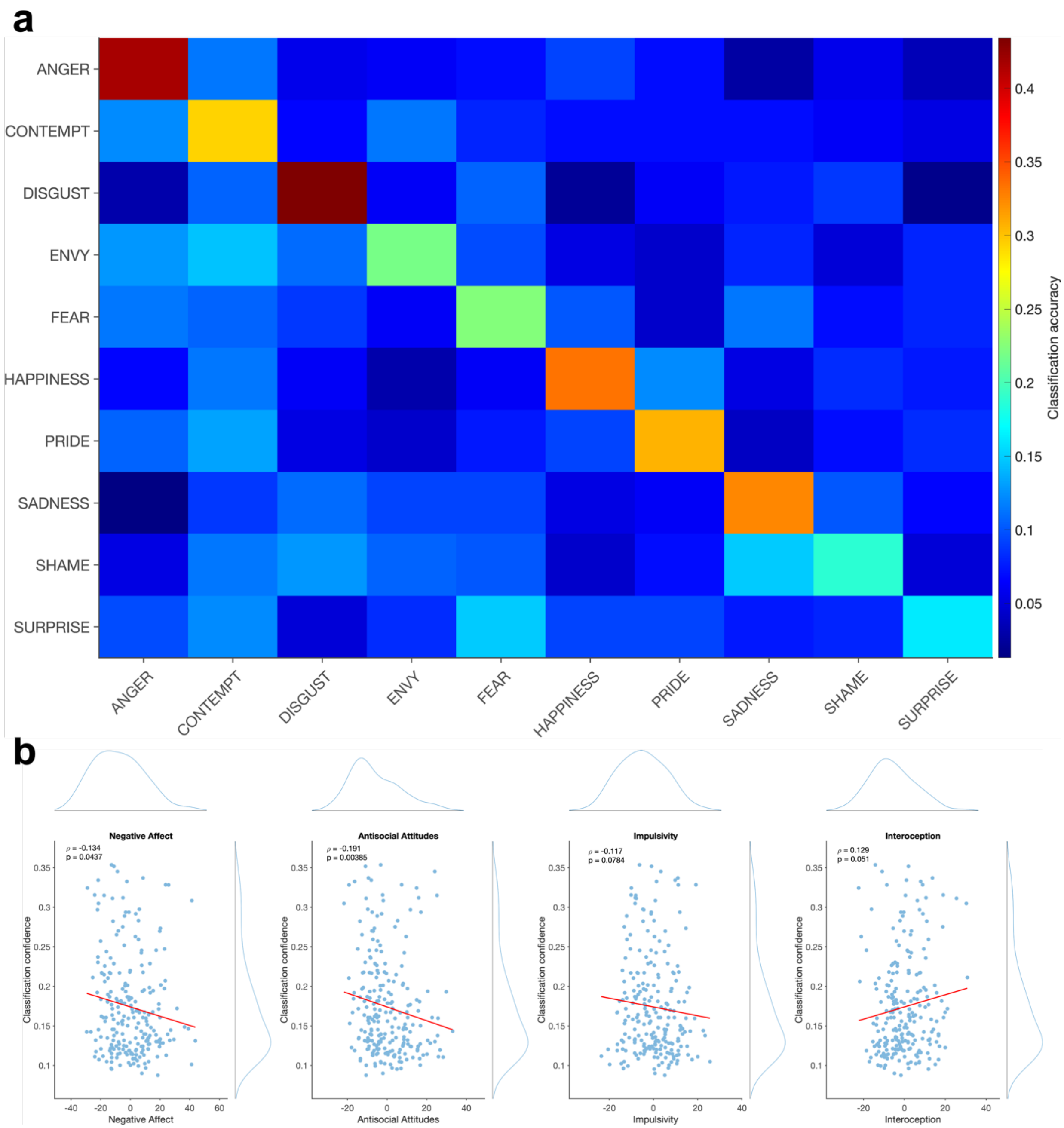

Figure 2- 4: Linear discriminant analysis classifier confidence and its association with personality.

Figure 4. Linear discriminant analysis classifier confidence and its association with personality. A) Confusion matrix for the linear discriminant analysis classifier predicting emotion label from participants' BSM data. B) Correlations of classifier confidence with personality PCA components. Classifier confidence was computed as the posterior probability that an emotion is accurately classified as its true label, averaged over emotions for each subject. Spearman's ρ and uncorrected p-values are indicated. Histograms show the distribution of each variable.

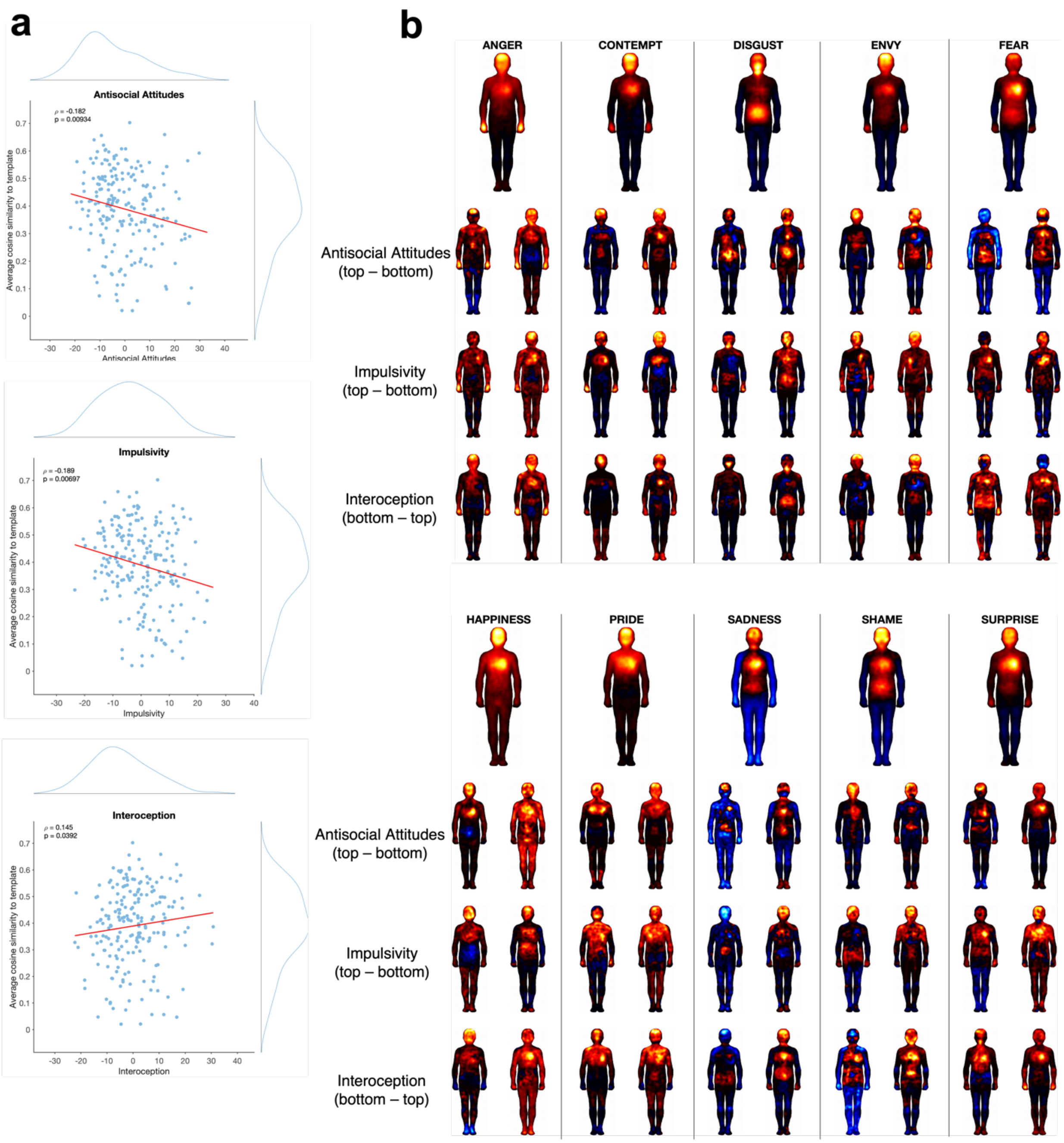

Figure 2- 5: Relationship of body map representativeness and differentiation with personality PCA components.

Figure 5. Relationship of body map representativeness and differentiation with personality PCA components. A) Correlations of BSM representativeness with personality PCA components; Spearman's ρ and the corresponding p-value are plotted. Histograms show the distribution of

each variable. B) Average body maps for the bottom 5% and top 5% of each personality factor (empathy, interoception: bottom 5% on the left, top 5% on the right; impulsivity: top 5% on the left, bottom 5% on the right). Group average maps are shown above.

Chapter 3: Natural differences in upright body posture are associated with prosociality

Soren Wainio-Theberge, Jorge Armony

Manuscript in preparation

Connecting chapters 2 and 3

In the previous chapter, we examined the role of individual differences in emotional somatosensation in personality. As discussed previously, somatosensory processes in emotion are usually linked to emotional physiology, which is conceived in an evolutionary context. However, studies have shown that physiological responses to emotion vary contextually, and factors such as interoception can shape the degree to which somatic sensations are represented within the brain and within individuals' awareness. In the previous study, we found that this variability is systematically related to personality: specifically, we found that visceral and cardiac sensations in emotion were associated with greater empathy and less psychopathy and antisocial tendencies.

In the subsequent chapter, we will investigate the same question, but in the motor domain: that is, do individual differences in body posture have associations with personality factors? Emotional body postures, much like emotional somatosensation, are typically thought of in terms of evolutionarily-determined state modulations; considering individual variability in these processes is novel. However, unlike with emotional somatosensation, in this case we are interested not in variation of how these states are enacted, but in trait versions of these states: that is, whether individuals' body postures at rest exhibit features like emotional body language, and whether these features play a role in individual differences. Interestingly, the same personality factor (dominance and antisocial tendencies) will again play a role, this time in relation to dominant and submissive body postures.

Natural differences in upright body posture are associated with prosociality

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Abstract

Social dominance has wide-ranging social and affective consequences, and body posture is an important medium of dominance/submission interactions. While transient displays of body posture in social and experimental contexts have been shown to affect social cognition and emotion, little attention has been paid to stable individual differences in natural body posture. In our paper, we show that individual differences in postural expansion in a neutral, baseline context are robustly associated with individual differences in prosocial attitudes, particularly social dominance orientation. We also validate our measure of natural posture by correlating it with physiological data from relevant musculature and showing its stability over a one-month interval. Our work suggests that postural signalling of social dominance occurs not just in brief displays in social contexts, but exists as a stable individual trait with consequences for socioaffective processing.

Introduction

Social dominance behaviours are a set of verbal and nonverbal behaviours which guide competition for resources among individuals (Johnson et al., 2012). Dominance/submission interactions allow organisms to avoid potentially costly conflict either by intimidating other individuals (dominance) or by signaling that they wish to avoid a fight (submission; Koski et al., 2015); over time, these interactions instantiate social hierarchies among members of a species, where individuals at the top receive greater access to resources than individuals at the bottom. Dominance behaviour has consequences across the whole spectrum of socioaffective processing. Dominant, powerful individuals express greater optimism and take more risks (Anderson & Galinsky, 2006), but also exhibit less prosocial affect and behaviour than low-status individuals (Piff et al., 2010). In contrast, individuals lower in dominance and social status show elevated psychological and physiological stress (Kessler, 1979; Sapolsky, 1982), poorer health (Singh-Manoux et al., 2003), and elevated rates of psychiatric illness (Scott et al., 2014), particularly depression (Sloman & Gilbert, 2000).

Body posture is a crucial medium of dominance signalling (Burgoon & Dunbar, 2006). Both animals and humans display dominance using open, erect, and expanded postures and submission through closed, slumped, or contracted expressions (Burgoon & Dunbar, 2006). In humans, the use of these postural signals in social interactions affects perceptions of social status (Hall et al., 2005), competence and successfulness (Weisfeld & Beresford, 1982), and leadership (Cashdan, 1998), and are associated with actual personality traits such as extraversion and neuroticism (Breil et al., 2021). Moreover, the popular “power posing” paradigm (Carney et al., 2010) suggests that adoption of an expansive or contractive body position for a few minutes, as an experimental intervention, can subtly influence individuals’ moods and behaviours, increasing risk-taking and positive affect and encouraging more selfish moral choices (Elkjaer et al., 2020). Although this experimental paradigm has been controversial (Jonas et al., 2017), recent meta-analyses suggest that these behavioural and mood effects are robust, though earlier claims about hormonal changes remain unverified (Elkjaer et al., 2020).

In addition to enacting dominant or submissive displays in interactions with peers, individuals also vary in their habitual body postures outside of social contexts. Despite its potentially important role in dominance signalling and social cognition, this variation in natural posture has rarely been studied. Notably, "thin-slicing" studies of personality perception from photographs have found that the gaze direction and head tilt of isolated faces influence judgements of personality and dominance (Toscano et al., 2018; Witkower & Tracy, 2019; Zhang et al., 2020); however, only one such study has examined whole body posture, finding that ratings of energetic or tense stances were predictive of both observer-rated and self-rated big five personality traits (Naumann et al., 2009). Moreover, only a few studies have directly investigated correspondences between participants' neutral postures and measures of trait affect or personality, and these have had small sample sizes and used subjective measures of body posture unrelated to the expansive/contractive dimension emphasized by human and animal research on non-verbal behaviour (Guimond & Massrieh, 2012; Notarnicola et al., 2017). Therefore, while suggested by previous research, the existence of stable, meaningful individual differences in dominant and submissive body posture -- tested in large samples, using objective and quantitative measures -- has not been established and, more importantly, neither has their relationship to socioaffective processing.

To directly address this question, we used machine learning-based photogrammetric posture assessment and a large battery of well-validated personality scales. Using photos of participants and a AI-based pose estimation tool (Cao et al., 2019), we created a measure of postural submissiveness based on participants' head angle in the absence of any explicit social context. We also applied a battery of personality measures related to social cognition and trait affect, and applied dimensionality reduction techniques (Wainio-Theberge & Armony, 2023) to find personality factors which might be related to our measure of postural submissiveness. Critically, we replicated our findings in two independent samples differing in social context (one online and one in-person), conducted a physiological validation of our posture metric using electromyography of relevant muscles, and measured its test-retest reliability to ensure that it was truly a stable measure of trait posture. Briefly, we found that scales related to antisocial attitudes, and in particular the social dominance orientation construct (Pratto et al., 1994), were related to the erectness of participants' neutral or habitual postures. These results suggest that beyond serving as a transient signal in social interaction, habitual body posture is intimately connected to individuals' personality and social cognition.

Results

To address our hypothesis, we carried out three studies. In the first online study, we obtained photographs of participants' neutral postures and computed a measure of postural submissiveness related to participants' head angle. To find relevant dimensions of personality related to posture, we performed a principal components analysis on the personality measures and related these components to the posture metric. We next replicated our findings in an in-person sample, in order to validate our posture metric by relating it to the activity of relevant musculature and better control the characteristics of the posture photos. Finally, we conducted an additional online replication of the correlation between measures of interest derived from Study 1, in which we also assessed the test-retest reliability of our posture metric.

PCA decomposition of personality factors reveals constructs relating to social dominance, negative affect, and emotion awareness

The final sample for study 1 consisted of 229 subjects (mean age = 20.6, SD =1.6, 31 males), considering only participants with complete personality information and good quality posture photos. Following (Wainio-Theberge & Armony, 2023), we conducted a principal components analysis to reduce the number of personality variables. After parallel analysis, the principal components analysis yielded seven significant components (Figure 1): (1) negative affect dimensions of the PANAS-X, anxiety, and negatively on optimism, environmental mastery and self-acceptance (*Negative Affect*); (2) social dominance orientation and psychopathy, with negative loadings for empathy (*Antisocial Attitudes*); (3) positive affect and negatively on anxiety and depression (*Positive Affect*), (4) positively on conscientiousness and negatively on secondary psychopathy and several impulsivity factors (*Self-Control*), (5) positively on several subdimensions of interoceptive awareness and negatively on alexithymia (*Interoception*), (6) negatively on neuroticism and distress and positively on serenity and the "not-worrying" interoception subscale (*Calm*), and (7) positively on primary psychopathy and negatively on agreeableness and several empathy subdimensions (*Disagreeableness*). Full component loadings with bootstrap confidence intervals are reported in the supplementary materials (Supplementary Figure 1).

Dominant posture correlates with antisocial attitudes, social dominance orientation in two online samples

In an exploratory analysis, we sought to determine which of the above personality constructs might relate to our measure of postural submissiveness. We entered all the significant principal components obtained above into a linear model, with head angle as the dependent variable. Head angle was coded such that larger values indicated more forward head posture (i.e. more stooped/submissive postures). Only the coefficient for the *Antisocial Attitudes* principal component was statistically significant, corrected for multiple comparisons ($p = 0.002$, $p_{FDR} = 0.01$; $p_{FDR} > 0.1$ for all others; Table 1).

Table 1. Linear model predicting forward head posture from principal components of personality.

	Estimate	**Standard Error**	***t* Statistic**	***p* Value**	**Corrected *p* Value**
Negative Affect	0.014	0.059	0.25	0.80	1
Antisocial Attitudes	-0.17	0.055	-3.1	0.002	0.014
Positive Affect	-0.036	0.072	-0.51	0.61	1
Self-Control	0.053	0.090	0.59	0.56	1
Interoception	0.044	0.082	0.53	0.60	1
Calm	0.14	0.093	1.5	0.13	1
Disagreeableness	0.18	0.091	2.0	0.050	1

In order to move from principal component space, which will vary based on the specific personality battery administered, to individual personality scales, we refined our findings by selecting the scales contributing most to the second principal component and relating these to postural submissiveness. We took the top 3 loadings (Social Dominance Orientation, Primary Psychopathy, and Empathy) from the *Antisocial Attitudes* component and entered them into a linear model, with forward head posture as the dependent variable. Of these three, only Social Dominance Orientation (SDO) emerged as significant when controlling for the influence of the others (SDO: $p = 0.001$, $p_{FDR} = 0.004$; all others $p_{FDR} > 0.1$; Table 2). SDO was thus chosen as the metric of choice for the hypothesis-driven investigations of posture and personality in the In-person and Online 2 studies.

Table 2. Linear model predicting forward head posture from the top loadings making up the second principal component. Trait names are presented with abbreviations for the source scale in brackets (see Methods for references).

	Estimate	Standard Error	*t* Statistic	*p* Value	Corrected *p* Value
Social Dominance Orientation (SDO)	-0.19	0.058	-3.3	0.001	0.004
Primary Psychopathy (LSRP)	0.22	0.15	1.5	0.14	1
Empathy (IRI)	-0.13	0.18	-0.68	0.50	1

Replication in an in-person sample and validation of the head posture metric

We next sought to replicate our findings in an in-person sample, where noise in participants' posture photos could be minimized and a physiological validation of our head posture metric could be carried out. The final sample for study 2 consisted of 123 subjects (mean age = 21.8, SD = 3.6, 35 males), after removal of three participants who failed the attention check question. First, we validated our metric of forward head posture by relating it to EMG activity from relevant neck musculature. In agreement with previous studies (Rubine-Gatina et al., 2022), we found a negative relationship between EMG activity in the sternocleidomastoid muscle and our measure of forward head posture ($r = -0.26$; $p = 0.01$); the correlation with activity in the trapezius was not significant ($p = 0.54$). While counterintuitive given the sternocleidomastoid's role as a neck flexor, this finding is consistent with previous studies (Rubine-Gatina et al., 2022), and suggests that the forward head posture measured with our head angle metric is a passive (i.e., letting the head fall), rather than an active (e.g., bowing) process.

Importantly, we were able to replicate the previously observed correlation of forward head posture with SDO in this in-person sample, where posture photos were taken in a controlled setting with no variability in camera angles. Indeed, there was a significant prediction of forward head posture by SDO ($r = -0.15$, $p = 0.04$).

Replication in an additional online sample and test-retest reliability of the posture measure

Finally, we used a third online study to replicate again the observed correlation of SDO with forward head posture and assess the test-retest reliability of the head angle measure. The final sample for study 3 consisted of 124 subjects (mean age = 20.0, SD = 1.45, 10 males), considering only participants with complete personality information and good quality posture photos. Applying the exact same methods as in online study 1, we observed a significant relationship between social dominance orientation and forward head posture ($r = -0.19$; $p = 0.04$).

To assess test-retest reliability of personality and posture measure, we included a follow-up session in Study 3, consisting of the same measure of head angle and a subset of the same personality questionnaires (including the Social Dominance Orientation scale). Follow-ups were completed between 4 and 6 weeks after the first session and a total of 96 participants had personality scales and acceptable quality posture photos for both sessions (mean = 20.15, SD = 1.31; 8 males). To assess the test-retest reliability of our posture measure, we measured the intra-class correlation coefficient (ICC) of participants' head angles. Encouragingly, the ICC of the head angle measure was 0.72, on par with our relevant personality scales such as SDO (ICC = 0.77), Primary Psychopathy (ICC = 0.76) and Empathy (ICC = 0.68), and indicating moderate to good reliability according to the standards set out by Koo & Li (2016). This suggests that in line with our hypothesis, the head angle measure employed in this study does indeed reflect a trait measure of posture, which is stable among participants at least over month-long timescales.
In summary, all three studies revealed that a more upright upper body posture was associated higher scores on the social dominance orientation inventory. Combining the p-values from all three samples using a weighted z-test (Zaykin, 2011), we found that the relationship between social dominance orientation and forward head posture was highly significant (total n = 476,

combined p = $4x10^{-4}$); moreover, the robust regression estimates were highly concordant for all three samples.

Discussion

Dominance behaviour is a crucial social and affective process which is mediated by body posture. While the expansive and contractive postures which indicate dominance information have been investigated in the context of dyadic interactions and brief, experimentally manipulated displays ("power posing"), the existence and relevance of trait-level variation in dominant and submissive body language has not been established. Using objective and replicable methods and a large sample size, we created and validated a measure of natural, trait-level body posture, and observed a correlation between this postural variation and scores on the social dominance orientation scale. We replicated this in three separate samples, including different experimental contexts (online and in-person). Our results suggest that the influence of expansive and contractive body language extends beyond situational behaviours to the domain of stable, trait-like individual differences in personality and social cognition.

Our study suggests that posture is associated with stable, trait-level psychological traits, including the tendency to endorse social hierarchies. These findings are supported by several possible causal explanations. Firstly, if personality is a causal factor, it may be that individuals who endorse social hierarchies attempt to adjust their posture to dominate others; for those high in dominance motivation, the experience of being at the bottom of the heap can be intolerable, so one's upright posture may be an attempt to secure one's continued high status (Fodor et al., 2006). The scatterplots in figures 2A and 3A support such an interpretation; the correlation between SDO and head angle appears to be driven in part by the upright head postures of high-SDO individuals, while low-SDO individuals experience the full range of expansive and contractive postures. This is also supported by the finding that forward head postures tend to be reflective of more passive processes; taking this relationship in reverse, the upright head postures of high-SDO individuals seem to require more active muscular effort.

Alternatively, posture and personality may be engaged in a vicious cycle involving social perception. Individuals who may adopt a more stooped posture may be construed by others as behaving submissively, and be treated as such by their interlocutors; in turn, the individual may construe themselves as a submissive person because of their treatment by other (Buss, 1987). This powerful phenomenon is widespread in zero-acquaintance judgements, and cited as a prominent explanation for observed relationships between other physical features (such as facial structure: (Oosterhof & Todorov, 2008)) and personality (Zebrowitz & Collins, 1997). Finally, posture and personality may simply co-develop as individuals are forced to subordinate their desires in social settings or are faced with socially dominant others: they may learn and internalize both physical and psychological habits of submissive behaviour (and vice versa for dominance). Future studies with careful experimental design are needed to parse apart the potential causal pathways involved in the posture-personality relationship observed here.

The findings obtained here carry a number of implications for our understanding of dominance behaviour and its psychological consequences in humans. Firstly, our work carries implications for future work on non-verbal behaviour, including the “power posing” paradigm. While the “power posing” paradigm involves brief, conscious displays of dominant or submissive body language, our study suggests that natural, trait-level variation in such postures has effects on personality. As such, individuals do not enter into a “power posing” experiment as blank slates, but may find the expansive or contractive postures more or less familiar or novel depending on their individual baseline; accounting for this variability may bring clarity to a literature that has suffered considerable reproducibility problems (Jonas et al., 2017). Likewise, studies of non-verbal behaviour in dyadic interactions may benefit from accounting for these baseline differences.

Nevertheless, our study has a number of limitations, which future studies should address. Firstly, as most studies of self-reported personality, our study is correlational, and as discussed above multiple pathways exist where both cognitive and embodied processes may have causal influence. While it is difficult to study personality development without resorting to correlational designs, future studies of posture habituation over long time periods or more novel techniques such as Mendelian Randomization (Smith & Ebrahim, 2004) may be able to address this gap. Secondly, our study focuses on samples collected in a western country (Canada), primarily on young, female-identifying adults and university undergraduates; while our sample contains a large number of international students, the cultural influence of our data collection site is undeniably an important caveat (Henrich et al., 2010), and future studies should attempt to replicate the effect we found in other settings. Our physiological investigation was rather limited, as we only recorded from two muscles which were chosen a priori; future studies should focus on other relevant musculature which may be involved, as well as on the neural pathways which may be involved (Chiao, 2010; Poyo Solanas et al., 2020a). Finally, our study measured just one aspect of natural posture – namely, the erectness of participants' posture measured via head angle. Other methodologies, such as anatomical key point marking using 3D motion tracking system or multi-channel EMG, may yield cleaner data, as well as allow for measuring aspects of posture such as the horizontal dimension of postural expansion (Körner & Schütz, 2020), which was difficult to quantify using our method.

Conclusion

Social dominance interactions constitute important social and affective events, and body posture is an important medium of this communication. While dominance signalling by posture has been well-studied in social interactions and brief, experimental manipulations, the consequences of variation in natural postures has been comparatively neglected. We demonstrate a robust negative correlation between a measure of postural submissiveness (forward head posture) and the social dominance orientation construct, which reflects individuals' tendencies to endorse social hierarchies; moreover, we validate that our measure of body posture indeed reflects a stable individual trait related to relevant physiology. Our findings suggest that beyond deliberate signalling, individual body posture is associated with differences in social cognition and personality, carrying implications for future work on social hierarchies and for well-known and controversial paradigms such as "power posing".

Methods

Study 1: online study of posture and personality using webcam-based posture assessment

Participants

Participants for study 1 were recruited from the general public using social media advertisements and from the McGill University Department of Psychology extra credit participant pool. A total of 362 participants were tested for study 1 (mean age = 20.9 years, SD = 2.0; 54 males). Both studies were larger investigations of posture, personality, and emotional somatosensation which include data not presented here; data from study 1 were previously presented in (Wainio-Theberge & Armony, 2023). The study was approved by the McGill University Faculty of Medicine Institutional Review Board (IRB# A00-B62-21A) and written informed consent was obtained from all participants. Participants were either compensated with CAD 15$ for their participation or received course credit. The study procedures were carried out in accordance with the Declaration of Helsinki.

Experimental procedure

Study 1 consisted of four 15-minute experimental modules run on a JATOS server (Lange et al., 2015) hosted by the International Laboratory for Brain, Music, and Sound Research (BRAMS), using the jsPsych library (de Leeuw, 2015). In addition to two other experimental tasks (an emotional face perception task and an emotional somatosensation task), included a battery of personality questionnaires (see Table 1, below) and a webcam-based postural assessment. Additional data from the other modules of study 1 were reported in (Wainio-Theberge & Armony, 2023).

To assess participants' neutral postures, we used a photogrammetric approach (Singla et al., 2017). Our approach was inspired by the PostureScreen software, a well-validated scale used in physiotherapy applications which measures individuals' posture based on keypoints annotated on four photos: front view, profile looking both directions, and behind (Szucs & Brown, 2018). As studies 1 and 2 were conducted online, participants were asked to take photos of themselves with their webcams using a custom-coded interface made in Javascript. Participants were instructed to take the photos from the front, in profile on both sides, and from the rear, with the camera angled minimally and positioned an appropriate distance away so that their entire body was in the frame. If participants did not have a webcam on their laptop, they were provided with a link where they could take the photos with other means and upload them. Participants were provided with examples of good quality posture photos.

Participants' photos underwent a manual quality check to remove major noncompliance with the instructions. Photos were discarded if they exhibited large shear or barrel distortion, if the participant's whole body was not in the frame, if the camera angle or the participant's body position differed greatly from the instructions, or if the participant's head was turned towards the camera in the side view photos, as this would bias the head angle estimate.

Data preprocessing and analysis: data exploration using PCA and selection of scales for hypothesis-driven follow-ups

To quantify the submissiveness of participants' neutral postures, we relied on a large literature on slumped postures (Körner & Schütz, 2020). As reviewed in (Körner & Schütz, 2020), slumped postures reflect the vertical dimension of postural contractiveness, in contrast to the horizontal expansion and contraction of the limbs in "power posing". This vertical dimension of posture was chosen for our study as it is present in both "power posing" studies and early studies of postural feedback (Riskind & Gotay, 1982), and, importantly, because it reflects subtle variation that can likely be measured in participants resting posture absent of a social context. To measure this, we calculated an approximation of the angle of the participant's head relative to their spine, referred to as the craniovertebral angle in physiotherapy studies (Singla et al., 2017). To annotate key points on participants photos without introducing human error and the need for multiple raters, we used a well-known machine learning library called OpenPOSE (Cao et al., 2019). OpenPOSE automatically finds human bodies in photos and videos and fits a 25-point skeleton to these bodies; it has been previously used in work on body posture and emotion to measure postural and kinematic features of emotional body expressions (Poyo Solanas et al., 2020b). Using the OpenPOSE skeletons, we calculated forward head posture as the angle between OpenPOSE's ear keypoint and shoulder keypoint (see Supplementary figure S2), averaged between the profile view photos on each side.

For the exploratory analysis in study 1, we subjected all the personality scales in this study to a principal components analysis, roughly following the methods of (Wainio-Theberge & Armony, 2023). The number of components was chosen using the Hong et al. (2020) permutation method: briefly, a matrix of random sign-flips is applied 1000 times to the data to create a null distribution of eigenvalues, and the eigenvalues from the original dataset are compared with this null distribution to estimate the significance of each component. Quartimax rotation was then applied to improve the interpretability of each of the significant components.

Significant loadings of each component were then determined using 1000 bootstrap samples to estimate the loadings' standard errors. We then used these components to determine hypotheses for individual personality constructs which might correlate with postural submissiveness (see below).

To explore which broad-scale personality factors might be related to submissive posture, we entered all the significant personality PCA components into a linear model, with forward head posture as the dependent variable. Robust regression was used in order to account for the presence of outliers in the distribution of the head angle variable. Following this, for the significant *Antisocial Attitudes* component, we took the top three loadings (in terms of absolute value) and entered these into a linear model with forward head posture in order to select specific personality constructs which are most strongly related to postural submissiveness. Significant scales from this linear model were then selected for inclusion in the linear model in the replication sample (studies 2 and 3), where forward head posture was again the dependent variable. Multiple comparisons were corrected for using False Discovery Rate correction (Benjamini & Yekutieli, 2001).

Personality measures

All three studies included multiple validated personality scales, with slightly different sets of scales due to the different aims of the studies. Study 1 was aimed at data exploration, using multiple personality measures and data reduction techniques to explore which personality constructs were related to our measure of submissive posture. As such, a large variety of scales were administered relating to different aspects of affect and social cognition, including the Barratt Impulsivity Scale (BIS-11; Patton et al., 1995), the Big Five Inventory (BFI; John et al., 1991), the Interpersonal Reactivity Index (IRI; Davis, 1983), the Multidimensional Assessment of Interoceptive Abilities Version 2 (MAIA-2; Mehling et al., 2018), the Levenson Self-Report Psychopathy Scale (Levenson et al., 1995), the Social Dominance Orientation scale (SDO; Pratto et al., 1994), the Life Orientation Test Revised (LOT-R; Scheier et al., 1994), the Positive and Negative Affect Schedule – Expanded (PANAS-X; Watson & Clark, 1999), the Spielberger State-Trait Personality Inventory (STPI; Spielberger & Reheiser, 2009), the State-Trait Anger Expression Inventory (STAXI; Spielberger et al., 1999), the Toronto Alexithymia Scale (TAS;

Bagby et al., 1994), the Cognitive Emotion Regulation Questionnaire (CERQ; Garnefski & Kraaij, 2006), and the Psychological Well-Being Scale (PWB; Ryff, 1989). These scales were chosen due to their relevance to trait affect and social cognition in healthy populations. For studies 2 and 3, only the SDO was included in the present analysis, though a full battery of other personality scales were administered. Data from these scales will be presented in another publication.

Study 2: Replication of posture-personality relationship in an in-person sample with peripheral physiology

Participants

A total of 126 participants (mean age = 21.8, SD = 3.6, 36 males) were recruited from online advertisements and through the McGill University Department of Psychology extra credit participant pool. The study was approved by the McGill University Faculty of Medicine Institutional Review Board (IRB# A11-B62-21A) and written informed consent was obtained from all participants. They were either compensated with CAD 50$ for their participation or received course credit. The study procedures were carried out in accordance with the Declaration of Helsinki.

Experimental procedures

Data for study 2 came from a larger study on the neural mechanisms of postural feedback effects on emotion, the results and detailed procedures of which will be reported at a later date. In the week before the in-person experiment, participants completed an online battery of personality questionnaires, containing personality scales relevant to trait emotionality, emotion processing, personality, and social attitudes, and including the social dominance orientation scale selected earlier.

Photogrammetric posture assessment proceeded similarly as in study 1. Upon arrival at the lab, participants were first told to remove their shoes, and four photos were taken of each participant to measure their neutral posture. Photos were taken with a Panasonic Lumix GX-85 mirrorless camera, with a 12mm Panasonic lens. Participants were positioned 2 m away from the camera, and photos were taken of them face on, in profile looking both directions, and from behind.

Participants then underwent a set of physiological recordings. Bipolar surface EMG was recorded from the sternocleidomastoid muscle and the upper trapezius on the participant's dominant side using a BioSemi ActiveTwo amplifier and Ag/AgCl electrodes. EMG electrodes were positioned according to Falla et al. (2002) for the sternocleidomastoid and according to the SENIAM 8 guidelines for the upper trapezius (Hermens et al., 2000). EMG was recorded at the start of the experiment during a 3 minute seated resting state recording, and during three other resting states throughout the experiment for 3 minutes each. Briefly, the experiment consisted of alternating blocks of a perceptual decision-making task including emotional faces and self-report mood questionnaires, as well as an expansive or contractive posture which the participant would take for 3 minutes in the middle of the experiment. Further details of this study will be reported at a later date.

Data preprocessing: extraction of relevant features of personality and posture

Personality measures were screened for random responding using attention check questions; participants who failed these attention checks were excluded from the dataset. Quality check was not needed on the posture photos, as these were carried out in the lab by the experimenters so good quality was ensured. EMG data were preprocessed according to the SENIAM guidelines (Stegeman & Hermens, 2007). First, raw EMG signals were re-referenced to a bipolar montage for each muscle. Next, bipolar EMG signals were bandpass filtered from 10 to 500 Hz to remove low-frequency drift. Finally, the filtered signals were rectified and lowpass filtered at 20 Hz to create the EMG power time series. These power time series were averaged within each resting state to gain a measure of raw EMG power for each resting state, and these four resting-state values were averaged to create a measure of EMG power for each participant. Large outliers (> 3 median absolute deviations from the median) reflecting were removed, as these likely reflect bad electrode-to-skin contact.

Linear modelling of personality, forward head posture, and EMG

As in study 1, the significant individual scale from the exploratory study (social dominance orientation) was entered into a linear model with forward head posture as the dependent variable, in order to replicate this relationship. Moreover, to ensure that our measure of forward head posture was physiologically valid, we entered this measure into a linear model with EMG activity from the sternocleidomastoid and trapezius, as these muscles are neck flexors and neck extensors, respectively (Brennan et al., 2015).

Study 3: Online replication study concerning the reliability of the posture measure

Study 3 was carried out in order to replicate the findings in a third sample and to assess the test-retest reliability of our head angle metric, in order to determine whether our measure was a stable representation of individual differences in body posture. Initially, a total of 154 participants were recruited for study 3 (mean age = 19.9 years, SD 1.4; 14 males) from the psychology department participant pool; participants then completed a follow-up session between 4 and 6 weeks after the first session. A total of 135 participants returned for session 2 (mean age = 20.1 years, SD = 1.38; 13 males).

Data cleaning and analysis proceeded as in the previous studies. The head angle measure was calculated from participants' webcam photos, and photos were manually screened for data quality. Based on study 1, the Social Dominance Orientation scale was chosen as the measure of interest of social hierarchy processing, and this scale was related to head angle using robust regression using the first session data only.

Finally, to measure the reliability of our measure of forward head posture, we computed the intra-class correlation coefficient (ICC). Following the recommendation of (Koo & Li, 2016), we used the two-way mixed effects model with a single measurement, corresponding to the ICC(3,1) of the Shrout & Fleiss convention (Shrout & Fleiss, 1979). ICC was assessed for the head angle measure and also for the three scales included in Table 2, to serve as reference values of acceptable reliability for our sample.

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Figures

Figure 3- 1: Results of the exploratory principal component analysis of personality scales in online study 1.

Figure 1. Results of the exploratory principal component analysis of personality scales in online study 1. A) Eigenvalue plot showing the distribution of eigenvalues by component and the permuted eigenvalues. Light blue line shows the unrotated eigenvalues; the dashed part reflects eigenvalues not significant following the permutation test. Dark blue shows the eigenvalues of the components following quartimax rotation. Black shows the permuted eigenvalues, with grey shading for their 95% confidence interval (see Methods for details). B) Loadings of all significant components (determined by the permutation procedure). The size of the word corresponds to the magnitude of the loading, and red words reflect positive loadings while blue words reflect negative loadings. The top 4 positive and negative loadings are highlighted in bold colour.

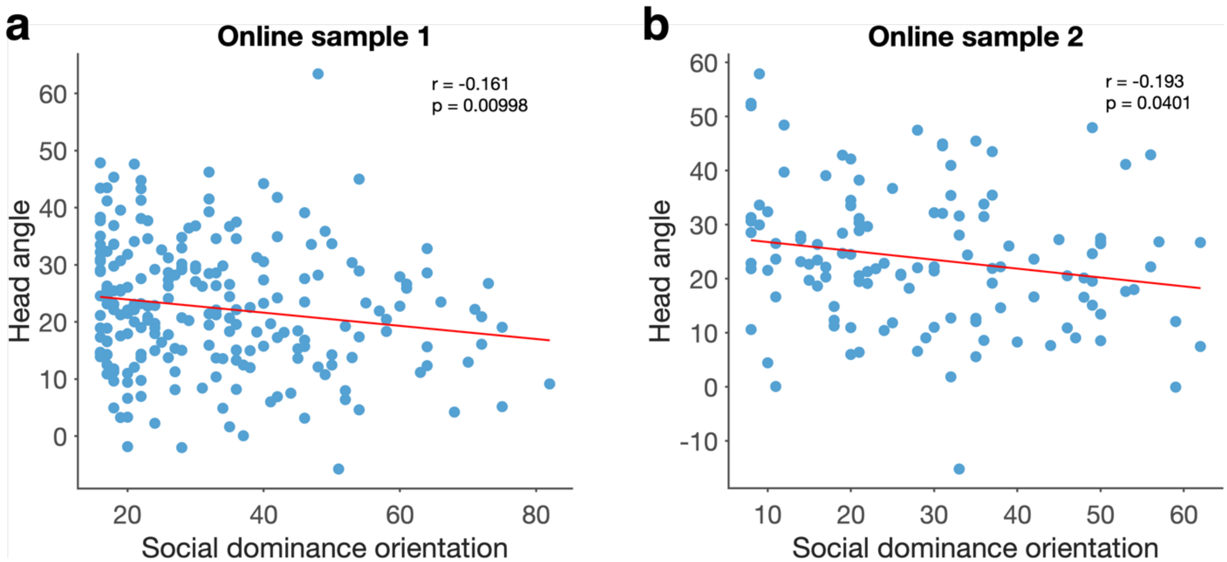

Figure 3- 2: Scatterplots showing the correlation of head angle and social dominance orientation in A) online sample 1 and B) online sample 2.

Figure 2. Scatterplots showing the correlation of head angle and social dominance orientation in A) online sample 1 and B) online sample 2. P values presented in the figure are drawn from the robust regression procedure detailed in the methods.

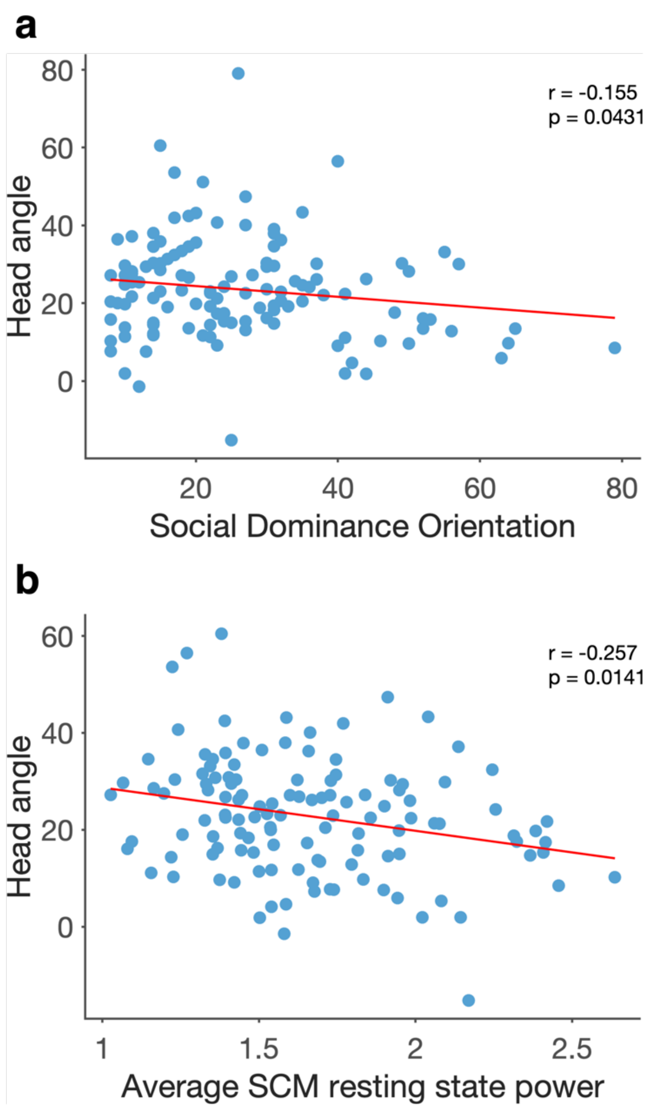

Figure 3- 3: Scatterplots showing results from the in-person study.

Figure 3. Scatterplots showing results from the in-person study. A) Replication of the head angle-SDO correlation in the in-person sample. B) Validation of the head angle metric by correlation with EMG power in the sternocleidomastoid muscle. As in figure 2, p values are from the robust regression procedure used in the paper.

Chapter 4: High-frequency brain activity mediates the psychological effects of expansive and contractive postures

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Manuscript in preparation

Connecting chapters 3 and 4

While chapters 2 and 3 were linked by their focus on individual differences, chapters 3 and 4 are linked by the central theme of expansive and contractive body postures. The previous chapter considered these postures from a trait perspective: we developed a method of quantifying individuals' neutral postures, and related this systematically to personality. Specifically, focusing on expansive and contractive postures associated with dominance and submission, we found that head angle, a measure of postural uprightness and therefore expansion, was associated with social dominance orientation, a measure of attitudes towards social hierarchy.

The next chapter addresses the same question, from the more traditional state perspective. Postural feedback paradigms are a well-studied manipulation in which participants are placed in expansive and contractive postures experimentally; they provide the proof of principle for the relationship of trait body posture and personality. Chapter 4 addresses the neural mechanisms of postural feedback using neuroimaging, a question that has been neglected by the literature. The answer to this question relevant is for the interpretation of the previous chapter's results, as well as their relationship to somatosensation: in the next chapter, we find tentative evidence that somatosensory mechanisms are involved in postural feedback, connecting the themes of all three manuscripts.

High-frequency brain activity mediates the psychological effects of expansive and contractive postures

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Abstract

The "power posing" paradigm is a popular experimental method aimed at studying dominance and submission. Participants are placed into expansive and contractive postures, which induce mood and behavioural changes corresponding to increased or decreased social rank, respectively. Despite this effect's robustness and social relevance, no study has ever examined the neural mechanisms of this effect, and neural evidence on social rank in general is limited. In this study, we used EEG combined with a "power posing" paradigm to address these open questions. We found that expansive and contractive postures differed with respect to beta and gamma power, bands with known associations with somatomotor processing; moreover, these changes were correlated with the affective outcomes of the postures, though muscle artefacts preclude a strong conclusion about this effect. Overall, our results provide the first neural data on the "power posing" effect and suggest the involvement of somatosensory processing as a mediator of this effect.

Introduction

Dominance and submission interactions are crucial behavioural processes in both humans and animals. As physical conflict with conspecifics and other organisms is dangerous and costly, dominance communication allows organisms to avoid paying the price of conflict, while submission allows organisms to avoid conflicts they cannot win (Johnson et al., 2012). The power and resources that dominant individuals gain affects many aspects of their behaviour and affect. For example, dominant individuals exhibit more risk taking, given that the consequences of risk are buffered for them (Anderson & Galinsky, 2006); moreover, they exhibit more positive affect due to the breadth of resources and affordances that they enjoy, and exhibit more individualistic behaviour and self-concepts as their actions are not constrained by others (Kraus et al., 2012). In contrast, submissive individuals who chronically lack access to resources tend to accept less risk, exhibit more negative affect, and have more interdependent self-concepts; the stress of this condition can lead to poorer health outcomes, even when controlling for differences in material resources (Sapolsky, 1982).

In many organisms, dominance and submission are signalled using expansive and contractive body postures: expansive body postures make organisms look larger and more threatening, while contractive body postures make organisms appear smaller and weaker (Burgoon & Dunbar, 2006). More recently, dominance and submission have come to the fore in psychology in the context of the "power posing" experimental paradigm (Carney et al., 2010). In this design, participants are placed artificially into an expansive or contractive pose, and these poses are compared with respect to their effects on mood, behaviour, or cognition. Expansive postures have been shown to reduce negative mood (Veenstra et al., 2017) and increase feelings of power and self-worth (Carney et al., 2010; Körner et al., 2019), seemingly producing the psychological characteristics of dominant individuals outlined above. Similarly, power poses increase risk-taking behaviour (Carney et al., 2010), performance in cognitive tasks (Förster & Stepper, 2000) , as well as moral violations such as lying, cheating, and stealing (Yap et al., 2013). Despite considerable controversy (Jonas et al., 2017), recent meta-analyses of the effects of expansive and contractive postures found robust effects across behavioural and self-report domains, though hormonal effects claimed by early studies have not been replicated (Elkjaer et al., 2020; Körner et al., 2022).

However, the neural mechanisms of power posing have never been investigated. As the procedure involves adopting emotional body postures, one hypothesis is that it involves somatosensory feedback. Analogous to classic studies of arousal attribution (Dutton & Aron, 1974; Schachter & Singer, 1962), participants may perceive that they are in a powerful pose, interpret that they are in a powerful position and act accordingly. Concurrent with this view, studies have found that emotional body language and motor programs do have somatosensory feedback effects: for example, in an experiment involving emotional face perception Kragel & LaBar (2016) found a somatotopic correspondence between emotion-related motor activity in the observed face and activity in the face region of somatosensory cortex (SSC), and Sel et al. (2020) found similar results using somatosensory-evoked potentials. Alternatively, expansive and contractive postures may have direct effects not mediated by somatosensory feedback. Evidence from animal studies on the processing of status signals in the brain suggests the involvement of subcortical reward areas such as the nucleus accumbens, amygdala, and ventral tegmental area (Dwortz et al., 2022; Korzan et al., 2006). In humans, fMRI studies have also implicated cortical areas such as the medial prefrontal cortex (mPFC), dorsolateral prefrontal cortex (DLPFC), and inferior parietal sulcus in making status judgements about individuals (IPS; Chiao, 2010; Koski et al., 2015; Li et al., 2021). These regions may likewise be involved in mediating the effects of power posing.

Studying the neural mechanisms of expansive and contractive postures is difficult using popular approaches such as functional magnetic resonance imaging (fMRI) because of the restrictions these methods place on participants' motion; participants must lie flat in the scanner, and even small motions create large artefacts which are problematic for analysis. Electroencephalography (EEG) allows participants more freedom of motion, though muscle artefacts can still be problematic (Muthukumaraswamy, 2013). Moreover, modern source localization approaches combined with anatomically accurate head models (Oostendorp & van Oosterom, 1989) can achieve acceptable resolution to distinguish major brain structures such as those that might be implicated in hierarchy processing (Lantz et al., 2003), and EEG features such as beta power are known to be markers of somatomotor processing (Barone & Rossiter, 2021). Thus, the aim of the present study was to use EEG to examine the neural mechanisms of the power posing paradigm.

Methods

Participants

One hundred and fifty-five participants were recruited from the McGill Psychology Department Participant Pool and the general public via social media advertisements. The study was approved by the McGill University Faculty of Medicine Institutional Review Board (IRB# A01-B03-15A) and written informed consent was obtained from all participants. Participants were either compensated with CAD 50$ for their participation or received course credit. The study procedures were carried out in accordance with the Declaration of Helsinki.

Study procedures

The experiment involved a series of resting-state EEG recordings with accompanying mood questionnaires, interspersed with blocks of a perceptual task. The structure of the study was divided into two study sessions conducted back to back, described in figure 1. In session 1, participants began the study with a set of mood questionnaires, followed by a 3-minute resting-state; these included the Affect Valuation Index (AVI; Tsai et al., 2006), as well as the authentic pride scale (AP; Tracy & Robins, 2007) and the Toronto Hospital Alertness Test (THAT; Shapiro et al., 2006) to distract from the true intention of the questionnaires and support the cognitive cover story (see below). Participants then completed the task from (Chadwick et al., 2019): briefly, this involved presenting participants with emotional faces superimposed on scenes, and asking them to judge either the sex of the face or the content of the scene (indoor or outdoor). Results of this task will be reported in future publications. Participants then completed the same set of questionnaires and the resting state after this task. Subsequently, participants were asked to hold either an expansive or contractive posture for three minutes. They then repeated the first session (questionnaire, rest, task, questionnaire, rest), but with expansive and contractive postures interspersed within blocks of the Chadwick et al. task.

Crucially, this structure resulted in having a resting state and questionnaire positioned on either side of the posture, while disguising these as baseline recordings for the tasks. A cover story was also used to prevent participants from discovering the intention of the task. Participants were told that the study was about the effect of body posture and heart-rate variability on cognitive performance; body posture was meant to affect heart-rate variability, and thereby performance in the task. Participants were debriefed afterwards, and participants who suspected any effects of the posture on mood or emotion were noted for further subgroup analyses.

Participants were randomly assigned to an expansive or contractive posture group. Postures were defined as in Carney et al. (2010). In the expansive condition, participants were instructed to raise their head, straighten their spine, and bring their shoulders back; in the contractive condition, participants were instructed to lower their head, curve their spine, and bring their shoulders together in front. Experimenters did not demonstrate the posture so as to avoid the confounding influence of viewing the experimenter's posture. Experimenters checked the participant's understanding of the posture and participants were monitored with video during the experiment to ensure compliance.

EEG was recorded throughout the experiment with a 96-channel BioSemi ActiveTwo system with active Ag/AgCl electrodes at a sampling rate of 2048 Hz. The montage was based on the standard BioSemi 64-channel headcap, with 32 additional electrodes added following the BrainVision setup. Channel DC offsets were maintained below 50 mV during recording. EMG and electrocardiography (ECG) were recorded using the external channels of the same system. EMG placement for the sternocleidomastoid followed (Falla et al., 2002), while placement for the trapezius followed the SENIAM guidelines (Stegeman & Hermens, 2007).

Behavioural analysis

To reduce the data and to improve the interpretability of the findings, the AVI subscales were combined into two dimensions reflecting the two axes of the affective circumplex (Posner et al., 2005). The composite arousal dimension (COMP-A) was calculated by subtracting the low arousal (LA), low arousal negative (LAN), and low arousal positive (LAP) subscales from the high arousal (HA), high arousal positive (HAP), and high arousal negative subscales (HAN), while the composite valence dimension (COMP-V) was created by subtracting the negative (N), HAN, and LAN from positive (P), HAP, and LAP. The Authentic Pride Scale (AP) was analyzed separately. Focusing on the time points immediately preceding and following the posture, we computed the difference between post-posture and pre-posture for COMP-A, COMP-V, AP. We then conducted a two-sample t-test on these difference scores between the expansive and contractive conditions; follow-up one-sample t-tests were then carried out on the difference scores within each posture group to examine which posture drove the effects. COMP-A, COMP-V, and AP difference scores were also used for correlations with the EEG data. To control for the influence of participant knowledge, we entered whether participants suspected the manipulation (coded as 0 or 1) into a linear model, with posture, participant knowledge, and their interaction as independent variables and change scores for COMP-A, COMP-V, and AP as the dependent variables.

Physiology preprocessing and analysis

Following recording, EEG data were downsampled to 256 Hz and preprocessed according to the HAPPE pipeline (Gabard-Durnam et al., 2018). Data were first filtered with a 1-Hz FIR high-pass filter in EEGLAB (Delorme & Makeig, 2004). Data were then notch filtered at 60 and 120 Hz to remove line noise (this step replaced the Cleanline procedure in the HAPPE, as it failed to suppress non-stationary line noise in our data). Bad channels were rejected using HAPPE's normalized log-power heuristic, and wavelet-thresholded ICA was performed to clean data for ICA decomposition. ICA was performed using the Infomax algorithm in EEGLAB, and artifactual ICA components were rejected using MARA (Winkler et al., 2011). Data were then segmented into 2-second consecutive non-overlapping epochs, and bad channels and segments were repaired using FASTER (Nolan et al., 2010). No segments were rejected outright at this step to avoid introducing discontinuities which could affect frequency analysis. Finally, data were re-referenced to a common average reference.

To further clean the data, we conducted a k-means clustering analysis using three of the HAPPE pipeline's preprocessing metrics (median residual artefact probability, number of channels initially rejected, and number of ICA components rejected). A cluster of recordings with high values of all of these metrics was identified (n = 46 recordings from 32 unique subjects), and these subjects were excluded from further analysis.

EMG preprocessing followed the recommendations of the SENIAM committee (Stegeman & Hermens, 2007). First, raw EMG signals were re-referenced to a bipolar montage for each muscle. Next, bipolar EMG signals were bandpass filtered from 10 to 500 Hz to remove low-frequency drift. Finally, the filtered signals were rectified and lowpass filtered at 20 Hz to create the EMG power time series. These power time series were averaged within each resting state to gain a measure of raw EMG power. Two large outliers (> 3 median absolute deviations from the median) reflecting were removed, as these likely reflect bad electrode-to-skin contact.

Frequency band power in EEG was calculated as follows. Power spectra were calculated for each channel using Welch's method (Welch, 1967). Frequency bands were defined as 1-4 Hz delta, 4-8 Hz theta, 8-13 Hz alpha, 13-30 Hz beta, 30-80 Hz low gamma, and 80-120 Hz high gamma (Buzsáki, 2006). Power in each band was calculated by integrating the power spectral density within each frequency band using Simpson's rule. Frequency-band power were then log-transformed for normality (Smulders et al., 2018). At this step, three additional subjects were removed for being a large outliers (> 3 median absolute deviations) in all measures of power in at least one recording.

Statistical analyses of frequency-band power were carried out using the Fieldtrip package (Oostenveld et al., 2011) in MATLAB 2020a. We assessed neural effects of the expansive and contractive posture conditions by taking the change in power in each band between the during-posture and pre-posture resting states and comparing this change between the expansive and contractive conditions using a cluster-based permutation test (Maris & Oostenveld, 2007). Cluster tests are a non-parametric method of statistical testing which take advantage of correlations between neighbouring channels and brain regions in EEG/MEG data. The procedure involves applying a univariate statistical test at each channel, then summing the test statistics over adjacent significant channels; data are then shuffled to generate a permutation distribution of this summed cluster statistic, and a p-value is generated from this distribution. In our study, the procedure was carried out using an unpaired t-test at each channel between the expansive and contractive conditions, and shuffling 2000 times. The procedure was then repeated using the change in power between the post-posture and pre-posture resting states; this was done both to conduct a cleaner, artefact-free comparison between posture conditions, and because the effects of the posture are presumed to last several minutes in order to be psychologically relevant for subsequent tasks or mood measures. To relate these neural changes to the behavioural effects, we computed summary indices of the change in power in each band by summing the change in power over all sensors found to be part of a significant cluster (Wainio-Theberge et al., 2021); this was done for both the during-pre and post-pre comparisons. We then correlated these summary indices with the changes in arousal and valence scores using Spearman correlation, correcting for multiple comparisons (6 bands x 3 scales) using false discovery rate correction (Benjamini & Yekutieli, 2001).

To further control for the influence of muscle artefacts during the posture, we then computed changes in EMG power for both the sternocleidomastoid and the trapezius and entered these into linear models. To compute changes in EEG power during the posture unbiased by EMG effects, we first regressed changes in EMG power out of the changes in EEG power by creating a linear model at each channel with both measures of EMG power, and taking the residuals of this model. This residualized EEG power was then subjected to the same cluster-based permutation test and correlation procedure described above.

Source localization of EEG data

We further attempted to characterize the brain areas involved in power posing using source localization. To this end, we applied exact Low Resolution Electromagnetic Tomography (eLORETA) to examine the cortical sources of our findings (Pascual-Marqui et al., 2011); eLORETA was chosen as it compares favourably to other source-localization approaches in multiple contexts (Halder et al., 2019; Pascual-Marqui et al., 2018). As individualized headmodels would have been too computationally costly to compute, we used a standard boundary element method head model obtained from the Colin27 template, which had three compartments: scalp, skull, and brain (Oostenveld et al., 2003). As a source model, we used the Conte69 surface template (Van Essen et al., 2012). Standard 10-20 system electrode locations were projected onto the surface of the head model.

We used a “virtual channel” approach to reconstruct source-level dipole moment time series at each vertex of the Conte69 template, as described in the Fieldtrip documentation and in Wainio-Theberge et al. (2022). We then applied the parcellation from Glasser et al. (2016) to reduce the size of our data, generating time series for each parcel by averaging the time series of the vertices within each region. From these parcel-level time series, we then carried out the same frequency and statistical analyses described above for the sensor-space data, focusing on the EMG-residualized data. Clustering at the source level was performed on the basis of adjacent regions.

Results

Expansive postures increase positive valence and arousal

After excluding bad recordings and taking only participants with data for all parts of the experiment, a final sample of 91 participants was obtained (mean age = 21.6, SD = 3.26; 25 males; 49 expansive, 42 contractive). Examining the changes in mood as a function of posture, we found that the expansive posture increased both COMP-A (arousal) and COMP-V (valence), relative to the contractive posture (COMP-A: $t(89) = 2.11$, $p = .038$; COMP-V: $t(89) = 3.33$, $p = .001$; Figure 2). For arousal, this effect occurred mainly due to a decrease in arousal in the contractive condition (expansive: $t(48) = 0.68$, $p = .50$; contractive: $t(41) = -2.5$, $p = .017$), while for valence, the increase for expansive postures was significant while the decrease in contractive postures was marginal (expansive: $t(48) = 2.92$, $p = .0054$; contractive: $t(41) = -1.83$, $p = .075$). Controlling for participant knowledge of the manipulation, the valence effect remained significant ($t(87) = -2.15$, $p = .035$) while the arousal effect was marginal ($t(87) = -1.73$, $p = .087$); no main effects or interactions with participant knowledge were significant, though there was a marginally significant interaction of posture and knowledge for valence ($t(87) = -1.73$, $p = 0.087$). Posture also affected scores on the authentic pride scale, with expansive postures increasing pride and contractive postures decreasing it, though subgroup effects were not significant (expansive: $t(48) = 1.52$, $p = .14$; contractive: $t(41) = -1.59$, $p = .12$; difference: $t(89) = 2.20$, $p = .031$); this effect was marginally significant controlling for participant knowledge ($t(87) = -1.81$, $p = .074$).

Posture modulates high-frequency EEG power

We next considered the effects of posture on power in the canonical EEG frequency bands. Considering changes during the posture, we found that contractive postures increased power in all frequency bands, while expansive postures had minimal effects; the differences between expansive and contractive conditions were significant in all bands (Delta: $p = .003$; Theta: $p = .005$; Alpha: $p = .022$; Beta: $p = .002$; Low gamma: $p = .001$; High gamma: $p = .001$; Figure 3). Effects were largest in occipital and temporal sensors, as well as in a frontal cluster for alpha and low and high gamma. We found that low and high gamma power changes were correlated with changes in both COMP-V and AP (Low gamma: $\rho_{COMP\text{-}V} = -0.31$, $p_{COMP\text{-}V} = .0032$, $\rho_{AP} = -0.22$, $p_{AP} = .032$; High gamma: $\rho_{COMP\text{-}V} = -0.34$, $p_{COMP\text{-}V} = .0011$, $\rho_{AP} = -0.27$, $p_{AP} = .0099$); moreover, changes in beta power were correlated with COMP-V and changes in delta power were correlated with AP (beta: $\rho = -0.21$ $p = .042$; delta: $\rho = -0.23$, $p = .029$). Of these, only the low and high gamma correlations with COMP-V survived FDR correction for multiple comparisons (low gamma: $p_{FDR} = .029$; high gamma: $p_{FDR} = .02$), while the high gamma correlation with AP was marginal ($p_{FDR} = .059$). For all correlations, greater increases in power were associated with smaller increases in positive affect and pride; these effects were driven by the contractive condition.

Considering changes in the post-posture resting state, we saw significant differences between expansive and contractive conditions only in the beta band ($p = .021$): expansive postures increased beta power in a frontal cluster, while contractive postures reduced it. These changes were not significantly correlated with any psychological scales.

Muscle artefacts confound the association of EEG power and behaviour

Examining the during posture – pre-posture power changes residualized for EMG activity, we found that differences between the expansive and contractive postures were largely maintained, though effects in theta power and the previously observed frontal clusters in low and high gamma were not significant (Delta: $p = .007$; Theta: $p = .085$; Alpha: $p = .036$; Beta: $p = .015$; Low gamma: $p = .002$; High gamma: $p = .002$; Figure 4). However, correlations between EEG power and mood questionnaires were significantly attenuated, and none reached significance ($p > 0.1$ for all cases).

Source localization of power differences between expansive and contractive postures

Finally, we used eLORETA to examine the cortical sources of the effects of expansive and contractive postures. Considering the EMG-residualized source-space data for the difference of during posture – pre-posture, we found a left medial occipital and subcortical cluster showed greater activity in the contractive posture for alpha ($p = .004$), beta ($p = .016$), low gamma ($p =$

.001), and high gamma ($p = .002$; Figure 5). Using the cluster-based permutation test, we found no significant effects of posture on changes in the source-localized post-posture resting state ($p > 0.1$ in all cases); however, several individual regions were significant, including the dorsolateral prefrontal cortex in delta and gamma (see Figure 5). For the beta band, where posture effects were significant at the channel level, the parieto-occipital sulcus was the region which most strongly distinguished the expansive and contractive postures in terms of their changes from pre-posture to post-posture.

Discussion

While the power posing paradigm has been a popular, if controversial, experimental design in psychology, no studies have directly investigated its neural mechanisms. We addressed this open question using EEG recorded during a standard power posing paradigm, taking advantage of this method's flexibility in allowing participants greater freedom of motion. We found that expansive and contractive postures had the expected effects on mood, with expansive postures increasing positive affect and arousal and contractive postures decreasing these. Moreover, we found that expansive and contractive postures differed with respect to their effects on EEG power, with contractive postures increasing power particularly in high frequency bands during the posture, but with contractive and expansive postures differing in beta power changes following the posture. While the effects during the posture were correlated with the mood questionnaires, the effects of muscle activity prevent a clear interpretation of neural mediation of the psychological effects. Despite this, the study provides the first neural data on the mechanisms of power posing, which will be elaborated below.

Beta and gamma oscillations: somatosensory processing in power posing

During the posture, we found the largest effects of postural contraction in high-frequency bands such as beta and gamma. Moreover, beta was the only band in which significant differences were found in the post-posture resting state. Beta has been long studied as a marker of somatosensory and motor processing. Spontaneous fluctuations of beta power correlate inversely with fMRI activity in the somatosensory cortex (Ritter et al., 2009); resting beta power is also associated with GABA signalling (Jensen et al., 2005), suggesting that beta is an "idling rhythm" of somatosensory cortex (much like alpha in occipital cortex; Ben-Simon et al., 2008). The initiation of movement strongly attenuates beta power, while following movement completion beta power rebounds to above normal levels (Barone & Rossiter, 2021); this, along with the above findings has led researchers to suggest an inhibitory role for beta in maintaining the current sensorimotor state, while beta desynchronization allows for movement and transition between steady states (Engel & Fries, 2010). In contrast, low gamma oscillations are often tonically active during movement (Crone et al., 1998), while high gamma appears at movement initiation and offset (Szurhaj et al., 2005); these latter findings are hypothesized to reflect afferent motor commands and efferent somatosensory feedback, respectively (Ulloa, 2022)

The modulation of beta and gamma oscillations by expansive and contractive postures suggests that, in accordance with our hypotheses, somatosensory activity is involved in the effects of expansive and contractive postures. With respect to effects during the posture, consistent with gamma's role as a prokinetic oscillation, we found gamma power increased markedly in the contractive posture, but not in the expansive one; we suggest that this effect may be due to the contractive posture requiring greater motor coordination to maintain, as it reflects a more extreme deviation from normal resting posture. However, as effects were found in all frequency bands, muscle artefacts may be suspected (see below); alternatively, broadband, aperiodic cortical dynamics could be implicated, which future analyses should address (Donoghue et al., 2020). The perspective above on beta power as a sensorimotor idling rhythm, combined with our findings of reduced beta power in the post-posture resting state suggests that SSC is more active following the contractive posture than the expansive one; we suggest that this may be due to the brain processing somatosensory feedback from the contractive posture, which has been suggested by our study and others (Elkjaer et al., 2020) to drive the effects of the power posing manipulation. Moreover, the increased GABAergic signalling implied by the higher beta power in the expansive post-posture resting state may suggest that this state is lower in anxiety (Lydiard, 2003), in accordance with our behavioural findings.

The confounding influence of muscle artefacts

In our data recorded during the postures, we found a significant confounding influence of muscle artefacts. As previously noted, muscle artefacts manifest themselves most strongly in high-frequency activity, particularly in the gamma band (Muthukumaraswamy, 2013); this is particularly pernicious for our study as these are the bands of interest which are relevant for somatomotor processing. In our preprocessing, we rejected ICA components whose topographies and frequencies resembled those of muscle artefacts (Winkler et al., 2011); however, this was clearly insufficient, as EMG power retained significant correlations with EEG activity during the posture. While effects were significant even when regressing out EMG power, there remains the suspicion of muscle contamination in our source localization findings: we localized changes in EEG power mainly to subcortical structures, which, though implicated in previous studies of hierarchy processing (Dwortz et al., 2022), typically are not well-represented in EEG signals (Attal & Schwartz, 2013). Thus, these localization findings lend credence to the idea that residual muscle artefact remains in the signal. These residual artefacts may be attenuated by a different choice of source localization approach: while eLORETA is highly accurate, beamforming has the additional property of suppressing non-brain artefacts (Cheyne et al., 2007), making it a potentially useful tool for our data. However, beamforming also struggles with localizing bilateral source topographies, as the beamforming approach attempts to suppress signals from sources other than the original target (Hillebrand & Barnes, 2005); as such, we found that the approach resulted in abnormal distributions of power for our data.

However, with respect to the EEG-behaviour correlations, regressing out all EMG activity may over-control for this effect. We also observed correlations between EMG sternocleidomastoid power change during the posture and EEG gamma power in the post-posture resting state ($\rho = 0.24$, $p = .028$). Since we did not observe differences in EMG power between pre- and post-posture resting states, this implies that part of the EMG-EEG correlations may reflect that different participants adopted the posture to different degrees: those who adopted a more extreme version of the posture (or who needed to move more from their baseline to adopt the posture) may have greater behavioural effects, greater EMG power, and greater neural effects, implying a true (non-artefactual) correlation between EMG power and neural activity. Analysis of participants' postural angles during the expansive and contractive postures could help to address this question by providing an independent measure of the extent to which participants adopted the posture.

Conclusion

Expansive and contractive postures are crucial media for dominance signalling, and feedback from these postures, as in the popular "power posing" experimental design, can influence mood, behaviour, and cognition. However, the neural mechanisms of power posing have never been investigated, and little work has been done in general on neuroimaging of dominance signalling in humans. Here, we used EEG combined with peripheral physiology and a simple "power posing" design to investigate the neural mechanisms of postural feedback. We found that expansive and contractive postures modulated beta and gamma power, frequency bands known to be involved in somatomotor processing. While the influence of muscle artefacts confounds a clear interpretation of the findings, this study provides the first neuroimaging evidence on power posing, and suggests that somatosensory feedback may be implicated in this procedure.

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Figures

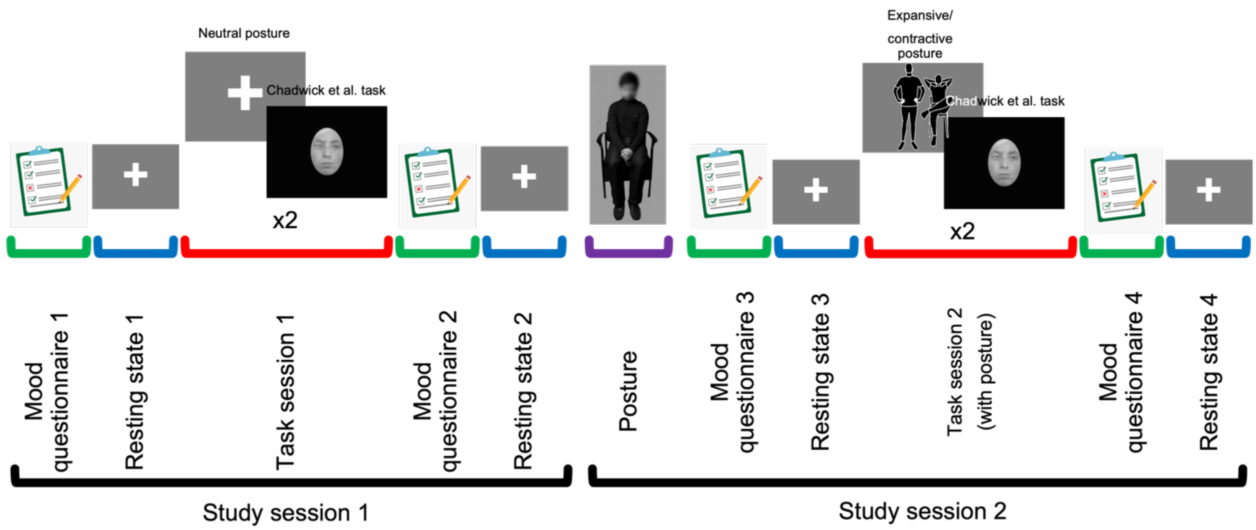


Figure 4- 1: Schematic of the study structure.

Figure 1. Schematic of the study structure. Study sessions were carried out on the same day, in immediate succession.

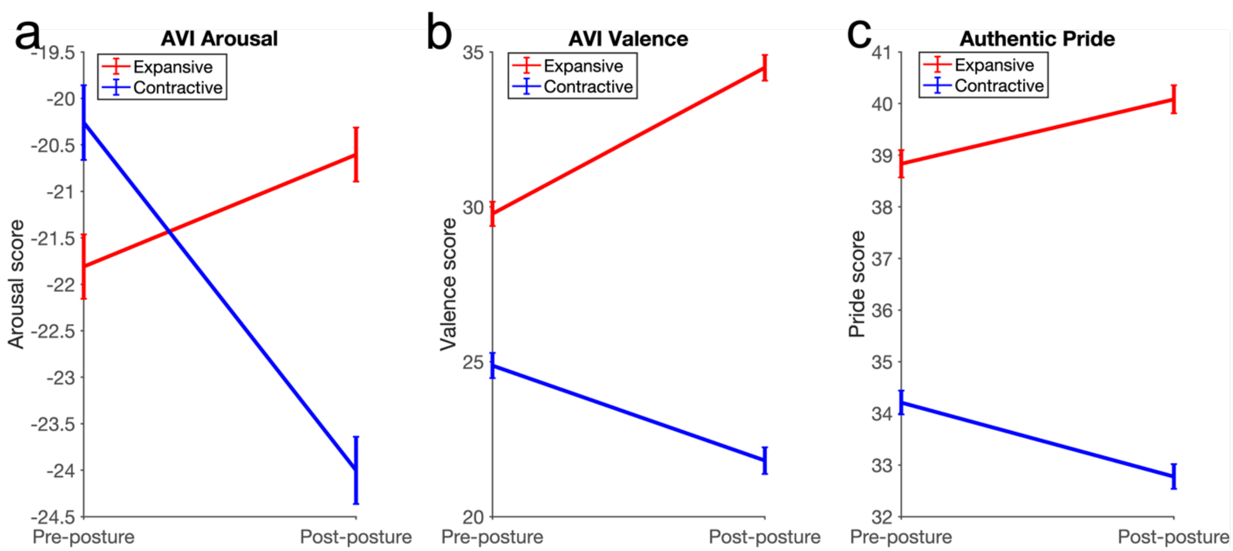


Figure 4- 2: Behavioural effects of posture on arousal, valence, and pride.

Figure 2. Behavioural effects of posture on arousal, valence, and pride. Means ± standard error are plotted.

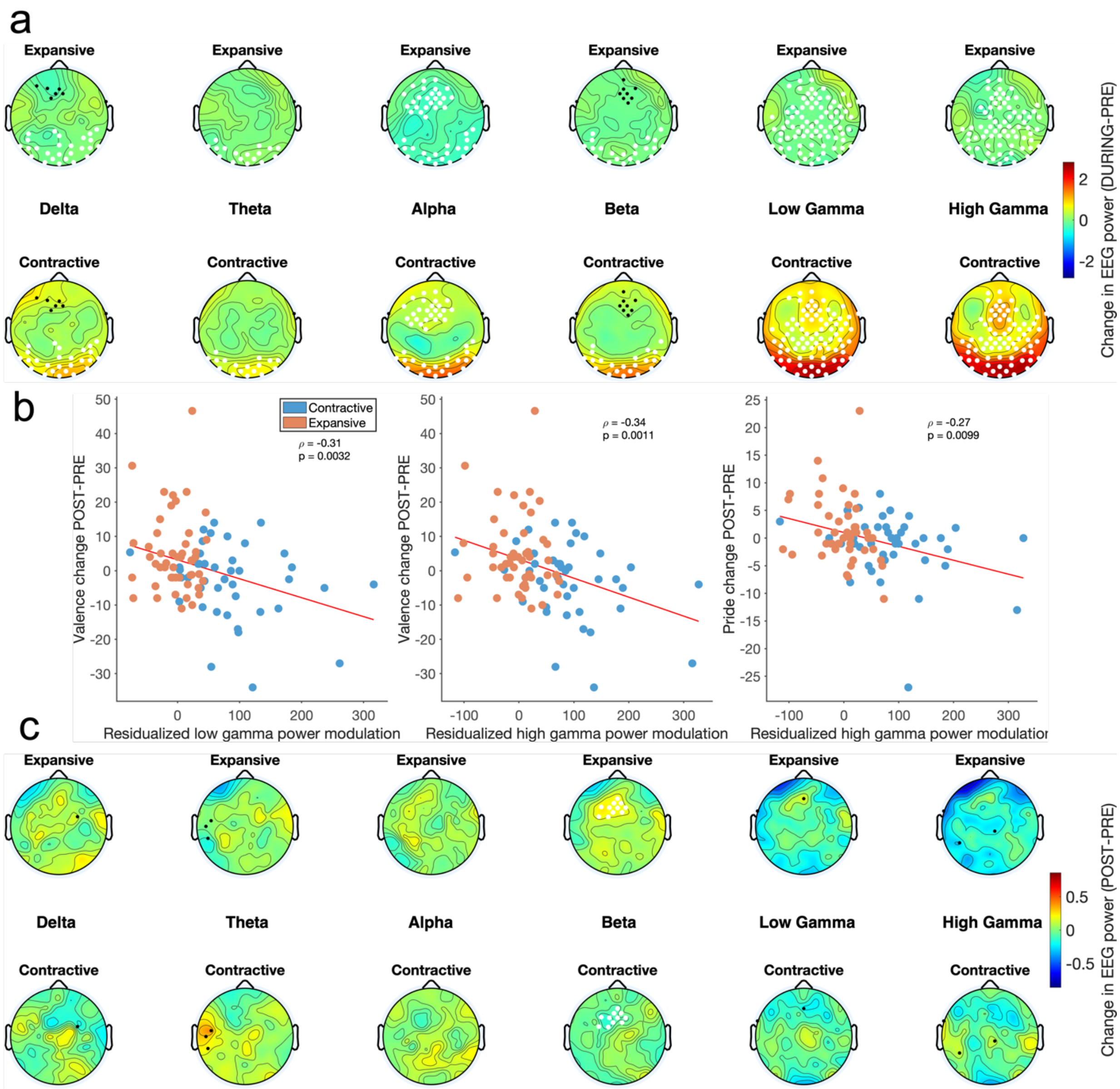


Figure 4- 3: Effects of expansive and contractive postures on EEG power.

Figure 3. Effects of expansive and contractive postures on EEG power. A) EEG power changes during expansive and contractive postures. Topoplots show the difference in log EEG power between the during-posture recording and the post-posture recording. Sensor dots indicate the significance of differences between expansive and contractive: white dots indicate electrodes which form part of a significant cluster, while black dots indicate channel-level significance that did not survive multiple comparison correction. B) Correlations between EEG power modulation during the posture and changes in behavioural scales. Power modulation was calculated by summing the EEG changes within significant clusters (see Methods for details. Each dot

represents one subject, line of best fit is plotted in red. C) EEG power changes in the post-posture resting state, as a function of the preceding posture. As A.

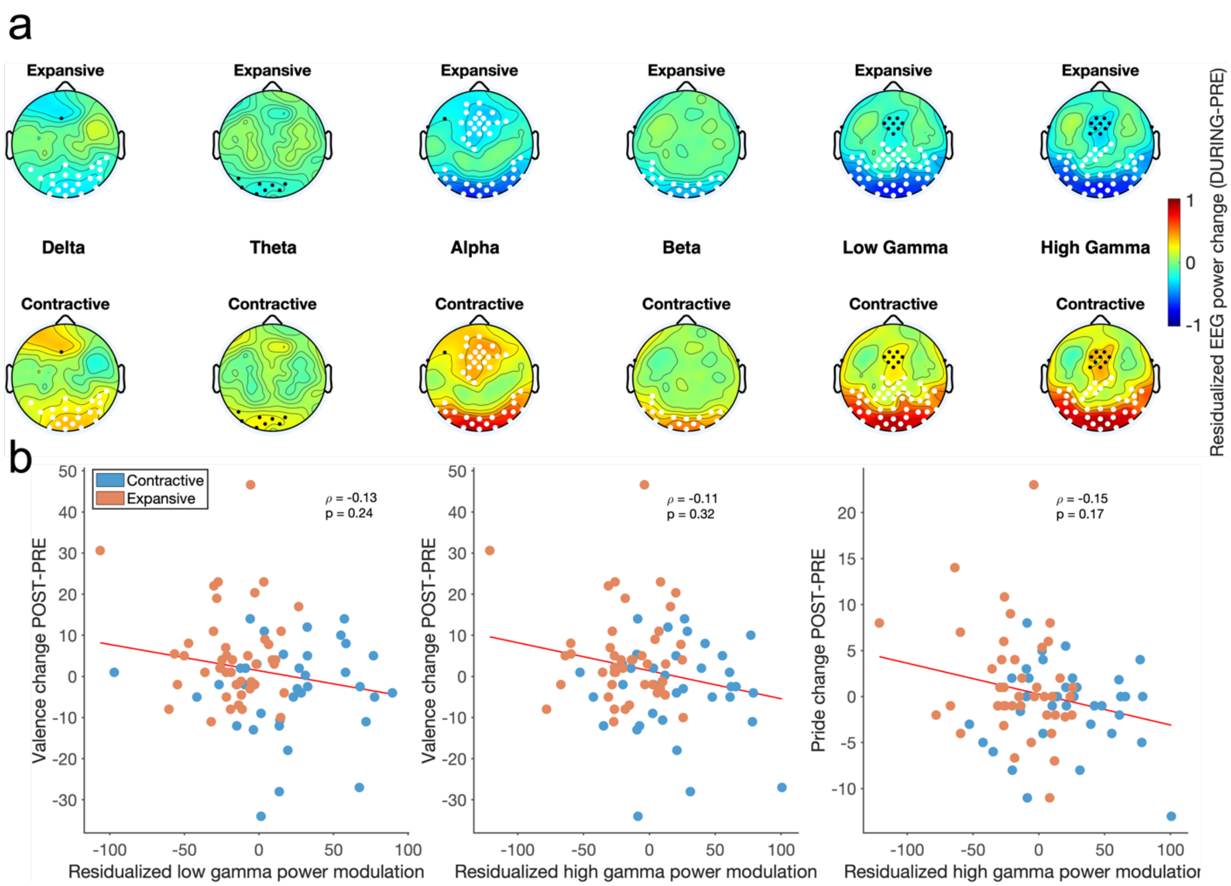
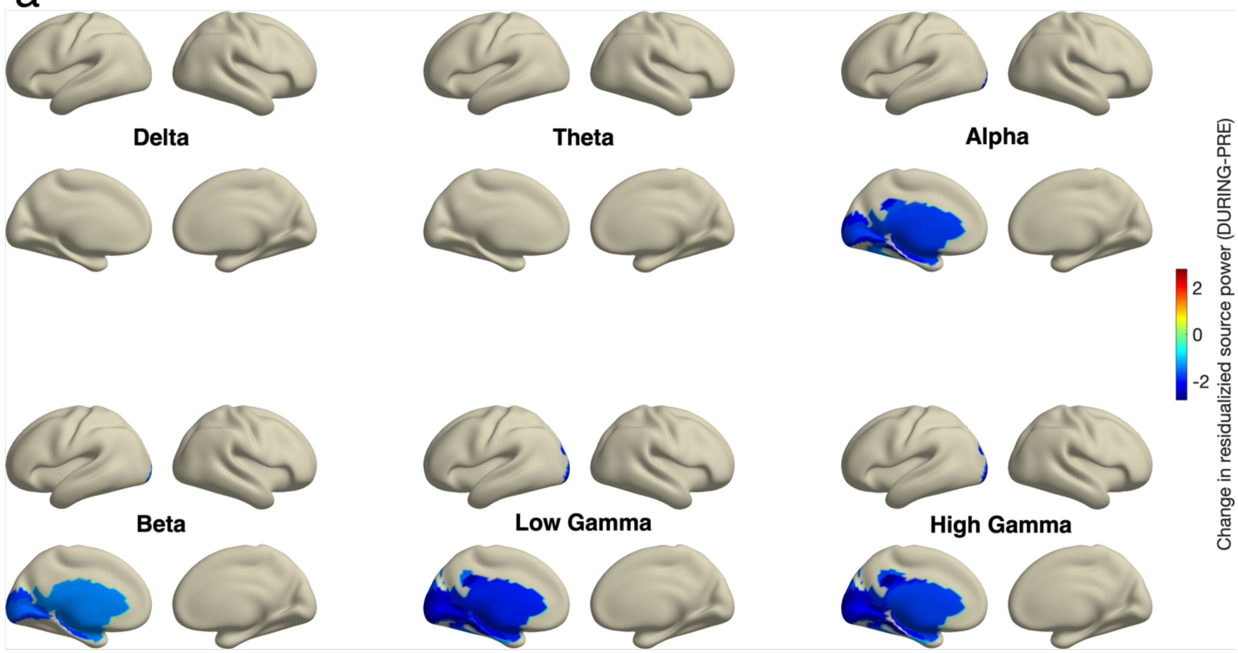


Figure 4- 4: Effects of expansive and contractive postures on EEG power controlling for the influence of muscle activity.

Figure 4. Effects of expansive and contractive postures on EEG power controlling for the influence of muscle activity. As figure 3 A and B, but residuals after regressing out EMG power at each electrode are plotted.

a



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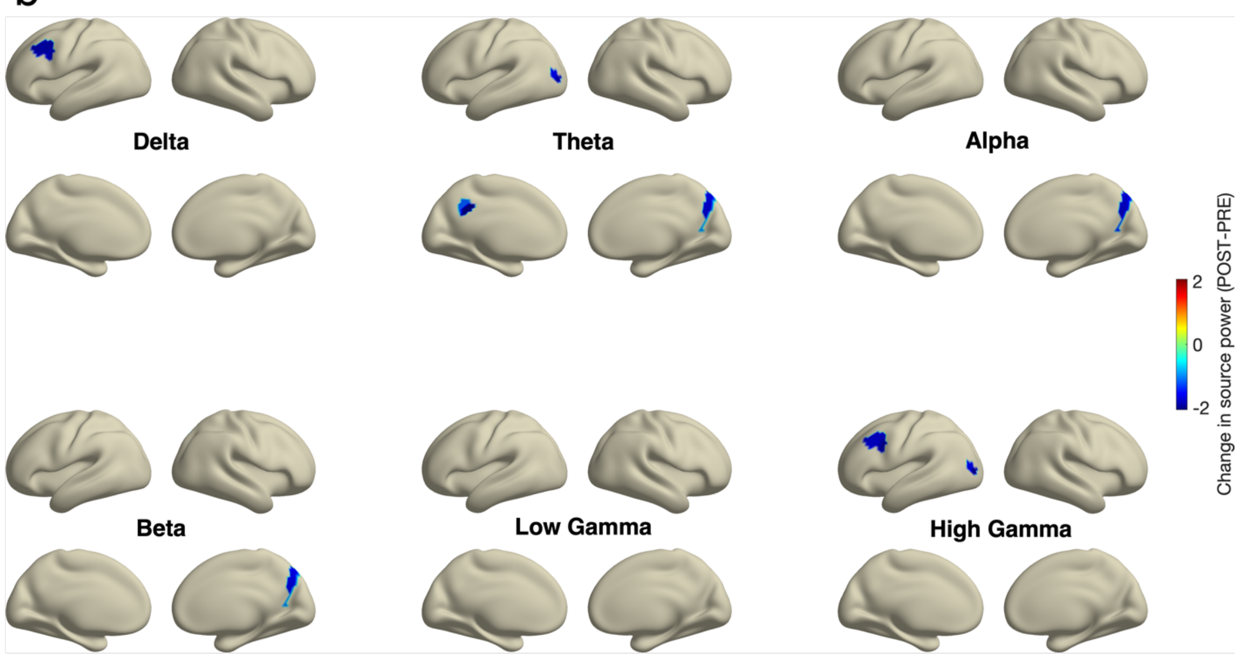

Figure 4- 5: Source-localized differences between expansive and contractive postures.

Figure 5. Source-localized differences between expansive and contractive postures. Plots show the difference between expansive and contractive postures in A) During posture minus pre-posture power modulation and B) Post-posture minus pre-posture power modulation. In A), only

significant clusters are shown. Since no significant clusters were found in B), individual significant regions (which did not survive multiple comparison correction) are plotted instead.

Chapter 5: General discussion and conclusion

Discussion

Individual differences in somatosensory and motor processes

The first two manuscripts in the thesis were primarily concerned with the theme of individual differences in somatosensory and motor phenomena in emotion. As outlined in the introduction, somatomotor and physiological processes in emotion are generally considered from the standpoint of evolutionary processes: the motor and physiological outputs of emotion are thought of as evolutionarily optimized responses to specific environmental contingencies, and are viewed as conserved across species, leaving little room for individual intra-species variation. Individual differences have been instead considered at the level of pre-cognitive appraisal and meta-cognitive representation (see Scherer, 2022 for the distinction of these components). For example, studies of anxiety and neuroticism suggest that individual high in these traits appraise emotion-related situations as more threatening, resulting in increased negative affect (Etkin et al., 2004). Similarly, studies considering alexithymia and emotional granularity have considered individual variation within meta-representations of emotion; that is, how individuals perceive and cognize their emotional states (Smidt & Suvak, 2015). However, variation in the motor and sensory aspects of emotion have been less considered.

We suggest that this variation at the sensorimotor level may act as a mediating mechanism by which individual habits (e.g. of dominance and submission, approach or avoidance) maintain themselves. Laboratory studies have established that the effects of emotion-related motor activity are bi-directional: for example, expansive postures are adopted more by dominant individuals (Hall et al., 2005), but adopting expansive postures also increases behavioural signatures of dominance (Elkjaer et al., 2020). Thus, the habitual use of either dominant postures, or the habitual occupation of dominant social roles, may reinforce itself in a positive feedback loop. To express dominance, individuals adopt dominant postures: in turn, the individual perceives themselves in such a posture, reinforcing the initial expression (this feedback loop can also include perception by others, in the sense of personality "evocation"; Buss, 1987). In this way, the sensorimotor loop may reinforce behaviours which were initially situation-specific, transforming them into stable personality traits.

Individual differences in somatosensory feedback in emotion may have multiple causal origins or relationships to personality. Individual, biological differences in interoceptive sensitivity or physiological activity may mediate these effects (Critchley & Garfinkel, 2017). Alternatively, differences in physiology may have impacts on cognition and personality. For example, patients with atrial fibrillation exhibit significantly increased risk of psychiatric problems due to this conditions impacts on the autonomic nervous system (Ladwig et al., 2020), and irritable bowel syndrome has been linked with numerous psychiatric disorders, potentially through its effects on the perception of visceral signals (Fadgyas-Stanculete et al., 2014); these examples show the impact that individual differences in biological factors can have on mental traits. Finally, and interestingly given the above focus on individual differences in body posture, learned motor habits may affect somatosensory feedback (Ostry & Gribble, 2016). If motor learning generates changes in somatosensation (Kumar et al., 2019; Ostry et al., 2010), then learned patterns of body posture such as those discussed in chapter 3 might have corresponding somatosensory effects, an intriguing possibility that would link the first two manuscripts.

Overall, the present work extends perspectives on embodied cognition to the level of individual differences and personality. Embodied cognition, a perspective gaining traction in the cognitive and neurosciences, is the view that many cognitive processes inherently involve representations in the body, rather than abstract representations in the brain (Varela et al., 2017). There is a growing view that concepts such as the self in particular have a particular embodied basis, with experimental findings showing the importance of heart-brain coupling for self-referential processing (Azzalini et al., 2019; Tallon-Baudry et al., 2018), and the involvement of interoceptive regions such as the insula in self-reflection (Modinos et al., 2009). As such, the extension of embodied perspectives to personality and individual differences is timely and needed (Robinson et al., 2021); the present work gives two examples of how mental conceptions of the self (e.g. as dominant or submissive) might also be represented in the body.

The role of somatosensory and motor phenomena in empathy and antisocial attitudes

Interestingly, the first two manuscripts both described correlations with a dimension of personality referred to as “antisocial attitudes”. This principal component, which was similar in both manuscripts and in all the samples where it was assessed, generally loaded strongly on scales such as Social Dominance Orientation (SDO), psychopathy, and negatively on empathy and agreeableness. While empathy has been well-described in the context of somatosensation (e.g. the embodied simulation account of empathy, described in the introduction) and in the context of dominance (e.g. dominant individuals being lower in empathy), its converse in psychopathy and anti-social tendencies have not usually been thought of in this context.

As personality traits generally reflect a continuum with clinical phenotypes (Cuthbert & Insel, 2013), the present studies may be relevant to clinical work in antisocial personality disorders and clinical psychopathy. Other psychiatric conditions such as schizophrenia (Torregrossa et al., 2019) and major depression (Lyons et al., 2021) have been shown to exhibit anomalous bodily sensation maps; moreover, depression has also been associated with stooped head posture (Wilkes et al., 2017). However, psychopathy and antisocial disorders have rarely been thought of in terms of somatomotor abnormalities, despite a growing body of evidence suggesting somatomotor alterations across a wide spectrum of clinical phenotypes (Bunse et al., 2014; Kebets et al., 2019; Northoff et al., 2020). While much more research needs to be done, the present work suggests that interventions aimed at increasing interoceptive awareness, which form part of mindfulness interventions which have been gaining popularity across psychiatry (Keng et al., 2011), may be effective in alleviating psychopathy and clinical antisocial traits.

The relationship of both trait body posture and individual somatosensory representations of emotion to similar principal components reflecting empathy and antisocial attitudes raises the question of whether body posture and somatosensory representations of emotion are themselves related. Indeed, this seems plausible and likely, especially given the findings discussed in the literature review that emotional body language corresponds somatotopically with SSC responses to emotional stimuli (Kragel & LaBar, 2016; Sel et al., 2020), and the findings discussed above that motor learning affects somatosensory activity (Ostry & Gribble, 2016). These findings are also supported by the third manuscript of this thesis, which suggested an involvement of somatosensory mechanisms in the “power posing” paradigm. We suggest that the relationship of dominance and submission to somatosensory activity can be conceived in terms of differences in agency, similar to the perspective advanced by Kraus et al. (2012) in their discussion of self-concepts and power. Because of their power and access to resources, dominant individuals have greater agency in the world, and thus are more able to enact their desires; in contrast, submissive individuals are more passive, and more frequently must adapt to the constraints of the environment. Submissive individuals are thus primed for somatosensory perception (i.e. perceiving the feedback of the environment upon them), while dominant individuals take on a motor role (i.e. acting upon the environment); this results in reduced somatosensation.

Unfortunately, the present studies were not sufficiently powered to detect such an association. The posture measure and the bodily maps of emotion measure both contain significant sources of noise and error variance. For the posture, differences in participants' camera angles and distances can affect the head angle, as well as more subtle methodological issues with the OpenPOSE estimation; since OpenPOSE estimates a keypoint on the shoulder, rather than an anatomical key point on the spine, participants with more protracted shoulders may have artificially lower head angles, creating an additional source of noise. For the BSMs, different interpretations of the task may result in individual differences in overall painting intensity which may not be meaningful, and (as mentioned in the limitations of chapter 2) numerous cognitive processes, such as memory recall, affect the final paintings. While we have partially addressed the former issue in follow-up experiments, in which we showed that heart/stomach/head painting in non-emotional body sensations has minimal relationship with personality, the task remains a noisy measure of emotional somatosensation. Thus, the power required to detect an association between two noisy measures is significantly greater than the power to detect an association between a single noisy measure (head angle or BSMs) and a measure closer to the ground truth (validated personality scales).

Future directions

While the first two manuscripts of this thesis have outlined two successful approaches at relating emotional somatosensation and personality, data from both the bodily maps of emotion procedure and the OpenPOSE-based trait posture assessment are rich and multivariate, and could be used to test numerous other hypotheses and uncover other relationships. For example, with respect to the BSM data, we focused on somatosensation from particular areas of interest. However, it may also be appropriate to examine global patterns of somatosensory activity. Focal regions of interest emerged in our procedure largely because of the use of factor rotation in the principal component analysis, which encourages loadings on a small number of variables (i.e. pixels). Unrotated components may reveal broader patterns of somatosensation which may be associated with different personality features. Alternatively, the use of multivariate associative techniques could reveal associations between BSM features and personality on a purely data driven basis (McIntosh & Mišić, 2013). Finally, techniques such as parallel factor analysis (Schmitz et al., 2015), an analogue of principal component analysis which allows the decomposition of three-dimensional data such as the body maps (i.e. pixels x emotions x participants), may be appropriate and useful in finding underlying dimensions of emotional somatosensation.

With respect to the posture data, while most postural feedback research has focused on expansive and contractive postures as signals of dominance, a small but consistent literature has also emerged demonstrating that posture can also index approach/avoidance behaviour: studies have shown that leaning forward increases behavioural and neural markers of approach behaviour (Harmon-Jones et al., 2011). Trait "postural leans" could also be quantified using our procedure, for example by using participants' postural angles to estimate their centre of mass. Moreover, while we focused on head angle, the quantification of other postural parameters (such as head tilt; Witkower & Tracy, 2019), or the use of multivariate associative techniques could be relevant in uncovering additional relationships between trait body posture and personality.

Given the suggestions by the third manuscript and by the literature that somatosensory feedback processes are involved in power posing, a prudent next step would be to test the involvement of somatosensory cortex in a causal manner. Transcranial magnetic stimulation (TMS) is a non-invasive brain stimulation method which can selectively inhibit target cortical areas, allowing for causal tests of the involvement of a brain region in a given process. If somatosensory feedback is indeed necessary for power posing, then inhibition of SSC via TMS should abolish the effects of the posture. As discussed previously, TMS has been used effectively in studies of empathy and emotion processing, demonstrating the involvement of SSC in these processes (Bufalari et al., 2007); as such, it may be an effective tool in further elucidating the mechanisms of postural feedback.

Finally, the framework discussed in the first section of the discussion begs the question of the relationship between trait and state body posture. Postural feedback paradigms assume that individuals enter the study as "blank slates", with neither expansive nor contractive postures at baseline. However, previously, we proposed that individual differences in trait body posture reflect a sensorimotor loop which reinforces repeated motor and psychological states; moreover, we discussed how these learned motor behaviours have impacts on associated somatosensation. As such, it is reasonable to assume that these baseline postures may impact the procedure: for example, individuals with habitually more expansive postures may be either more sensitive to an expansive posture condition (if the posture reinforces the self-concept that has developed as a result of repeated dominant behaviours and postures), or more sensitive to a contractive posture condition (because this reflects a larger difference from baseline which may be more salient to them). Including these baseline postures as a covariate may help in accounting for the large heterogeneity of posture effects in the literature, as well as for trends observed in the literature, such as that effects are larger in individualistic countries (Körner et al., 2022).

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Conclusion

The present thesis details an investigation of several overlooked aspects of sensorimotor processes in emotion. Centrally, individual differences in both motor and somatosensory representations of emotion were shown to be relevant for a cluster of personality traits revolving around empathy, psychopathy, and social dominance: these results corroborate theories in the literature around empathy and vicarious somatosensation, and support the extension of work on emotional body postures to the level of trait-like individual variation. Moreover, the thesis examines the link between somatosensation and posture by investigating the neural mechanisms of the "power posing" paradigm. We find tentative evidence of the involvement of somatosensory mechanisms in this design, completing the loop between emotion, bodily action, and somatosensation. In summary, this work provides several lines of evidence reinforcing the importance of embodied perspectives in emotion science, and particularly in the study of individual differences, where they have been sorely neglected.

Appendix S1: Supplementary materials to manuscript 1

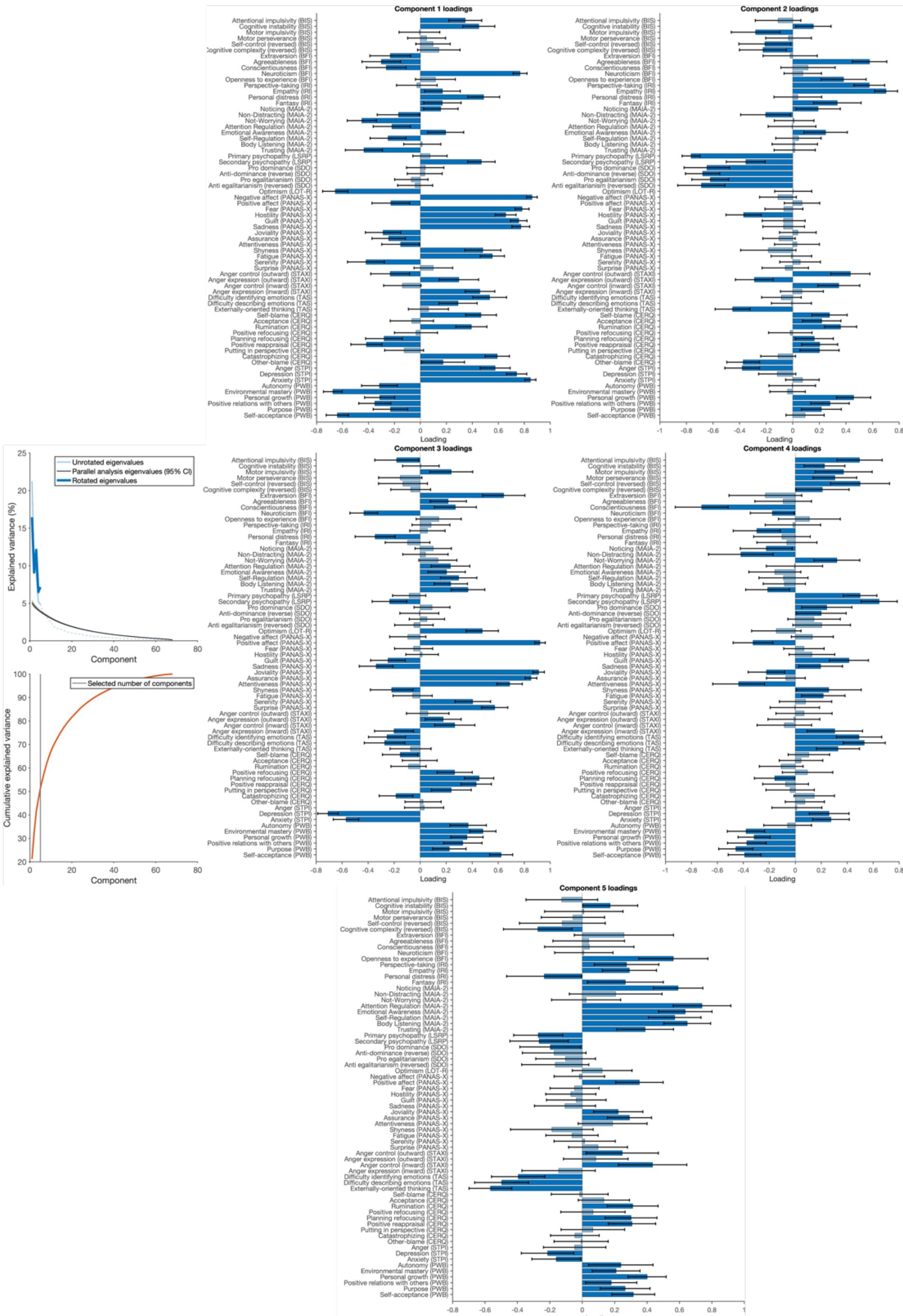

Figure S1. Full loadings for the personality PCA decomposition. Left: Eigenvalue plots as in figure 2. Bold blue line shows the eigenvalues of the rotated components. Light blue line shows the eigenvalues of the unrotated components; the dashed part reflects eigenvalues not significant following the permutation test. Black line shows the eigenvalues from the permutation test and the 95% confidence interval of these (grey shading). Right: loadings for each component on all personality scales. Bars represent loadings, error bars reflect bootstrap confidence intervals. Bars are shaded dark blue if they are significant (bootstrap CI excludes 0), light blue if they are not significant.

Appendix S2: Supplementary materials to manuscript 2

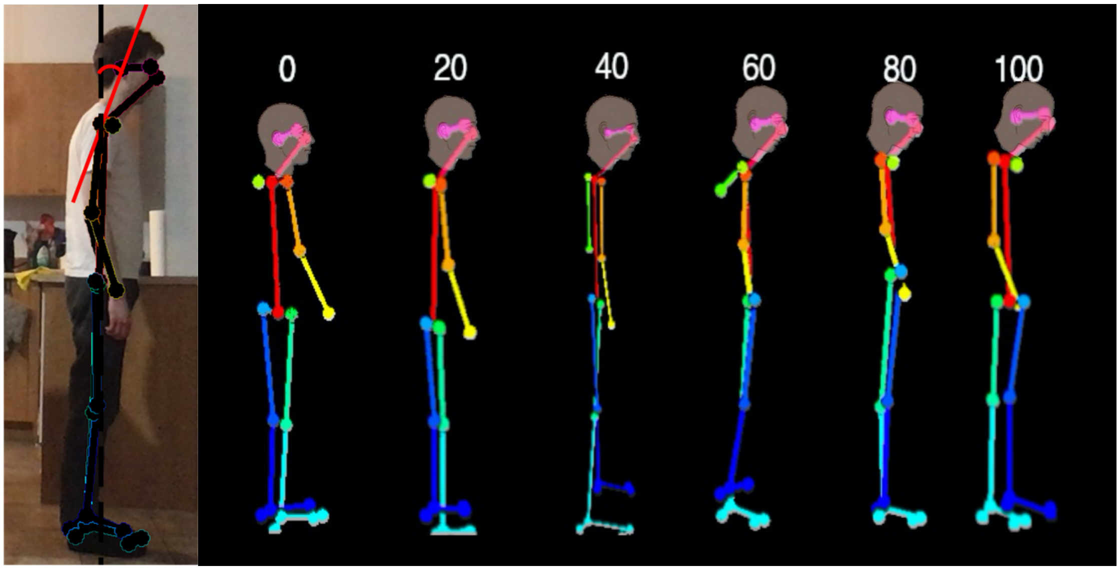

Figure S1. Left: Example of the head angle calculation from OpenPOSE's annotation of key points. The head angle is calculated by drawing a line between the shoulder and ear OpenPOSE keypoints, and calculating the angle with the vertical of the photograph. This is done on both the left and right view photos, and the angles are averaged. The subject shown is one of the experimenters, who was not included in the sample. Right: OpenPOSE skeletons for the 0th, 20th, 40th, 60th, 80th, and 100th percentiles of head angle. Examples shown reflect percentiles of head angle only for the left view photos, for illustrative purposes – the actual head angle measure used in the study reflects the average of the left and right view photos.