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My body, your emotions: Viscerosomatic modulation of facial expression discrimination

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ABSTRACT

Interoception reflects the ability to observe one's innermost bodily states. Here, we assessed whether interoceptive accuracy (IA) is related to the empathic ability to discriminate others' emotions. Participants (N = 111) completed a heartbeat tracking task, as well as an emotional go/no-go task with fearful and disgusted faces. Empathic facial mimicry during the go/no-go task was measured using electromyography (EMG) of the *Corrugator Supercilii* muscle. Higher IA was associated with higher perceptual sensitivity for emotional faces but was unrelated to response bias. Individuals higher in IA had stronger coupling between facial EMG and task performance. IA and facial EMG were associated with Go but not with NoGo trials, consistent with a specific modulation of perceptual sensitivity. These results suggest that tuning into one's own viscerosomatic signals relates to empathic mimicry and perception of others' emotional states.

1. Introduction

The degree to which an individual is able to perceive or "tune into" their own internal signals is an important factor in emotional experience. The perception of one's own bodily signals is called interoception (Khalsa, Rudrauf, Feinstein, & Tranel, 2009). In particular, the correspondence between objective somatic events (e.g., heartbeats) and perception of these events (i.e., interoceptive accuracy, IA) has been linked to enhanced emotional experience. In one study, individuals with higher IA (measured in a heartbeat counting task) had more subjective arousal, and more vagal reactivity, when viewing emotional scenes (Herbert, Pollatos, Flor, Enck, & Schandry, 2010). Disrupted interoceptive signaling has been observed in multiple affective disorders, including borderline personality disorder (Müller et al., 2015), anorexia nervosa (Pollatos et al., 2016), alexithymia (Brewer, Cook, & Bird, 2016), and autism (Garfinkel et al., 2016). Functional neuroimaging and neurostimulation studies have identified cortical areas that may facilitate the integration of interoceptive processing with perception of others' emotions (Terasawa, Fukushima, & Umeda, 2013; Motomura et al., 2019). These groups and others have observed overlapping brain activation in the anterior insula and the anterior cingulate cortex during cardiac interoception and viewing of emotional stimuli (Terasawa et al., 2013; Zaki, Davis, & Ochsner, 2012). This evidence is broadly consistent with the hypothesis that emotions involve the integration of bodily sensations with processing and valuation of exteroceptive events. Thus, evidence suggests that interoception may modulate how both healthy and affect-disordered individuals extract emotional significance (Khalsa et al., 2017). Here, we asked how interoception, indexed by the accuracy with which a person can monitor their own heart, modulates accuracy in discriminating others' emotions.

Early twentieth century models of emotion posited that processing of emotional events occurs separately from the somatic sensations associated with subjective emotional experience. Specifically, perceptual processing of exteroceptive inputs (and related conceptual interpretation) was thought to precede or occur in parallel to somatic processing (Dagleish, 2004; Darwin, 1955/1872Darwin, 1955/1872; James, 1950/1890James, 1950/1890). Contemporary work has refined these assumptions by suggesting that skeletomotor responses and somatic sensations can influence perception of emotional events. Facial mimicry, which describes the movements of one's own facial muscles when viewing another person's emotional facial expression, has been posited as an important method of identifying emotions in others (Goldman & Sripada, 2005; McIntosh, 1996). Evidence suggests that somatic input may be necessary for facial mimicry: Patients with locked-in syndrome (paralysis of voluntary facial movements) show impaired recognition of facial expressions (Pistoia et al., 2010), and healthy people show impaired facial expression recognition when facial mimicry is blocked (Oberman, Winkielman, & Ramachandran, 2007).

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Thus, external somatic mirroring is part of the process of emotional discrimination of other's mental states.

Facial mimicry may be understood as a component of emotional communication, in reading others' mental states (Goldman & Sripada, 2005; McIntosh, Reichmann-Decker, Winkielman, & Wilbarger, 2006). Access to one's own internal physiological states is not an overt act of communication, but represents an internal tuning toward one's bodily states and potentially a competence in reading others' mental states. Recent work suggests that, when presented during specific cardiac states, i.e., systole versus diastole, perception of threat-related signals is heightened (Garfinkel & Crichtley, 2016). This work relates objective cardiac states (i.e., outside of conscious awareness) to attention to, and perception of, external emotional stimuli. However, the relationship between one's ability to consciously tune into cardiac events (i.e., interoceptive accuracy) and the ability to discriminate others' emotional states remains unclear. In the current study, we assessed the relative contributions of both visceral and somatic inputs to facial emotion discrimination. In order to do so, we measured interoceptive accuracy (using a heart beat tracking task) and facial mimicry (using electromyography, EMG), examining their relationship to sensitivity and response bias when discriminating between other's emotional states as conveyed by facial expressions. We hypothesized that higher interoceptive accuracy and higher facial mimicry would be associated with better emotion discrimination when viewing others' facial expressions.

2. Methods

2.1. Participants

One hundred eleven college students (80 female), mean age 20.35 years (SEM = 0.17, range = 18–32) participated in the go/no-go and heartbeat tracking tasks. This sample size was selected based on a calculation assuming an effect size of .2 (as is typical of individual difference studies), and a one-sided alpha of .05 (given that our hypothesis was unidirectional), in order to achieve 75% power.

2.2. Procedure

In the laboratory, participants provided informed consent and then were set up with the physiological measuring equipment. They completed the emotional go/no-go task first, followed by the heartbeat tracking task. After completing both tasks, participants filled out surveys to measure traits that have previously been associated with interoceptive accuracy. These surveys included the Spielberger State-Trait Anxiety Inventory (STAI, Form Y) (Spielberger, 1983), a 12-item short form of Raven's Advanced Progressive Matrices (APM, a measure of general intelligence; Arthur & Day, 1994), and demographic information. Surveys were administered in Qualtrics software (Provo, UT). All procedures and materials were reviewed and approved by the Cornell University Institutional Review Board.

2.2.1. Physiological recordings

Electromyography (EMG) activity of the left *Corrugator Supercilii* muscle was measured using a BioPac MP150 amplifier/receiver and three wireless BioNomadix Ag/AgCl electrodes (4 cm inner diameter). Two electrodes were placed over the approximate location of the *Corrugator Supercilii* according to established guidelines (Fridlund & Cacioppo, 1986). A third electrode, which served as the "ground", was placed on the participant's right cheekbone. Prior to placement on the skin, a small amount of multipurpose conductive gel (SignaGel) was applied to each electrode, and the electrode sites on the skin were also first cleaned with a non-alcohol-based exfoliating gel, then thoroughly dried. EMG data were collected at a 1000 Hz sampling rate, and the amplified signal was digitally filtered with 10 Hz high-pass and 500 Hz low-pass thresholds. Impedance was not monitored due to the BioPac equipment's high Common Mode Rejection Ratio (90 dB minimum) and high Common Mode Input Impedance (1000 MΩ). EMG data were collected into Acqknowledge 4.0 software (BioPac, Inc., Goleto, CA), which was synchronized with PsychoPy (Pierce, 2007) via a parallel port cable. Pulse plethysmography (PPG) data were collected at 200 Hz sampling rate, using the same BioPac MP150, a wireless BioNomadix transponder, and an infrared sensor was attached to their non-dominant middle finger.

2.3. Materials

2.3.1. Avatar images

Facial images of avatars were created using FaceGen software (SingularInversions, 2015; www.facegen.com; Blanz & Vetter, 1999). Avatars were used in order to control the percentage of emotion expressed, and to avoid image degradation associated with morphing photographs of human faces. Ten avatars were created, representing five races (African, East Asian, European, South Asian, and Mixed Race) and two genders (male, female). Avatars were modified from prototypes available in FaceGen software; these prototypes were derived from a training set of 272 human faces across these five races and two genders (Blanz, 2007). Similar avatars from this software have been used in previous research on face perception (Stolier & Freeman, 2016). Facial expressions were standardized across races, such that each emotion was expressed via identical changes in the position of the eyes, mouth, nose, and cheeks (though these changes differed slightly between male and female faces). For representative examples of the avatar images, see Supplemental Fig. 1.

In order to measure perceptions of the emotions depicted by the faces used in the go/no-go task, we asked 111 participants (38 male, age: M = 21.27 (SEM = 0.11)) to interpret the 100% intensity image of each emotional face, for a total of 30 ratings per participant. This sample was separate from the sample that completed the go/no-go task but was drawn from the same pool of students, all of whom participated in exchange for course credit. Images and multiple-choice options were presented in randomized order via Qualtrics software (Qualtrics, Provo, UT). Participants were asked to choose the word that best described each face out of the following options: fearful, disgusted, or neutral (the order of options was randomized for each face, and randomization was conducted separately for each participant).

2.3.2. Go/no-go task

The emotional go/no-go task (Hare, Tottenham, Davidson, Glover, & Casey, 2005) measures the ability to withhold prepotent motor responses to emotional stimuli (Casey et al., 2011), allowing an examination of how IA and facial mimicry are related to perceptual discrimination versus motor responsiveness. Stimuli for Go and NoGo cues consisted of color images of ten avatars (5 female, 5 male) with facial expressions ranging from neutral to fearful or from neutral to disgusted in four equal increments (0, 33, 66, 100%). In total, 80 face stimuli were included. Stimuli were presented in PsychoPy. For exact wording of all task instructions, see Supplemental Methods.

Each participant completed two blocks in randomized order with either fear as target and disgust as distractor, or the opposite. Each task block contained 480 trials (360 emotional faces and 120 neutral faces). Of the emotional faces, 270 were the target emotion (90 at each percent emotion) and 90 were the distractor emotion (30 at each percent emotion), comprising a 3:1 "target:distractor" ratio. The overall "target:distractor" ratio, counting both emotional and neutral distractors, was 270 : 210, or 9 : 7.

Faces were presented in the center of the screen for 500 ms each. The interstimulus interval (ISI) was pseudorandomized from 1,250 to 1,750 ms (mean per block = 1,500 ms) to discourage anticipatory responses. A fixation cross was displayed in the center of the screen during the ISI. Responses were entered by pressing the space bar, and were recorded for up to 2000 ms after the face onset.

2.3.3. Heartbeat tracking task

In order to assess interoceptive accuracy, we asked participants to complete three rounds of a heartbeat tracking task (Garfinkel et al., 2016; Schandry & Specht, 1981). Participants were instructed, “Do NOT touch your pulse points. Just tune into your body and feel your heart beating.” The rounds lasted 25, 35, and 45 s, presented in randomized order and separated by 30 s of rest. Between rounds, participants were instructed, “Please take a few deep breaths. The next portion will begin momentarily.” Participants were not told nor shown the duration of each round; they were visually cued to start and stop heart beat counting at the beginning of each round, then enter their count on the computer. Stimuli were administered, and responses recorded, in Psychopy. For exact wording of all task instructions, see Supplemental Methods.

2.4. Data analysis

2.4.1. Heartbeat tracking task

An error score for the heartbeat tracking task was calculated by subtracting the perceived number of beats from the actual number, and dividing by the actual number (Brener & Ring, 2016). Error scores from all three rounds were averaged. The absolute value of this interoceptive error score was computed, given that our hypothesis regarded the magnitude of difference between actual and perceived heartbeats, rather than the direction of that difference (Brener & Ring, 2016). The error score is interpreted as the percent error in heartbeat tracking (e.g., an error score of .32 would indicate that the perceived number of heartbeats was 32% higher or lower than the actual number). Lower error scores indicate higher IA. Subsequently, IA scores were calculated as 1 – error score, with higher values indicating higher IA (Brener & Ring, 2016). For analyses, IA scores were natural-log-transformed in order to meet assumptions of normal distribution.

2.4.2. Facial electromyography (EMG)

EMG analyses were conducted in MATLAB using custom scripts. EMG data were filtered at a high-pass threshold of 2 Hz (Filter Order = 3300, Transition Bandwidth = 1 Hz), and then at a low-pass threshold of 400 Hz (Filter order = 660, Transition Bandwidth = 5 Hz), both using Hamming windowed-sinc FIR filters implemented in EEGLAB (Delorme et al., 2004). Trials were extracted, and time-locked to onset of face stimuli, from 500 ms pre-onset to 2000 ms post-onset. Root-mean-square of the EMG data (rmsEMG) was computed by squaring each data point, averaging across 20-ms bin (i.e., 20 data points, with zero overlap), and then computing the square-root of the mean within each bin (Dimberg, Thunberg, & Grunedal, 2002; Merletti & Di Torino, 1999).

The rmsEMG of bins within the critical window of interest, 200–600 ms post-onset of face stimulus for each trial, were averaged together to generate the face-evoked EMG value for that trial. This critical window was selected based on previous research demonstrating that involuntary facial mimicry occurs at this post-stimulus latency (McIntosh et al., 2006). Any trial with a critical window mean in excess of 5 standard deviations (SD) from the condition mean (across subjects) was excluded. For each trial, a baseline window, consisting of the 500 ms prior to stimulus onset, was also computed by averaging across the rmsEMG of bins within that window. The critical and baseline windows were natural-log-transformed in order to meet assumptions of normality. These values were then z-transformed within subject and within condition, using the formula: $x_{\text{Ztransformed}} = (x - \text{mean}_{\text{condition}})/\text{SD}_{\text{condition}}$. For each trial, the log- and z-transformed baseline was then subtracted from the log- and z-transformed critical window, creating a difference score that was used in subsequent statistical analyses.

2.4.3. Emotional Go/No-Go task behavior

Hit rate was calculated as the number of correct responses on Go trials divided by the number of Go trials; false alarm rate was calculated as the number of incorrect responses on NoGo trials divided by the number of NoGo trials (Green & Swets, 1966; Stanislaw & Todorov, 1999). Sensitivity (d’) measures the ability to discriminate between targets and distractors and is independent of the participant’s overall tendency to respond. Sensitivity was calculated by subtracting the z-transformed false alarm rate from the z-transformed hit rate (Stanislaw & Todorov, 1999). Larger values of d’ indicate better performance; a d’ value of 0 would indicate an inability to distinguish targets from distractors. Criterion (C; i.e., response bias) represents each participant’s threshold for responding to a given stimulus (Snodgrass & Corwin, 1988). C was calculated by summing z-transformed hit rate and z-transformed false alarm rate, then multiplying by $-1/2$ (Snodgrass & Corwin, 1988). Positive values of C indicate a conservative bias (the tendency to withhold response), negative values indicate a liberal bias (the tendency to respond), and a value of zero indicates no bias.

Note that criterion and sensitivity could not be computed for the zero-percent-emotion condition (i.e., neutral faces), because trials in this condition were always distractors. Therefore, criterion and sensitivity were only computed for the following Percents Emotion: 33%, 66%, and 100%. Neutral faces served as the implicit baseline against which these conditions were compared. Statistical analyses were run in SPSS Version 25 (IBM SPSS, Inc., Sanborn, NY, USA).

2.4.4. Repeated-measures analyses

Separate models were run on the following dependent variables: DPrime, Criterion, Response, RT, and facial EMG. In order to account for repeated measurements within subjects, analyses were run as mixed or generalized mixed models with a random intercept (Baayen, Davidson, & Bates, 2008). For continuous dependent variables (DPrime, Criterion, RT, and EMG), a multilevel linear mixed effects model was run. For the binary dependent variable (Response), a generalized estimating equation was run. Subject, Target Emotion, and Percent Emotion were modeled as levels of repeated observation. (Models of Response, RT, and facial EMG included an additional term reflecting repeated observations at the level of individual trials.) We included main effect terms for Target Emotion (Fear, Disgust), Percent Emotion (33%, 66%, and 100%; some models also included 0%, as described in the next paragraph), Age (in years), Gender (male, female), and IA (i.e., log-transformed heartbeat dividend). We included the following interaction terms: Target Emotion X Percent Emotion, Target Emotion X IA, Percent Emotion X IA, and IAˆ2. In trial-level models (of Response, RT, and EMG), we included a main effect term for the number of preceding Go trials, which previous research has identified as an index of trial difficulty. A prepotent response builds up over the course of repeated Go trials, increasing the difficulty of withholding a response on a subsequent NoGo trial (Hare, Tottenham & Casey, 2005). In models of Response and RT, an additional main effect term for trial-level facial EMG was included, as were the following interaction terms: EMG X IA, EMG X Target Emotion, EMG X Percent Emotion, and EMG X Target Emotion X Percent Emotion.

For models of DPrime and Criterion, the Percent Emotion variable had three levels (33%, 66%, and 100%; recall that neutral faces served as the implicit baseline). For models of Response, RT, and EMG on Go trials, the Percent Emotion variable also had three levels (33%, 66%, and 100%), because neutral faces were never Go trials. For models of Response, RT and EMG on NoGo trials, the Percent Emotion variable had four levels (0%, 33%, 66%, 100%), because neutral faces were always NoGo trials. For Response, RT, and facial EMG, separate models were run for Go and NoGo trials (to decompose the summary effects of DPrime and Criterion). Two-tailed significance testing is reported for all analyses.

2.4.5. Correlations

Bivariate Spearman correlations were run to assess the potential relationship between IA and the following variables: age, actual heartbeat (beats per minute), perceived heartbeat (beats per minute), Trait Anxiety, State Anxiety, and Advanced Progressive Matrices mean score.

3. Results

3.1. Heartbeat tracking task

Mean overall perception score was 0.717, SEM = 0.023. This indicates an error rate of approximately 28%, comparable with previous studies (Ring, Brener, Knapp, & Mailloux, 2015; Schandry & Specht, 1981). Cronbach's alpha across all three heartbeat-tracking trials was .837, indicating good internal reliability.

3.2. Avatar image ratings

Correct response rates were as follows: Neutral, M = 74.80%, SEM = 1.88%; Fear, M = 63.20%, SEM = 2.61%; Disgust, M = 73.51%, SEM = 2.58%. Accuracy did not differ significantly between Disgust and Neutral faces, *t*(df = 110) = .487, *p* = .628. However, accuracy was significantly lower for Fear faces than for Disgust faces, *t*(df = 110) = 4.556, *p* < .001, and Neutral faces, *t* (df = 110) = 4.334, *p* < .001.

3.3. Go/no-go task behavior

Mean Sensitivity, Criterion, Hit Rate, False Alarm rate, and Reaction Time by Target Emotion and Percent Emotion are presented in Table 1. Due to space limitations, only significant effects of IA and EMG are presented in the main text. Main effects of Target Emotion and Percent Emotion were significant in most analyses; for complete results, see Supplemental Materials.

3.3.1. Sensitivity (d')

Emotion discrimination sensitivity increased with increasing IA, standardized Beta = 3.125, F(1, 109.937) = 10.323, p = .002. However, the benefits of increasing IA diminished when the level of IA was already moderate or high, as reflected in a negative quadratic term, standardized Beta = −2.710, F(1, 109.912) = 7.344, p = .008. As illustrated in Fig. 1, for IA values at or below the mean, higher IA conferred increased sensitivity at every level of Percent Emotion. Increases in IA above the mean conferred no additional gains in sensitivity.

3.3.2. Criterion

No main effects or interactions of IA or EMG on criterion were significant, all p > .28 (Fig. 1).

3.3.3. Response

In order to decompose whether effects of IA and facial EMG on sensitivity were driven by hit rate (correct commission responses on Go trials) or false alarm rate (commission errors on NoGo trials), we conducted separate follow-up analyses by trial type. In analyses of Go trials, hits increased with increasing IA, standardized Beta = 2.401, Wald chi-square (df = 1) = 14.251, p < .001. Hits also increased with increasing facial EMG, standardized Beta = 1.853, Wald chi-square (df = 1) = 4.036, p = .045. These main effects were modified by a marginally significant interaction, such that individuals with higher IA responded to hits at lower amplitudes of facial EMG than did individuals with lower IA, Wald chi-square (df = 1) = 2.896, p = .089. In analyses of NoGo trials, facial EMG was less predictive of false alarms to Fear distractors than of false alarms to Disgust distractors, standardized Beta = −3.200, Wald chi-square (df = 1) = 8.941, p = .003. No other main effects or interactions involving IA or facial EMG were significant in analyses of false alarms, all p > .1.

3.3.4. Reaction time

For Go trials, RTs became faster with increasing facial EMG amplitude, standardized Beta = −1.829, F(1, 2798.366) = 5.126, p = .024. Higher IA was associated with faster responses to Disgust targets, standardized Beta = −5.163, F(1, 3848.323) = 26.652, p < .001. Across emotions, we also observed an IA X EMG interaction, standardized Beta = 2.383, F(1, 4977.938) = 5.669, p = .017. As illustrated in Fig. 2, increasing IA conferred faster RTs when EMG amplitude was at or below the mean. Above the mean EMG amplitude, increasing IA did not confer additional changes to RT. For NoGo trials, An IA X Emotion interaction, F(1, 899.680) = 4.492, p = .034, indicated that higher IA was associated with faster responses to NoGo trials in Disgust blocks (i.e. faster false alarms to Fear distractors), standardized Beta = −2.119.

3.3.5. Facial EMG

Amplitude of facial EMG during Go trials increased with increasing IA, standardized Beta = .887, F(1, 81.805) = 20.268, p < .001. The effect of IA was more pronounced during Go trials with Disgust faces than during Go trials with Fear faces, standardized Beta = 4.224, F(1, 809.345) = 17.845, p < .001. See Fig. 3. During NoGo trials with Fear faces, facial EMG amplitude decreased with increasing IA, standardized Beta = −3.069, F(1, 757.249) = 9.421, p = .002.

3.4. Correlations

Interoceptive accuracy was unrelated to age (rho (N = 111) = -0.36, p = .709), intelligence (rho (N = 111) = .072, p = .457), trait anxiety (rho (N = 106) = .032, p = .745), or state anxiety (rho (N = 110) = .037, p = .277). Higher perceived heart rate was associated with higher actual heart rate (raw values), rho (N=111) = .262, p = .006.

4. Discussion

We assessed the degree to which interoception interacts with somatic and visual information to influence discrimination of other's emotional states. To do so, we administered an emotional go/no-go task with fearful and disgusted faces, as well as measuring interoceptive accuracy in perceived heart beats (IA). Higher IA was associated with

Table 1
Sensitivity, Criterion, Hit Rate, False Alarm Rate, and RT by Target Emotion and Percent Emotion.

Percent Emotion	Target Emotion	Sensitivity (d') *M (SEM)*	Criterion *M (SEM)*	Hit Rate *M (SEM)*	False Alarm Rate *M (SEM)*	RT (sec) *M (SEM)*
0%	Disgust	–	–	–	0.032 (.006)	–
	Fear	–	–	–	0.039 (.007)	–
33%	Disgust	0.151 (.059)	1.316 (.053)	0.131 (.012)	0.119 (.015)	0.694 (.018)
	Fear	1.084 (.055)	1.201 (.048)	0.289 (.018)	0.054 (.008)	0.685 (.016)
66%	Disgust	1.259 (.114)	0.345 (.053)	0.595 (.022)	0.225 (.023)	0.692 (.013)
	Fear	2.189 (.072)	0.399 (.052)	0.709 (.019)	0.096 (.010)	0.630 (.013)
100%	Disgust	1.598 (.126)	0.047 (.056)	0.734 (.019)	0.257 (.026)	0.646 (.012)
	Fear	2.681 (.078)	−0.010 (.051)	0.859 (.015)	0.124 (.012)	0.587 (.012)

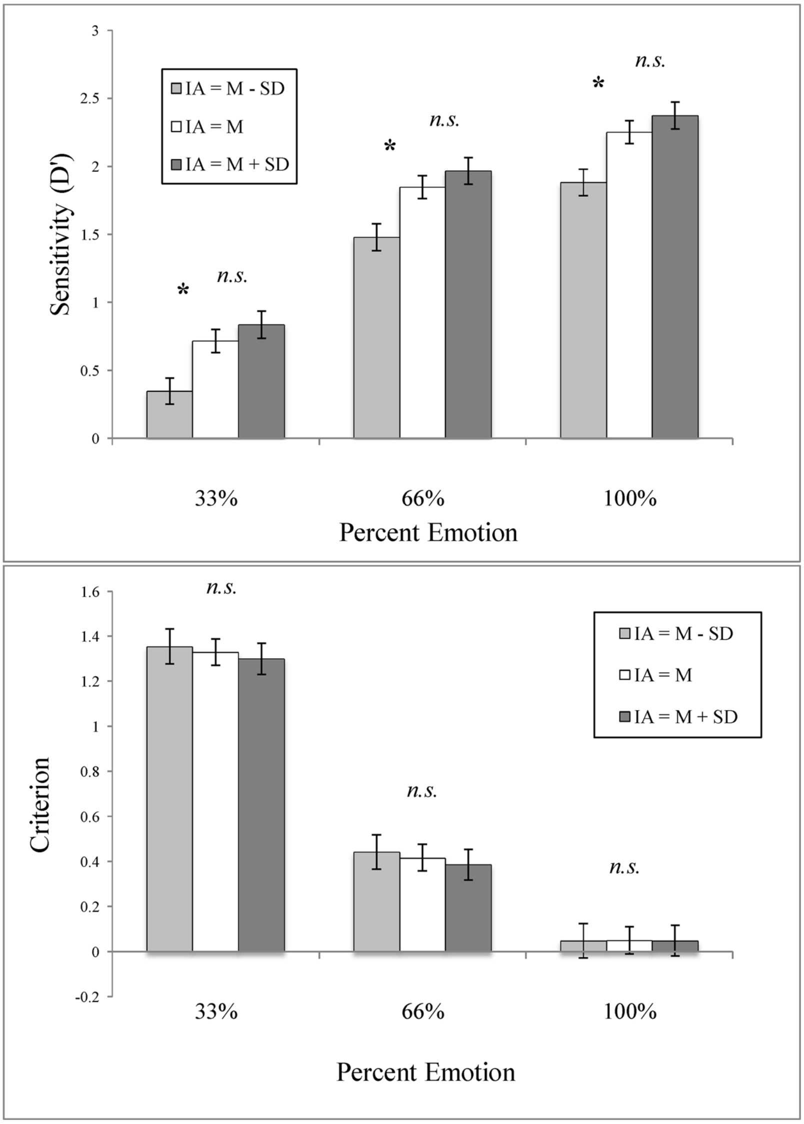

Fig. 1. Sensitivity (d') and criterion (response bias) by interoceptive accuracy (IA). Sensitivity and criterion are displayed at the mean IA, one SD below the mean IA, and one SD above the mean IA. Higher IA was associated with higher sensitivity (top) but was unrelated to response bias (bottom). Error bars represent SEM. * $p < .05$. n.s., not significant.

higher perceptual sensitivity when discriminating facial emotions but was unrelated to criterion (response bias). In other words, people with higher IA were better able to discriminate between different emotions but did not differ in overall tendency to respond.

To assess the potential contributions of somatic skeletomotor information to facial emotion discrimination, we measured facial mimicry by recording *Corrugator Supercilii* EMG during the go/no-go task.[2] Consistent with a role for facial mimicry in correctly interpreting facial expressions, facial EMG was associated with both accuracy and RT on Go trials. This, however, depended on the participant's level of IA. When facial EMG was at or below the mean, higher IA supported faster reaction times. In contrast, when facial EMG was above the mean, higher IA did not provide additional benefits to reaction time (Fig. 2). A plausible interpretation, though speculative, is that higher-IA individuals used somatic information from facial mimicry more efficiently in order to inform emotional face discrimination. According to this interpretation, higher-IA individuals would gain perceptual facilitation from even subtle facial mimicry, whereas lower-IA individuals would fail to benefit from these subtle somatic signals. Consistent with this interpretation, facial EMG corresponded more closely to objective stimulus features (i.e., Fear vs. Disgust), and was more strongly modulated by response requirements (i.e., Go vs. NoGo trials), in individuals with higher IA. Thus, not only did higher IA confer more efficient use of a somatic signal (i.e., facial mimicry), but this somatic signal may also have been more informative (i.e., reflective of objective stimulus features) in higher-IA individuals.

These results raise an interesting question about the mechanism by which interoception and facial mimicry interact during emotion discrimination. In this study, facial EMG preceded responses; we modeled EMG signal from 200 to 600 ms after the face onset, whereas average response times exceeded .66 s. Given this temporal precedence, it is possible that facial mimicry was informed by early visual processing, and subsequently served as an input to late-stage visual processing. If this were true, we would predict that individuals with higher IA would more effectively incorporate afferent EMG signal into perception and response planning. Consistent with this prediction, we observed an interaction between IA and facial EMG in analyses of RT on Go trials (this interaction was marginally significant in analyses of Response).

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[2] Recall that we modeled EMG response at 200-600 ms post-stimulus onset, which corresponds to involuntary facial mimicry (McIntosh et al., 2006).

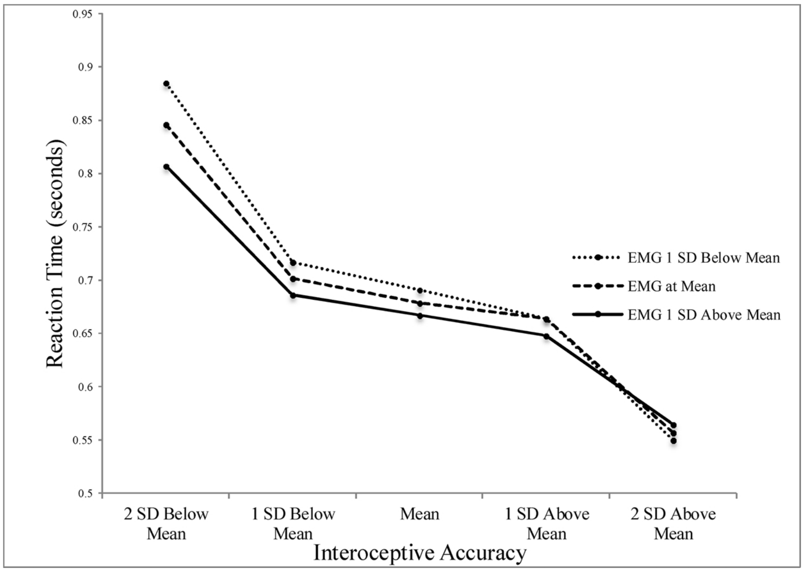

Fig. 2. Reaction times on Go trials by facial EMG and interoceptive accuracy. RTs are displayed for correct responses (i.e., hits) only. * $p < .05$. *n.s.*, not significant.

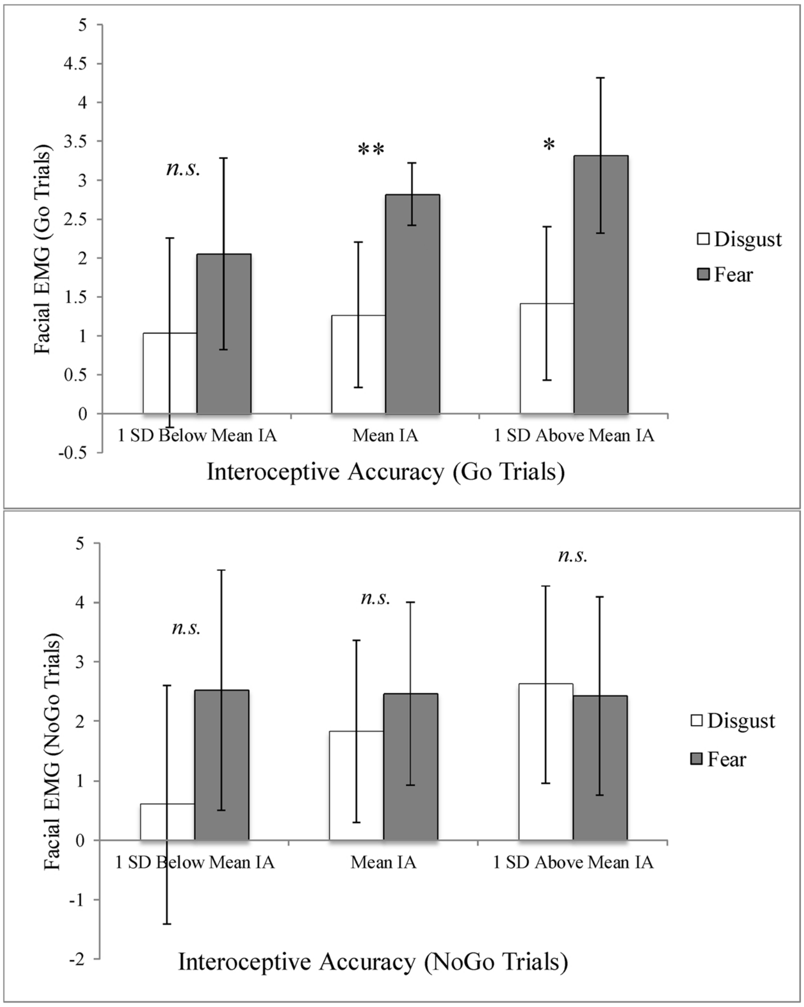

Fig. 3. Facial EMG by emotion and interoceptive accuracy for Go trials (top) and NoGo trials (bottom). Top: Facial EMG discriminated between Disgust targets and Fear targets only on Go trials. Bottom: Regardless of IA, facial EMG did not discriminate between Disgust distractors and Fear distractors on NoGo trials. Error bars represent SEM. **$p < .05$ two-tailed. * $p < .05$ one-tailed. *n.s.*, not significant.

This suggests the ability to look inward facilitates perception of outward signs of emotion, and potentially of others' internal emotional states.

An alternative explanation for the observed relationship between IA and emotion discrimination is that people with higher IA and those with higher accuracy on the go/no-go task were simply more engaged while completing both tasks. However, if this were true, we would expect lower IA to be associated with a higher false alarm rate and higher miss rate, which were not significant effects. Moreover, the association between IA and task performance was specific to sensitivity (driven by hit rate), and was unrelated to response bias, suggesting that the observed relationship reflects perceptual acuity rather than overall task engagement. Although there were differences in accuracy ratings for fear versus disgust, both fearful and disgusted faces were rated as significantly more negative and more arousing than were neutral faces, and accuracy was comparable to that reported for other published face sets (Tottenham et al., 2009). Importantly, the IA X EMG interaction was significant for both fearful and disgusted faces, indicating that the nature of the relationship between interoception and emotion discrimination (or RT) was similar for both emotions.

Since this study was not designed to address whether the relationship between IA and perceptual sensitivity is specific to emotional stimuli, we cannot rule out the possibility that people higher in IA generally have higher perceptual sensitivity. Some studies have found cardiac-phase modulation of non-emotional perception (Park & Thayer, 2014; Pramme, Larra, Schächinger, & Frings, 2016; Requin & Brouchon, 1964), though others have found no effect (Elliott & Graf, 1972). Cardiac phase studies have found enhanced effects on perception of fearful faces (vs. disgusted or neutral faces), suggesting heightened effects for highly salient emotional stimuli (Garfinkel et al., 2014; Wiens, Mezzacappa, & Katkin, 2000). Future work should clarify the role of IA and facial EMG in responding to neutral versus emotional stimuli.

A limitation of the go/no-go task is that correct responses require both perceptual sensitivity and inhibition. To disentangle these processes, separate trial-by-trial analyses of Go and NoGo trials allowed us to infer whether the association between IA and sensitivity (d') was driven by increasing hits or by decreasing false alarms. Consistent with the interpretation that IA benefits task performance by enhancing perceptual sensitivity during emotion discrimination, higher IA was associated with a higher hit rate and with faster correct responses on Go trials (see Fig. 2 and Supplemental Fig. 2). In contrast, results did not support the alternative possibility that the relationship between IA and emotion discrimination was driven by inhibition, as there was no significant main effect of IA on responses during NoGo trials. Thus, the relationship between IA and task performance was not driven by effects on inhibition.

The construct validity of the heartbeat tracking task has been criticized (Brener & Ring, 2016). In particular, research has found that the task can be influenced by feedback (Phillips, Jones, Rieger, & Snell, 1999; Ring & Brener, 1996; Ring et al., 2015) and by prior knowledge of resting heart rate (Essau & Jamieson, 1987; Pennebaker & Hoover, 1984; Phillips et al., 1999; Ring & Brener, 1996; Ring et al., 2015; Windmann, Schonecke, Fröhlig, & Maldener, 1999). In the current study, we did not provide feedback to subjects about their actual heart rate. Although it is possible that some subjects had prior knowledge of their resting heart rate, they were not informed of the duration of each counting interval, which would make estimation based on prior knowledge more difficult. Other work shows that the task may serve as a proxy measure for other psychological characteristics, including age (Khalsa et al., 2009; Murphy, Geary, Millgate, Catmur, & Bird, 2018), intelligence (Mash, Schauder, Cochran, Park, & Cascio, 2017; Murphy et al., 2018), or anxiety (Khalsa & Lapidus, 2016; Pollatos, Traut-Mattausch & Schandry, 2009). In the current study, we found no significant relationship between interoceptive accuracy and age, intelligence, state anxiety, or trait anxiety (all $p > .25$). Given the nonsignificant relationship between these characteristics and interoceptive accuracy, these measures are unlikely to explain the significant effect of interoceptive accuracy on emotional discrimination.

The reliability of the heartbeat tracking task has also been criticized (Brener & Ring, 2016). Correlations across different methodologies of cardiac interoception tasks have been null (Phillips et al., 1999; Schulz, Lass-Hennemann, Sütterlin, Schächinger, & Vögele, 2013) or low-to-moderate (Hart, McGowan, Minati, & Crichtley, 2013; Knoll & Hodapp, 1992). Additionally, a recent study found inconsistencies in the correlation of raw subjective counts with raw counts of actual heart beats (Zamariola, Maurage, Luminet, & Corneille, 2018). In the current study, we observed a significant positive correlation between perceived and actual heart rate ($p = .006$). Another recent study (Kleckner, Wormwood, Simmons, Barrett, & Quigley, 2015) showed that in a different cardiac interoception task, 40 trials per individual were required to achieve acceptable reliability. However, the recommendations made by (Kleckner et al., 2015) were for a different and more complex task (matching heart beats to external auditory stimuli), which may account for the lower reliability. In contrast to these criticisms, in the current study, repeated measurements within individuals showed moderate-to-high reliability (Cronbach's alpha = .837). Although the heartbeat tracking task may be an imperfect measure of cardiac interoception, it showed acceptable reliability in our study and does not appear to have been affected by confounds identified in other studies. Future research should continue to refine interpretations of the processes that contribute to accuracy on the heartbeat detection task.

In summary, we found that both IA and facial mimicry enhanced emotion discrimination. Based on the results of this study, we cannot conclude any causal relationship between these processes. It is tempting, however, to speculate that facial mimicry, in addition to receiving the products of early visual processing, also served secondarily as an input to inform subjective perception during later stages of visual processing. Such a mechanism would be consistent with our finding that individuals higher in IA were able to respond correctly on trials in which the level of facial mimicry was more subtle. This mechanism is plausible in light of evidence showing that, following early perceptual input to the amygdala, feedback from the amygdala subsequently modulates later-stage input from the perceptual cortex to the prefrontal cortex (Liu, Hadj-Bouziane, Moran, Ungerleider, & Ishai, 2016; Méndez-Bértolo et al., 2016), and that the firing of human amygdala neurons predicts subjective perception, even when subjective perception does not match objective stimulus features (Wang et al., 2014). Regarding how interoception and emotion might interact at a neural level, previous research has identified activation during interoception in the middle and anterior insula and the subgenual cingulate during cardiac interoception (Hassanpour et al., 2018; Khalsa et al., 2009; Strigo & Craig, 2016); moreover, overlapping activation has been observed in the anterior insula during both cardiac interoception and viewing of emotional video clips (Zaki et al., 2012). The subgenual cingulate has anatomical projections to the amygdala, and functional connectivity between these regions has been observed during emotion regulation (Etkin, Egner, Peraza, Kandel, & Hirsch, 2006; Pezawas et al., 2005; Stein et al., 2007). Thus, previous research suggests a physiologically plausible—though speculative—means by which the neural substrates of cardiac interoception might interact with those supporting emotion perception. Our results suggest that some people incorporate information from their own bodies with visual inputs in order to more accurately interpret other people's emotions. In this way, looking inward can enhance a person's ability to understand the external emotional world.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.biopsycho.2019.107779.

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