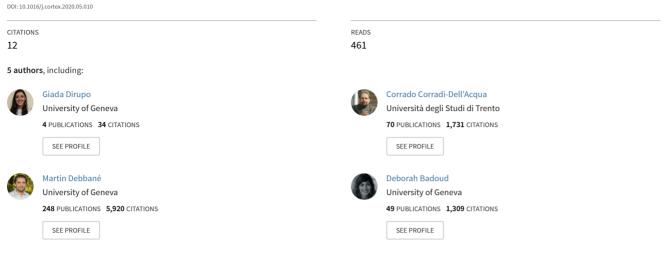
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The role of interoception in understanding others' affect.

Dissociation between superficial and detailed appraisal of facial expressions.

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Abstract

Embodied models of social cognition argue that others' emotional states are processed by re-enacting a representation of the same state in the observer, along with associated somatic and physiological responses. In this framework, previous studies tested whether a strong sensitivity to interoceptive signals (i.e., inputs arising from within one's body) facilitates the understanding of others' affect, leading to mixed results. Such heterogeneity in the literature could reflect methodological differences in paradigms employed, with some probing classification of a precise condition, and others requiring the assessment of supra-ordinal dimensions orthogonal to many states. Here, we engaged fifty young women in a study where they evaluated others' naturalistic facial reactions to painful and disgusting stimuli of comparable unpleasantness. Separately, we measured their interoceptive abilities through a well-known heartbeat counting task. We found that individuals that were more accurate in tracking their heartbeats across time were also more prone to judge facial expressions as more unpleasant (supra-ordinal assessment). However, when specifically asked to discriminate between comparably-unpleasant pain and disgust (state-specific assessment), participants' performance was not influenced by their interoceptive abilities. Although confined to a female sample, this study extends our knowledge on the role of interoception in the understanding of others, which influences only the evaluation of general features such as unpleasantness (common between pain and disgust), without extending to the appraisal of a precise state. This finding supports multi-componential models of social cognition, suggesting that only part of our ability to assess others' affect is mediated by a representation of one's affective/somatic responses.

1

3.1 Introduction

How we understand other people's affective states is a relevant but still heavily debated topic in cognitive-affective psychology. One influential model suggests that this might be achieved by accessing representations of homologous states in one's own body (Bernhardt & Singer, 2012; Goldman & de Vignemont, 2009). A rich literature supports this hypothesis through varied empirical evidence. First, brain responses evoked by ones' and others' emotional/somatic states often overlap, suggesting at least a partially common underlying neural representation (Corradi-Dell'Acqua, Hofstetter, & Vuilleumier, 2011; Lamm, Decety, & Singer, 2011; Wicker et al., 2003). Furthermore, observing people's injuries affects the muscular reactivity in homologous portions of one's body (Avenanti, Bueti, Galati, & Aglioti, 2005; Avenanti, Minio-Paluello, Bufalari, & Aglioti, 2009; Avenanti, Paluello, Bufalari, & Aglioti, 2006; Avenanti, Sirigu, & Aglioti, 2010; Fecteau, Pascual-Leone, & Théoret, 2008; Minio-Paluello, Avenanti, & Aglioti, 2006). Lastly, the understanding others' affect (e.g., classifying a specific state, quantifying dimensions such unpleasantness) is frequently biased by the self's own state, as people often project onto others what they are currently experiencing (Antico, Cataldo, & Corradi-Dell'Acqua, 2019; Qiao-Tasserit et al., 2017; Silani, Lamm, Ruff, & Singer, 2013). Overall, these studies act as a cornerstone for embodied accounts, according to which high-level cognitive (Gallese & Cuccio, 2018; Fischer & Brugger, 2011) and social (Bernhardt & Singer, 2012; Goldman & de Vignemont, 2009) abilities do not result only from an amodal computation, but also rely on a representation of one's own somatic and affective experience.

Embodied accounts work under the premise that an accurate understanding of others' states is dependent on an equally accurate sensitivity of one's own affective response. In line with this assumption, individuals who are unable to experience and express their own emotions (alexithymia) (Haviland, Louise Warren, & Riggs, 2002) also show reduced responses to others' affect, as measured through empathy questionnaires (Grynberg, Luminet, Corneille, Grèzes, & Berthoz, 2010), or physiological (Bogdanov et al., 2013) and neural responses to the sight of others' suffering (Bird et al., 2010; Moriguchi

et al., 2007; Silani et al., 2008). Furthermore, individuals that are highly sensitive to pain in their own body (low pain threshold) often show high behavioral and neural responses to visual/auditory cues about others pain (Chen et al., 2017; Liu et al., 2019; but see, Danziger, Faillenot, & Peyron, 2009). Finally, analgesic manipulations undertaken to decrease one's own sensitivity to nociceptive stimulations (e.g., paracetamol, placebo, hypnosis) cause a comparable decrease of behavioral and neural response to others' pain (Braboszcz, Brandao-Farinelli, & Vuilleumier, 2017; Mischkowski, Crocker, & Way, 2016; Rütgen et al., 2018; Rütgen et al., 2015). Overall, there is a wealth of evidence that sensitivity to signals on one's own affective response influences social cognition. However, previous studies shed little light on the nature of these signals, and whether they relate exclusively to exteroceptive information on the outer world (a frightening picture, an unpleasant touch, etc.) or also include interoceptive input from within the body (palpitations, breathing rhythm).

Though they play a primary role in homeostatic control and allostatic adaptation (Berntson, Cacioppo, & Quigley, 1993), interoceptive signals have only recently been recognized as agents of influence in a wide range of processes, including attention, motivation, self-awareness, decision-making, and personal affect (Craig, 2009; Tsakiris & Critchley, 2016). More specifically, individuals that are good at monitoring their own interoceptive (e.g. cardiac) signals show enhanced sensitivity to acute (Pollatos, Füstös, & Critchley, 2012; Scheuren, Sütterlin, & Anton, 2014) and chronic pain (Di Lernia, Serino, & Riva, 2016). These individuals also report stronger emotional arousal/intensity to the sight of affective images (Pollatos, Herbert, Matthias, & Schandry, 2007) or videos (Wiens, Mezzacappa, & Katkin, 2000), and are more eager to engage in regulation strategies such as suppression or reappraisal (Kever, Pollatos, Vermeulen, & Grynberg, 2015). Critically, many studies have attempted to investigate the role played by interoception on our social skills, and specifically on the ability to appraise others' (as opposed one's own) affect. These experiments vary extensively in their methodology, leading to differing results. Some report

that one's cardiac activity can influence the sensitivity towards others' affect (Fukushima, Terasawa, & Umeda, 2011; Garfinkel et al., 2014; Gray et al., 2012; Grynberg & Pollatos, 2015; Terasawa et al., 2014), while others failed to find an effect, even with high statistical power and a considerable range of paradigms employed (Ainley et al., 2015). To our knowledge, the factors underlying mixed results from the literature have not been explored systematically.

One possible source of heterogeneity from previous studies might be the method employed to measure interoception. Some experiments found that individuals were more sensitive to affective facial expressions (both at the behavioral and neural level) when these were presented in synchrony with their own heartbeats (Garfinkel et al., 2014; Gray et al., 2012). Likewise, cardiac-evoked neural activity was enhanced when synchronized with the evaluation of emotional faces (Fukushima, Terasawa, & Umeda, 2011). These studies show a clear interaction between interoceptive inputs and social cognition at an implicit level, without however shedding any light on an individual's ability to access bodily signals. In other studies, participants were explicitly asked to track their cardiac response, in order to quantify an individual's accuracy on their own interoceptive signals (Interoceptive Accuracy [IAcc], Garfinkel, Seth, Barrett, Suzuki, & Critchley, 2015). With this methodology, some studies showed that participants with high IAcc were more sensitive towards stimuli of others' emotional/affective states (Grynberg & Pollatos, 2015; Terasawa et al., 2014), whereas others reported null effects (Ainley, Maister, & Tsakiris, 2015). Finally, Garfinkel and colleagues (2015) reviewed two other methods to investigate interoception: subjective self-reports on questionnaires/scales (referred to as interoceptive sensitivity) and a metacognitive index obtained by combining *IAcc* and self-reports (interoceptive awareness). To our knowledge, these last two measures have never been modeled in relation to individual social abilities, at least in typically-developed population (but see Mul et al., 2018, for testing individuals with autism).

4

A second source of methodological heterogeneity lies in the information about others' affect that individuals have to appraise. For instance, Ainley and colleagues (2015) modeled *IAcc* on participants' responses in classification task, requiring the attribution of a specific emotional/affective state to a facial (eye) expression, and found no relationship. Instead, *IAcc* influenced a task requiring to quantify others' pain on dimensions such as arousal (Grynberg & Pollatos, 2015), or an hybrid paradigm involving face classification across different levels of emotional intensities (Terasawa et al., 2014). Hence, the only studies reporting significant effects probed an evaluation of supramodal dimensions (arousal, intensity, etc.) common to different states (Grynberg & Pollatos, 2015; Terasawa et al., 2014). Thus, based on the literature, we can hypothesize that individual interoceptive abilities do influence our understanding of others, but only to a limited extent. Rather than promoting the diagnosis of a specific affective state (*"this person is disgusted/hurt"*), they seem to influence the evaluation of supra-ordinal dimensions common to many states (*"this person is feeling bad"*). To our knowledge, this hypothesis has never been tested experimentally.

Finally, a last source of heterogeneity might be found in the population tested. All studies investigating the role of *IAcc* on social cognition reviewed above recruited typical individuals of both genders, but the percentage of women ranged between ~58% (e.g., Ainley et al., 2015, experiment using facial expressions) to more than 80% (Grynberg & Pollatos, 2015). It is plausible that effects in unbalanced samples (e.g. Grynberg & Pollatos, 2015) might reflect a stronger susceptibility of women to some elements of the manipulation employed. It is unlikely that women possess more pronounced interoceptive abilities, as many investigations using the HBCT in affective tasks failed to identify significant gender differences in *IAcc* (Grynberg & Pollatos, 2015; Herbert, Pollatos, & Schandry, 2007), with the exception of a study finding higher accuracy in men, as well as higher confidence in self-reported evaluations of interoceptive sensibility (Grabauskaite, Baranauskas, & Griškova-Bulanova, 2017).

Furthermore, males were associated with higher accuracy/sensitivity also in different paradigms testing interoception, such as a respiratory resistance task (Harver, Katkin, & Bloch, 1993), perception of stomach contractions (Whitehead & Drescher, 1980), blood-glucose levels detection in diabetes type 1 patients (Cox et al., 1985), sexual concordance (Suschinsky & Lalumière, 2012), etc. (see Harshav et al., 2015, as a review). Instead, previous research found that females are more sensitive than males to images of others' affect (such as emotional expressions), as shown in both behavioral (Montagne, Kessels, Frigerio, De Haan, & Perrett, 2005; Hoffmann, Kessler, Eppel, Rukavina, & Traue, 2010) and neuroimaging investigations (Derntl et al., 2009; Lee et al., 2002; Yang, Decety, Lee, Chen, & Cheng, 2008).

In the present study, we tested whether individual interoceptive abilities influence the ability to understand other people's emotional/affective state. Specifically, as one of the key elements of heterogeneity in the literature involves the methodology employed to assess others' affect, here we aim at disentangling the assessment of state-specific information from that of supra-ordinal features, common to many states. For this purpose, we created a video-database of naturalistic facial expressions, collected while individuals underwent painful (thermal) and disgusting (olfactory) events, carefully matched for unpleasantness (Dirupo, Garlasco, Chappuis, Sharvit, & Corradi-DellAcqua, 2020). Then we asked a group of female participants to observe these clips and to either classify them according to state (pain, disgust, neutral), or to rate the unpleasantness felt by the person in the video. This allowed us to dissociate an individual's ability to diagnose a specific affective state, from a generalized estimation of people's discomfort (common between pain and disgust). In an independent session, *IAcc* was measured through a widely used protocol comparing the objective and subjective tracking of one's heartbeats across predefined time-intervals (Heart Beat Counting Task" [HBCT], Schandry, 1981). Although criticized for being only in part connected to one's cardiac response, and potentially confounded by exteroceptive strategies (Desmedt, Luminet, & Corneille, 2018; Ring & Brener, 2018; Ring, Brener, Knapp, & Mailloux,

2015; Zamariola et al., 2018, but see Ainley, Tsakiris, Pollatos, Schulz, & Herbert, 2020), the HBCT was chosen in keeping with previous researches investigating emotion/affect recognition in others (Ainley et al., 2015; Grynberg & Pollatos, 2015; Terasawa et al., 2014). This allowed full comparability between the results of the present study and the literature, while at the same time potential confounds were monitored through control measures probing personal beliefs about their cardiac responses and the ability to track time. The critical test was whether individual differences in *IAcc* explained variability in the assessment of affective facial expressions in the two tasks. Based on the studies reviewed above, we expected *IAcc* to affect the estimation of unpleasantness in both pain and disgust expressions. We expect no meaningful influence of *IAcc* on the performance of the classification task.

3.2 Methods

Here, we report how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. No part of the study procedure/analysis has been pre-registered prior the research being conducted.

3.2.1 Participants

Fifty female participants initially took part in our experiment (age range 25-35 years, mean age = 26.93; Standard Deviation (SD) = 2.68). The inclusion/exclusion criteria were: no reported psychological, psychiatric, neurologic or cardiac conditions, and no reported abuse of alcohol or drugs and no one was a smoker. Twelve reported high Anxiety and Depression scores in the French version of the ASR auto-questionnaire (Mahr et al., 2018, cut-off: T = 64). All volunteers signed a consent form prior to the start of the experiment. The procedure has been approved by the Ethical committee of the Faculty of Psychology and Educational Sciences of the University of Geneva, and conducted in accordance with the declaration of Helsinki. No participant from the original sample was excluded from the analysis.

3.2.2 Pain and Disgust Expressions

We tested participants' ability to process naturalistic facial expressions of pain and disgust (plus a neutral control) with the aid of an *ad hoc* database of video-clips, created and validated through two independent populations. Pain and disgust present convenient choices in the study of naturalistic facial expressions, as they can be evoked experimentally in a controlled and quantified fashion through thermal and chemosensory stimulations respectively. Although of high ecological validity, these stimuli represent a departure from previous studies who focused prevalently on static images (Ainley et al., 2015; Grynberg & Pollatos, 2015; Terasawa et al., 2014).

3.2.2.1 Stimuli Editing and Validation

Twenty-nine participants (10 males, average age = 25.00, SD = 3.46) took part to a study, aimed at investigating naturalistic responses to pain and disgust (see for details Dirupo et al., 2020). In sum, during a session, they smelled odorants (see Figure 1A) aimed at evoking neutral to unpleasant disgust experiences (e.g., *isovaleric acid*, reminiscent of dirty socks), delivered through rubber cannulas in the nose. In a separate session, they received thermal stimulations neutral or of comparable unpleasantness to those of the previous olfactory session on their non-dominant forearm. After each thermal/olfactory event, participants rated its associated unpleasantness on a Visual Analog Scale. Facial reactions were continuously recorded through a Logitech USB HD Pro web camera C920 (Apples, Switzerland). At the time of the experiment, participants were aware of the camera, but were naïve to the purpose of the recording. For the creation of the video database we first used a lower cut-off of 4 out of 10 on the unpleasantness rating to identify unpleasant trials. We then selected the corresponding portion of the video-stream to create a brief clip (average duration = 7.61s, SD= 0.87s). Second, we excluded those clips where individuals showed no facial reaction to the stimulus (see Kunz & Lautenbacher, 2014 for a similar approach). Third, we paired the pain and disgust clips of each participant to create the smallest possible difference in unpleasantness between them (the remaining unpaired clips were discarded). Finally, we

associated to each pair a third neutral clip from the same participant, from among the thermal/olfactory events rated closest to 0, corresponding to a neutral subjective experience. This led to an initial database of 123 video-clips, organized in 41 triplets, each displaying the same individual undergoing painful, disgusting and neutral experiences where the painful and disgusting facial expressions come from similarly unpleasant perceived stimuli. These videos were then validated by an independent sample of 24 participants (7 males, average age = 23.54, SD = 4.12), who classified each expression as either painful, disgusting, or neutral. When either "Pain" or "Disgust" was selected, participants also rated the degree of unpleasantness they think the protagonist of the video has perceived. We selected a subset of 51 clips (17 triplets) from the initial database the statistical details of which are described in the following paragraph.

First, pain and disgust expressions showed only a marginal difference in terms of unpleasantness felt by the protagonist of the video ($F_{(1,9,51)} = 4.35$, p = 0.065; Figure 1B, left subplot). Second, pain and disgust expressions showed no difference in unpleasantness inferred by the participants in the validation study ($F_{(1,14.04)} = 2.07$, p = 0.172; Figure 1B, middle subplot). Finally, pain and disgust expressions were classified with comparable proficiency (Wald $\chi^2_{(1)} = 0.69$, p=0.407; ~70% of accuracy, Figure 1B, right subplot). See Data analysis subsection for more details about the statistical analysis. The tests performed above provide a measure of confidence in using the selected clips for our purpose, as they display spontaneous expressions of pain and disgust, both matched for unpleasantness from the protagonist's point of view, and from an independent sample of observers. Furthermore, spontaneous expressions of pain and disgust are sufficiently similar to at-times be confused with one another, yet sufficiently different to be discriminated with a higher than chance accuracy (see Figure 1). This procedure was ideated and executed to minimize the emergence of ceiling/floor effects in the main experiment.

3.2.2.2 Experimental Set-up

Having created and validated a suitable database of spontaneous aversive expressions, we asked participants to process each video-clip in two experimental tasks reminiscent of those used for the validation session. In one task ("Face Classification"), participants saw all the videos in a randomized order, preceded by a fixation cross of 1 second. After each video, we asked them to categorize the expression by pressing one of three different keys (1= Pain, 2= Disgust, 3= Neutral; order balanced across participants). Participants had 5 seconds to provide a response. In the other task ("Unpleasantness Rating"), participants saw the same list of video-clips in a different random order, and were asked to indicate the amount of unpleasantness they attributed to the displayed person. To do so, they had 6 seconds to slide a cursor horizontally on a Visual Analog Scale ranging from Neutral to Extremely Unpleasant. Both tasks were preceded by a brief familiarization session where they classified or rated three video-clips of posed expressions (from the Montreal Pain and Affective Face Clips of Simon, Craig, Gosselin, Rainville, & Belin, 2007). The two tasks lasted approximately 90 minutes altogether. Their order was counterbalanced across participants, and they were programmed and run with Matlab R2012a (Mathworks, Natick, MA) with the aid of the Cogent 2000 toolbox (Wellcome Dept., London, UK).

3.2.3 Interoceptive accuracy

In order to obtain insights on participants' interoceptive abilities, we employed the well-known "Heart Beat Counting Task" (HBCT) (Schandry, 1981), which requires mentally tracking one's heart beats across predefined temporal intervals. Cardiac activity was recorded through five electrodes applied on the participant torso, and connected with the Biopac System integrated with the Acqknowledge Software (Biopac Systems, Inc) for data analysis. After the installation of the recording equipment, participants underwent the following experimental session. First, they sat quietly on a comfortable chair for about 5 minutes. Subsequently, they were instructed to pay attention to their cardiac activity by counting the heartbeats within an interval signaled by two auditory stimuli. In this context, elements that could provide

exteroceptive information about cardiac activity (e.g., tight wristwatches) were removed. Participants underwent five randomly-presented counting intervals of 17, 24, 33, 36 and 40 seconds. After each interval, they were requested to type the number of counted beats on a computer keyboard and to indicate how confident they were about their estimation on a Visual Analogue Scale ranging from 1 (not confident at all) to 10 (extremely confident).

Subsequently, participants underwent a control task to account for potential confounds related to personal beliefs about one's cardiac response and time estimation (Desmedt, Luminet, & Corneille, 2018; Ring & Brener, 2018; Ring, Brener, Knapp, & Mailloux, 2015; Zamariola et al., 2018). It included a time estimation paradigm, where they were subject once more to the same five intervals (in a different random order). By contrast to the HBCT, they were asked to count the number of seconds within each interval. Finally, each participant was asked to report how many heartbeats they believed they normally experience within one minute (believed Beats per Minute, *believed BPM*). Participants received no feedback on their performance throughout the experimental session.

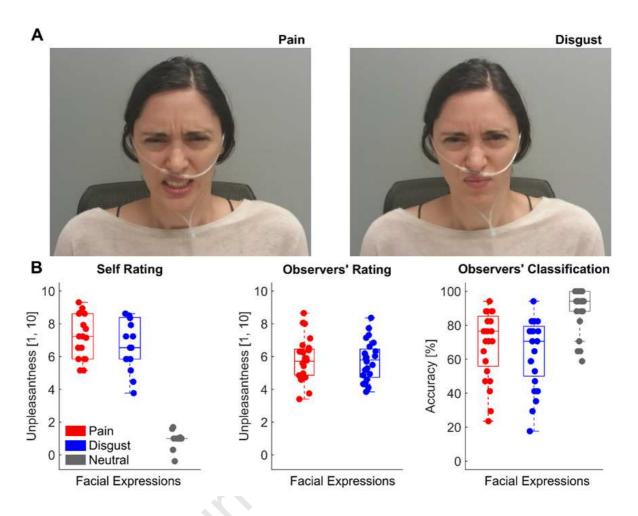


Figure 1. Database Creation and Validation. (A) For demonstrative purposes, one author of the study (GD) was placed in the experimental set-up and displayed pain (left subpanel) and disgust (right subpanel) expressions. (B) Boxplots describing the pilot data associated with the 51 video-clips used in the present study. Left subplot describes the self-reported unpleasantness ratings from the individuals displayed in the videos. Middle subplot describes the estimated unpleasantness from an independent sample of observers, whereas le right subplot describes the classification accuracy. In each boxplot, horizontal lines refer to the median value of the distribution, the box edges refer to the inter-quartile range, and whiskers refer to overall data range within 1.5 of the inter-quartile range. Individual data are also plotted as filled circles. Different expressions are associated with a specific color code.

3.2.4 Procedure

After having read and signed the consent form, participants underwent the experimental sessions on

interoceptive accuracy and the facial emotion evaluation tasks in counter-balanced order. Subsequently

they filled demographic questionnaires and the ASR (Mahr at al., 2018). The whole experiment took place at the psychology laboratory of the University of Geneva.

3.2.5 Data Analysis

Consistently with previous studies employing the HBCT (Zamariola et al., 2018), we calculated participants' accuracy for each interval through the following formula: $IAcc = \frac{|#detected heartbeats-#actual heartbeats|}{#actual heartbeats}$

In addition, we also inspected participants' cardiac frequency at each interval (in terms of Beats per Minute, *BPM*) as well as the frequency of heartbeats detected by participants (*detected* BPM). Similar measures were carried out for the time estimation control task, for which we calculated an accuracy score (temporal accuracy) and a detected seconds-per-minute frequency, in similar fashion to *IAcc* and *detected BPM*, by taking in consideration actual against detected seconds instead of heartbeats.

In our analyses, we employed a Linear Mixed Model, which allows us to account for multiple random factors simultaneously (identity of the participants, identity of the people displayed in the videoclips, etc.). Significance of the fixed effects was calculated with a Type III Analysis of Variance using the Satterthwaite approximation of the degrees of freedom. The only exception was the analysis of participants' choices in the classification task, for which we employed a Generalized Linear Mixed Model with a binomial distribution and Laplace approximation. In this case, significance of the fixed effects was assessed through a Type II Analysis of Deviance, using Wald χ^2 statistics. In all these models, null effects of interest were complemented with estimation of BIC-approximated Bayes Factor (Wagenmakers, 2007), which assesses whether the data are better explainable by a null model without the predictor of interest. The analysis was carried out as implemented in the ImerTest package (Kuznetsova, Brockhoff, & Christensen, 2017) from R.3.4.4 software (https://cran.r-project.org/).

3.3 Results

3.3.1 Heart Beat Counting Task

Table 1 displays the data from the HBCT and the time estimation control task for each of the five intervals. As first step, we tested whether the amount of detected heartbeats was reflective of the actual cardiac response, and whether individual interoceptive accuracy modulated such a relationship. We performed a Linear Mixed Model, where the detected BPM values for each participant, at each interval, were fitted against the BPM and IAcc. In this model, participants' identities and the temporal interval were specified as random factors with random intercept. This analysis led to a significant main effect of BPM (b = 0.54, $F_{(1,162.13)} = 36.32$, p < 0.001), suggesting that participants with higher heart rates detected more heartbeats. Furthermore, we found a main effect of *IAcc* (b = 63.08, $F_{(1,242.45)} = 493.98$, p < 0.001) suggesting that those participants with higher accuracy in the HBCT were on average detecting more heartbeats. Finally, we also found a BPM*IAcc interaction (b = 1.53, $F_{(1,248.32)} = 30.52$, p < 0.001), suggesting that the relationship between detected BPM and true BPM increased with participant accuracy. Following Zamariola et al., (2018), we divided the sample in 5 groups, ranked according to IAcc. For each of these groups we modeled detected BPM against BPM through a Linear Mixed Model with participants' identity and time interval as random factors. Results are displayed in Table 2 and reveal that, with the exception of the least proficient group, detected BPM was always explainable in terms of BPM (consistent with Zamariola et al., 2018). Furthermore, groups also differed in terms of intercept, with the most proficient group reporting a heart frequency close to the actual one, whereas less proficient participants showed a larger degree of underestimation.

		Intervals (sec)					
	_	17	24	33	36	40	
HR	BPM	74.14 (1.41)	71.80 (1.14)	71.82 (1.18)	71.33 (1.15)	72.97 (1.30)	
	detected BPM	52.64 (2.90)	50.20 (2.22)	50.14 (2.66)	49.27 (2.59)	48.00 (2.80)	
HBCT	IAcc	0.67 (0.03)	0.69 (0.03)	0.66 (0.03)	0.67 (0.03)	0.64 (0.04)	
	Confidence	4.74 (0.35)	4.82 (0.35)	4.66 (0.36)	4.74 (0.35)	4.6 (0.34)	
	Sec. per Min.	46.71 (3.04)	42.40 (2.92)	42.29 (3.21)	49.27 (2.30)	52.51 (2.09)	
Temporal Estimation	Temporal Acc	0.65 (0.03)	0.63 (0.37)	0.62 (0.04)	0.72 (0.02)	0.77 (0.02)	
	Confidence	6.88 (0.21)	7 (0.23)	7.12 (0.22)	6.96 (0.24)	6.86 (0.22)	

Table 1. Average (and standard error) data from the Heart Beat Counting Task (HBCT) and time estimation control task across the five intervals of interest. HR: actual heart rate; BPM: actual beats per minute; detected BPM: detected beats per minute; *IAcc*: Interoceptive Accuracy; Sec. per. Min,: detected seconds per minute; Temporal Acc.: Temporal Estimation Accuracy.

	Data Partitions						
	Lowest	Low	Average	High	Highest		
IAcc range	0-0.50	0.50-0.61	0.61-0.75	0.75-0.87	0.88-1.00		
BPM	75.68 (1.50)	73.78 (1.18)	72.39 (0.92)	70.75 (1.32)	69.46 (1.07)		
detected BPM (Intercept)	35.03 (5.93)	40.59 (0.35)	50.85 (2.04)	64.74 (1.78)	69.65 (0.92)		
detected BPM ~ BPM (slope)	-0.12 (0.35)	0.56 (0.04)	0.86 (0.14)	0.57 (0.20)	0.78 (0.09)		

Table 2. Results of a Linear Mixed Model, testing the relationship between actual and detected heart rate in data partitioned based on interoceptive accuracy. Each of the five groups is described in terms of IAcc range, cardiac frequency (average BPM, with standard error), and parameters of a Linear Mixed Model fitting detected BPM against true BPM. Parameters include the intercept (corresponding to the average detected BPM regardless of the actual heartrate) and a slope (how much detected BPM is explained by inter-individual difference in BPM). Slopes statistically larger than zero are highlighted in bold.

We then assessed whether participants detected BPM could be explained in terms of temporal counting

strategies, or personal beliefs about cardiac responses. For this reason, we repeated the same Linear

Mixed Model described above and replaced the *BPM* predictor with either the frequency of reported seconds in the time estimation task in equivalent intervals (detected seconds per minute), or participants' beliefs as collected at the end of the HBCT session (*believed BPM*, see methods). No effect was associated with *believed BPM* (b = 0.02, $F_{(1,52.36)} = 0.11$, p = 0.737). Instead, we found a significant modulation of detected seconds per minute (b = 0.11, $F_{(1,228.10)} = 10.10$, p = 0.002) with magnitude ~ 5 lower than that of *BPM*. Furthermore, the detected seconds interacted significantly with *IAcc* (b = -0.25, $F_{(1,239.49)} = 3.90$, p = 0.049). However, as opposed to the case of *BPM*, the parameter *b* was negative, suggesting the influence of detected seconds on the number of detected heartbeats was more pronounced in participants with low *IAcc*. Thus, although we cannot deny the potential role played by counting strategies in participants.

We also controlled if *IAcc* was itself modulated by the accuracy in the time estimation task, or by individuals' beliefs. A Linear Mixed Model (with subjects' identity and time interval as random factors) found no effect of temporal estimation accuracy (b = 0.02, $F_{(1,128.22)} = 0.16$, p = 0.688). As for beliefs, we modeled as predictor the absolute differential value between believed and actual BPM. This was done under the assumption that, if the HBCT was confounded by individual knowledge about their cardiac response, the lowest *IAcc* should be associated with those individuals in which believed and real BPM are most apart. This prediction was confirmed ($b = -7.04 \cdot 10^{-3}$, $F_{(1,290)} = -8.89$, p < 0.001). Hence, participants' performance in the HBCT is indeed influenced by individual knowledge about one's cardiac response.

3.3.2 Pain and Disgust Expressions

3.3.2.1 Unpleasantness Rating

Figure 2A reports the distribution of rating values for all 50 participants across the three states. Pain and Disgust expressions were both associated with comparable unpleasantness (~ 7 points on a scale ranging from 1 to 10), whereas lower values were attributed to neutral expressions (~ 2).

Single-trial ratings were input in a Linear Mixed Model with Expression (Pain, Disgust, Neutral) as a fixed factor and interoceptive accuracy (*IAcc*) as a between-subjects covariate (for each participant we estimated the average accuracy from all five intervals of the HBCT). Furthermore, the identity of the participants and of the person in the videos were modeled as random factors (both with random intercept and slope for Expression). This analysis led to a main effect of Expression ($F_{(2, 13.43)} = 73.19$, p <0.001), reflecting different degrees of unpleasantness between Neutral and Pain/Disgust expressions (Figure 2A) and a main effect of *IAcc* ($F_{(1, 48)} = 4.89$, p = 0.032). No interaction between *IAcc* and Expression was found to be significant ($F_{(2, 47.99)} = 0.09$, p = 0.916). Figure 2B-D shows *IAcc* from the HBCT plotted against participants' average ratings. For each kind of expression, individuals with higher accuracy are also more prone to rate other people's states as more unpleasant.

As participants' performance in the HBCT was partially confounded by counting strategies and beliefs about their cardiac response, we repeated the analysis by modeling instead residual *IAcc* values, obtained after regressing out the accuracy of the time estimation control task or the differential value between believed and actual heartbeats (|*believed BPM*– *BPM*|). This analysis confirmed the same effects obtained by using the raw *IAcc* scores (Expression: $F \ge 73.19$, p < 0.001; residual *IAcc*: $F \ge 5.03$, $p \le 0.029$; Interaction: $F \le 0.22$, $p \ge 0.790$).

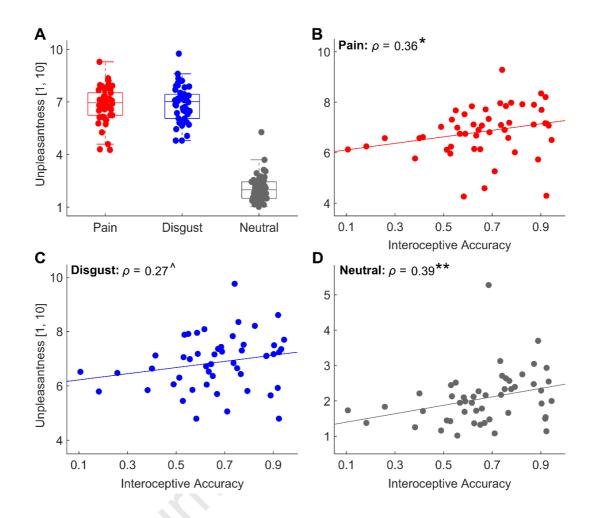


Figure 2. Unpleasantness Rating. (A) Boxplots describing the distribution of mean unpleasantness ratings for each expression across the overall population. Horizontal lines refer to the median value of the distribution, the box edges refer to the inter-quartile range, and whiskers refer to overall data range within 1.5 of the inter-quartile range. Individual data are also plotted as filled circles. Different expressions are associated with specific color codes. (B-D) Scatter plot with linear regression describing the relationship between individual mean unpleasantness ratings and interoceptive accuracy. Pain, Disgust and Neutral expressions are represented in separate subplots, and associated with a Spearman ρ correlation coefficient. Significant correlations are highlighted as follows ** p < 0.01; * p < 0.05, ^ p < 0.054

3.3.2.2 Face Classifications

Responses to the Classification task for each video category (Pain, Disgust and Neutral) are displayed in the scatterplot in Figure 3A. Responses to Neutral videos approached ceiling level (mean=94.00 \pm 7.74) with accuracy rates of 100% in 24 participants, while those for Pain and Disgust videos reflected the ambiguity found in the pilot study (Pain accuracy: 73.41 ± 11.16 , disgust accuracy: 66.00 ± 12.70 ; see also Figure 1B).

The accuracy for each trial (yes-no) was included in a Generalized Linear Mixed Model with a binomial distribution. We modeled Expression (Pain, Disgust) as a fixed factor, *IAcc* as a between-subjects covariate, and the identity of the participants and of the person in the videos as random factors, both with random intercept and slope for Expression. Neutral expressions were not included in the analysis, given that they were classified at ceiling, with detrimental effects on model estimation. Analysis of Deviance of Type II showed neither significant main effect nor interaction (Wald's $\chi^2 s \leq 2.46$, $ps \geq 0.116$). Thus, in contrast with the Unpleasantness Rating task, we found no evidence that *IAcc* influenced the classification (see also Figure 3B-D). On the contrary, when calculating BIC-approximated Bayes Factor, we found stronger support for a model where only the fixed factor Expression was specified, than for models including also *IAcc*, either only as main effect (Bayes Factor = 32.47), or also in interaction with Expression (Bayes Factor = 1334.75).

We repeated the analysis by modeling pain or disgust classifications instead of accuracy. For both we found a main effect of Expression (pain: $\chi^2 = 21.56$, p < 0.001; disgust $\chi^2 = 25.96$, p < 0.001) reflecting more frequent pain-classifications for pain videos, and disgust-classifications for disgust videos. *IAcc* was never significant, neither as main effect, nor as interaction ($\chi^2 s \le 0.31$; $ps \ge 0.832$; Bayes Factor ≥ 37.37).

We then modeled participants' Response Times (in milliseconds) for correct trials through a Linear Mixed Model with Expression (Pain, Disgust, Neutral) as a fixed factor, *IAcc* as a between-subject covariate, and the identity of the participants and of the person in the video as random factors, both with random intercept and slope for Expression. This analysis revealed a main effect of Expression ($F_{(2, 15.55)} = 73.19$, p < 0.001), suggesting faster responses to Neutral (average 848.83 ms) as opposed to Painful/Disgusting expressions (Pain = 931.55 ms; Disgust = 949.16 ms). No effect was significantly

associated with *IAcc*, either alone, or in interaction with Expression ($Fs \le 1.13$; $ps \ge 0.329$; Bayes Factor \ge 43.81).

3.3.4 HBCT Confidence

We repeated the (Generalized) Linear Mixed Models testing the relationship between interoceptive abilities and faces ratings/classifications, by replacing *IAcc* with participants' confidence about their performance in HBCT. This analysis revealed no significant main effect/interaction associated with HBCT confidence, neither when analyzing unpleasantness ratings ($Fs \le 2.01$, $ps \ge 0.163$), nor when focusing on participants choices (Wald's $\chi^2 s \le 2.32$, $ps \ge 0.127$) and response times ($Fs \le 1.36$, $ps \ge 0.259$) in the classification task (Bayes Factor ≥ 22.64).

3.3.5 Anxiety and Depression

As twelve of our participants displayed high level on the anxiety and depression scale of the ASR questionnaire (Mahr at al., 2018, cut-off: T = 64), we assessed weather our results were influenced by this potential confound. For this purpose, we repeated the (Generalized) Linear Mixed Models described above by adding the anxiety and depression score as covariate of no interest. This analysis revealed a global effect of anxiety and depression as participants with higher scores were both more accurate at classifying expressions and more prone to rate them as unpleasant (but not for neutral faces). However, this effect was independent from participants' interoceptive abilities, as in none of the analyses the score interacted significantly with *IAcc*. Full details are provided in Appendix A.

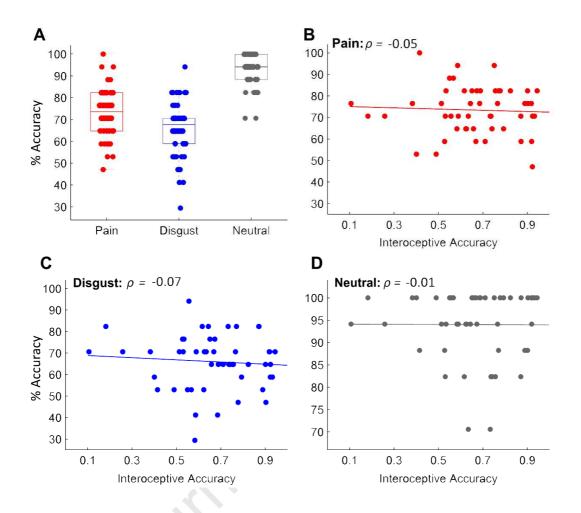


Figure 3. Face Classification. (A) Boxplots describing the distribution of percent accuracy for each expression across the overall population. Horizontal lines refer to the median value of the distribution, the box edges refer to the inter-quartile range, and whiskers refer to overall data range within 1.5 of the inter-quartile range. Individual data are also plotted as filled circles. Different expressions are associated with specific color codes. (B-D) Scatter plot with linear regression describing the relationship between individual classification accuracy and interoceptive accuracy. Pain, Disgust and Neutral expressions are represented in separate subplots, and associated with a Spearman ρ correlation coefficient.

3.4 Discussion

We recruited fifty young women in a study aimed at assessing the role played by interoceptive abilities in the evaluation and recognition of naturalistic facial expressions. To this end, we devised a paradigm dissociating the ability to classify specific states (e.g., pain, disgust), from a more general sensitivity to the dimension of unpleasantness. We found that interoceptive accuracy is involved in the latter, but not the former, with individuals more proficient at monitoring their own cardiac activity being more prone to evaluate any facial expression as more unpleasant. Our results converge with, but also extend, a wealthy line of research in social cognition pointing to a major role of personal affect in the coding of others' states through supra-ordinal dimensions such as unpleasantness (Antico, Cataldo, & Corradi-Dell'Acqua, 2019; Corradi-Dell'Acqua, Hofstetter, & Vuilleumier, 2011; Corradi-Dell'Acqua, Tusche, Vuilleumier, & Singer, 2016). Moreover, our study is in line with multi-componential models of social cognition, suggesting that only part of our ability to understand how others feel underlies access to one's interoceptive signals.

3.4.1 How interoceptive accuracy influences the understanding of others

The role played by interoceptive accuracy on social cognition has been thoroughly investigated in the last decades, leading to at least two different theoretical accounts. On the one hand, there is evidence that first-hand emotional experiences can be used as tools for interpreting behavioral and physiological signals in others, and consequently can make individuals more sensitive to their ongoing affective states. More specifically, embodied models of social affective cognition (Bernhardt & Singer, 2012; Goldman & de Vignemont, 2009) argue that the pain and disgust of another person are understood through a simulation of how these states influence oneself, with associated neural and physiological responses (Corradi-Dell'Acqua et al., 2011; Goldstein, Weissman-Fogel, & Shamay-Tsoory, 2017; Lamm, Decety, & Singer, 2011; Wicker et al., 2003). Within this framework, a more proficient capacity to detect one's internal bodily signals should allow for a more acute simulation of others' states on one's body, thus leading to a

better tuning to others' emotional and affective states. Therefore, interoceptive abilities can be considered elements that promote the sharing of others' states.

On the other hand, embodied models alone struggle to explain why projecting people's affective states on one's body does not lead to a confusion between which response belongs to oneself and which to someone else. For this reason, it has been suggested that mechanisms of affective simulation should be paralleled by a compensatory process that maintains a clear distinction between self and others (Silani et al., 2013). It has been suggested that interoception might serve this purpose, by strengthening the representation of one's real body properties, at the expense of vicarious simulations of those from other people (Palmer & Tsakiris, 2018). This hypothesis is supported by studies finding individuals with higher sensitivity to internal body signals to be more resistant to multisensory illusions, leading to a false sense of ownership towards alien body parts (Tajadura-Jiménez & Tsakiris, 2014; Tsakiris, Tajadura-Jiménez, & Costantini, 2011). It is conceivable that interoceptive abilities act in similar fashion for cases of social embodiment, by strengthening the representation of one's current emotional state, and therefore making individuals more resistant to sharing others' emotions and affect (Palmer & Tsakiris, 2018).

Our results allow us to disambiguate these opposing views by underscoring that a higher accuracy in detecting one's internal body signals increases unpleasantness evaluations of others' faces. Although higher ratings do not necessarily imply higher accuracy in estimating others' discomfort (also the rating of neutral faces increases with *IAcc*), our results clearly show a strong tendency to interpret any facial features (including reactions to neutral odorants/temperatures) as a sign of unpleasantness. This supports the view from embodied accounts that interoception promotes (and does not inhibits) individual receptivity to others' affect (in our case negative expressions). However, it should be noted that our task did not require participants to focus on the self-other distinction (volunteers presumably directed all their attention to the displayed facial expressions). It is therefore possible that interoceptive accuracy

influences the evaluation of others in two ways: by promoting it when there is no conflict with the self (as in our study) and by inhibiting it when the contrast between self and other is highly salient. Further studies are needed to better understand the role played by interoception in self-other distinction.

3.4.2 Two-way model of Social Affective Cognition

Our results show how interoception (as measured by the task HBCT) influences the appraisal of others' affect, specifically the evaluation of unpleasantness, but not the categorization between different states of comparable unpleasantness. This was achieved in a paradigm that made use of the same database of stimuli for both assessments, in a controlled and counter-balanced setting, thus ruling out the presence of design-related confounds. While it is possible that the two tasks differ in terms of sensitivity (unpleasantness is expressed through continuous ratings, whereas classification in a forced choice), it is unlikely that a potential effect on interoceptive accuracy in the classification task went undetected, given the remarkably strong support for a null model which does not take into account *IAcc* (Bayes Factor > 32). Instead, the most suitable interpretation is that the two tasks tap different components of participants' social abilities, with interoceptive accuracy influencing only one of these.

In the last decades, several authors proposed that individuals' abilities to appraise others' emotional states can be segregated in at least two pathways. In one, an "affective" pathway allows fast and automatic understanding of people's affect through a mechanism of resonance, through which observers embody the states seen in others as they would their own. On the other hand, a "cognitive" pathway provides the means for a slower and deliberate inference, relying on mechanisms reminiscent of those underlying perspective-taking and mentalizing (Shamay-Tsoory, Aharon-Peretz, & Perry, 2009; Stietz, Jauk, Krach, & Kanske, 2019). We argue that the unpleasantness rating task implemented in the present study taps selectively the "affective" pathways proposed in the literature.

In this perspective, our results might reflect the broad susceptibility of the cardiac response (here used to probe for people's interoceptive abilities) to a wide range of emotional/affective states (including

pain and disgust), as reported by individuals through either verbal descriptions (Oosterwijk, Snoek, Rotteveel, Barrett, & Steven Scholte, 2017) or graphical representations on body silhouettes (Nummenmaa, Hari, Hietanen, & Glerean, 2018). However, interoception is a complex and multidimensional capacity not limited to the tracking of one's heartbeats (Khalsa et al., 2018). It is therefore possible that other features of individual interoceptive abilities could contribute to statespecific estimation of others' affect. For instance, the ability to discriminate signals arising from different channels or organ systems (e.g. cardiac vs. gastric) could influence the discrimination of different states (pain vs. disgust) in others' expressions. While our data cannot exclude this possibility, it should be underscored that our results are in line with previous studies testing embodied accounts for social affective cognition, arguing that comprehensive experience of one's pain and disgust influences the appraisal of others' states, consistently with a supra-ordinal code of unpleasantness (Corradi-Dell'Acqua et al., 2011; 2016; Antico et al., 2019). This was observed through neuroimaging, which revealed that neural response common between ones' and others' pain is also shared across other painless unpleasant states (Corradi-Dell'Acqua et al., 2011; 2016). The same happens in behavioral priming, in which selfrelated aversive experiences influenced the subsequent appraisal of any facial expression diagnostic of unpleasantness (but not of arousal), regardless of whether it conveys the same or a different state (Antico et al., 2019). In this view, our data complement and extend previous research, pointing to a key role played by one's interoceptive abilities for a supra-ordinal assessment of others' unpleasantness.

In contrast to the unpleasantness rating, the classification task does not appear to be related to individual's interoceptive abilities, and therefore might not tap into the "affective" pathway for social cognition. Spontaneous disgusted and painful expressions share many properties, with only subtle differences in patterns of muscle contraction (Dirupo et al., 2020; Kunz, Peter, Huster, & Lautenbacher, 2013). Furthermore, automatic tools for detection of pain from facial responses can mistakenly

misclassify disgust expressions as painful (Dirupo et al., 2020). Finally, human observers can discriminate between these two states with moderate accuracy and considerable misclassifications (see Kunz & Lautenbacher, 2015; see also Figures 1B & 3). Interestingly, observers' proficiency increases when they are specifically trained at focusing on the relevant muscle contractions (Kunz & Lautenbacher, 2015). In this perspective, the classification between pain and disgust expressions may be the result of a complex scrutiny of observed facial movements, difficult to mimic by an automatic affective resonance mechanism.

Indeed, due to the flexible engagement of domain-specific functions, simulating others' reactions in one's own body might only be one possible component or strategy underlying our comprehension of others' emotions. Acknowledging such flexibility might explain the apparent inconsistency in the literature, with paradigms involving assessments of supra-ordinal dimensions describing positive effects of interoceptive abilities (e.g., Grynberg & Pollatos, 2015), whereas those requiring fine-grained appraisal failing to do so (Ainley et al., 2015).

3.4.3 Limitations of the study

In the present study, the population examined included only women. This was motivated by a wealthy evidence of gender differences in both interoceptive abilities (Cox et al., 1985; Grabauskaitė et al., 2017; Harver et al., 1993; Suschinsky & Lalumière, 2012; Whitehead & Drescher, 1980), in the evaluation of emotional facial expressions (Derntl et al., 2009; Hoffmann et al., 2010; Montagne et al., 2005), and by previous research documenting that *IAcc* influenced the evaluation of others' emotional and affective states in a gender-unbalanced population (80% women, Grynberg & Pollatos, 2015). Hence, in this experiment we selected the sample that was most sensitive to the main experimental manipulation. Unfortunately, our choice has a generalizability limitation as the conclusions cannot be extended to the whole population. In addition, a female's judgment on emotions can be influenced by the menstrual cycle

(Wu et al., 2014), an aspect that could have impacted our results. Future studies will need to account for these factors.

Furthermore, although our study provides clear evidence that interoceptive accuracy influences the evaluation of general (but not state-specific) information shared between pain and disgust, the nature of such supra-ordinal coding is not certain. Provided that the whole experimental set-up was designed and validated on the notion of "Unpleasantness", it is likely that our results highlight this dimension. Alternative interpretations are possible, under the assumption that participants' ratings would indirectly capture another affective dimension such as arousal or intensity (see Antico et al., 2019, for an extended discussion). Future research could extend the current experiment by including positive expressions, in order to understand whether *IAcc* acts along the dimension of intensity or valence.

Finally, in order to measure individual's interoceptive abilities, we implemented the well-known Heart Beat Counting Task which has been widely used in previous literature (Ainley, Brass, & Tsakiris, 2014; Ainley et al., 2015; Grynberg & Pollatos, 2015; Kever et al., 2015; Terasawa et al., 2014). Although advantageous in many respects (compatibility with the literature, simple experimental set-up) recent studies have criticized this paradigm, arguing that participants' responses might not reflect an exclusive monitoring of one's own cardiac responses, but could be contaminated by exteroceptive confounds, such as time estimation strategies or prior knowledge on cardiac physiology (Desmedt, Luminet, & Corneille, 2018; Ring & Brener, 2018; Ring, Brener, Knapp, & Mailloux, 2015; Zamariola et al., 2018, but see Ainley et al., 2020). In the present experiment we found that when performing this task, participants' estimated heartbeats were indeed correlated with their actual heartbeats (except in the 5th percentile of the sample with lowest *IAcc*, see also Zamariola et al., 2018). Parallelly, the performance in the HBCT was also influenced by control measures of time estimation and beliefs about cardiac frequency, thus confirming the presence of exteroceptive influences in participants' judgments. Critically, however, our main results

are independent from these confounds, as the relationship between *IAcc* and unpleasantness displayed in Figure 2 appeared conserved also when covarying for time estimation and beliefs about one's cardiac frequency. Unfortunately, in the present paradigm we did not collect measures such as Body Mass Index and Systolic Blood Pressure, which might account for potential exteroceptive confounds related to touch receptors on the chest (Murphy, Geary, Millgate, Catmur, & Bird, 2017). Furthermore, the Time-Estimation task was carried out under the same time-intervals than the HBCT, whereas this was not always the case in previous studies (Dunn et al., 2010; Murphy et al., 2017; Stevens et al., 2011; but see Knoll & Hodapp, 1992).

3.5 Conclusions

With this study, we demonstrate that interoceptive accuracy influences the appraisal of other people's affective states. By employing two independent paradigms, using carefully controlled stimuli, we demonstrated that this influence is restricted to a supra-ordinal processing of dimensions common to different states (such as unpleasantness), but not to a more fine-grained appraisal of the person's specific condition. This result is in keeping with multi-componential models of social cognition, positing the presence of two pathways for understanding others' affect, only one of which is influenced by a representation of one's own affective/somatic responses.

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3.6 Appendixes

3.6.1 Appendix A

We repeated the (Generalized) Linear Mixed Models carried out for assessing the interplay between *IAcc* and the appraisal of facial expressions, by adding the Anxiety & Depression Score from the ASR autoquestionnaire (Mahr at al., 2018) as covariate. The analysis of unpleasantness rating revealed a main effect of the score ($F_{(1,46)} = 5.49$, p = 0.024) and its' interaction with the factor *Expression* ($F_{(1,93.70)} = 3.37$, p = 0.038). Figure A1A shows that individuals with high scores have a stronger tendency to rate painful and disgusted (but not neutral) expressions as more unpleasant. The analysis confirmed the main effects of *Expression* ($F_{(2,13.47)} = 73.84$, p < 0.001) and *IAcc* described in the main text, although latter effect is now observed with marginal significance ($F_{(1,46)} = 3.39$, p = 0.072). No other effect was found to be significant ($Fs \le 0.40$, $ps \ge 0.669$).

As for the classification task, the analysis of Accuracy revealed only a main effect of the anxiety and depression (Wald's $\chi^2_{(1)} = 5.54$, p = 0.019; all other effects $\chi^2 s \le 0.80$, $ps \ge 0.370$), reflecting stronger accuracy in those individuals with high scores. Instead, the analysis of Response Times to correct classifications confirms only the main effect of Expression described in the main text ($F_{(2,13.73)} = 4.40$, p =0.033; all other effects $Fs \le 1.36$, $ps \ge 0.263$).

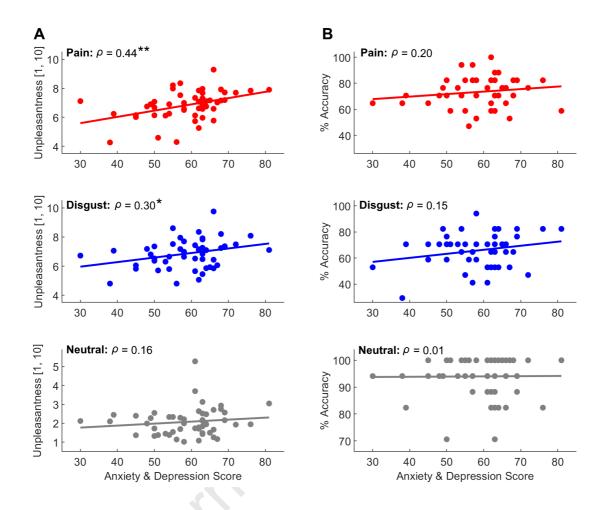


Figure A1. Effects of Anxiety and Depression. Scatter plots with linear regression describing the relationship between individual anxiety & depression and the appraisal of facial expressions. Left column (A) describes the data from the unpleasantness rating task, whereas left column (B) describes the accuracy of the classification task. Pain, Disgust and Neutral expressions are represented in separate subplots, and associated with a Spearman ρ correlation coefficient. Significant correlations are highlighted as follows ** p < 0.01; * p < 0.05

3.6.2 Appendix B

