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Listening to Your Heart: How Interoception Shapes Emotion Experience and Intuitive Decision Making

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Abstract

Theories proposing that how one thinks and feels is influenced by feedback from the body remain controversial. A central but untested prediction of many of these proposals is that how well individuals can perceive subtle bodily changes (interoception) determines the strength of the relationship between bodily reactions and cognitive-affective processing. In Study 1, we demonstrated that the more accurately participants could track their heartbeat, the stronger the observed link between their heart rate reactions and their subjective arousal (but not valence) ratings of emotional images. In Study 2, we found that increasing interoception ability either helped or hindered adaptive intuitive decision making, depending on whether the anticipatory bodily signals generated favored advantageous or disadvantageous choices. These findings identify both the generation and the perception of bodily responses as pivotal sources of variability in emotion experience and intuition, and offer strong supporting evidence for bodily feedback theories, suggesting that cognitive-affective processing does in significant part relate to "following the heart."

Keywords

interoception, emotion, decision making, arousal, bodily feedback, somatic marker hypothesis, James-Lange theory of emotion

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Some metaphorical expressions that are used daily, such as "brokenhearted" or "gut feelings," reflect the common belief that feelings and cognitions are partly grounded in bodily responses. This idea is reflected in early philosophical writings about embodiment (e.g., Descartes, 1649/1989) and was introduced to experimental psychology by William James (1884), who asserted that perception of changes in the body "as they occur is the emotion" (pp. 189–190). Since then, there has been considerable debate about the extent to which feelings and cognitions are in fact embodied. Much of this discussion has focused on emotion experience and decision making (e.g., Niedenthal, 2007). For example, Jamesian theory was modified to argue that emotion experience is a product of the cognitive appraisal of bodily arousal (Schachter & Singer, 1962). The somatic marker hypothesis (SMH; Damasio, 1994) proposes that emotional biasing signals emerging from the body influence intuitive decision making (see Dunn, Dalgleish, & Lawrence, 2006). These models remain controversial, and critics argue that bodily responses occur relatively late in the information-processing chain and are therefore best viewed as a consequence, rather than the cause, of cognitive-affective activity (see Moors, 2009).

The ability to detect subtle changes in bodily systems, including muscles, skin, joints, and viscera, is referred to as *interoception*. A lamina-I spinal-thalamo-cortical pathway culminating in the insula is believed to convey signals from the primary afferents that represent the body, resulting in bodily feelings such as pain, temperature changes, itching, and visceral sensations (Craig, 2002, 2009). It has been argued that representation of the homeostatic condition of the body in the insula and related regions crucially influences cognitive-affective processing (Craig, 2009; Critchley, 2005). In studies consistent with this position, the insula has been

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related to the accuracy of heartbeat perception (e.g., Critchley, Wiens, Rotshtein, Öhman, & Dolan, 2004), and has been implicated in emotion experience and decision making (e.g., Damasio et al., 2000; Mohr, Biele, & Heekeren, 2010).

If Jamesian accounts are correct, the more accurately individuals can perceive bodily activity, the stronger the relationship between such bodily changes and cognitive-affective processing should be (a moderation effect; Baron & Kenny, 1986). In other words, bodily changes should only relate to feelings and cognitions to the extent that one can accurately perceive them. The extant literature on bodily feedback has explored whether increased interoceptive awareness is simply related to superior decision making and stronger affective experience (e.g., Barrett, Quigley, Bliss-Moreau, & Aronson, 2004; Werner, Jung, Duschek, & Schandry, 2009). However, an inconsistent picture is emerging, and, surprisingly, James's pivotal moderation prediction has not been tested using optimal continuous designs (see Katkin, Wiens, & Öhman, 2001). In the studies presented in this article, we therefore examined whether interoception moderates the coupling of bodily responses to emotion experience (Study 1) and intuitive decision making (Study 2), to test a key aspect of bodily feedback theories.

Study 1

Embodiment theories of emotion have proliferated since James's (1884) proposal (see Moors, 2009). Early strong accounts argued that patterns of bodily responses are sufficient to differentiate between complex emotional states (e.g., determining stimulus valence or distinguishing feeling states such as fear and disgust). Later hybrid models (e.g., the two-factor theory; Schachter & Singer, 1962) suggested instead that the body contributes to emotional arousal, which is then cognitively appraised to generate more nuanced subjective affect.

In Study 1, we examined the extent to which interoceptive awareness moderates the relationship between bodily responses and these different kinds of emotion experience, using the circumplex model of affect (Russell, 1980). According to this model, all emotion experience can be classified as falling somewhere within two dimensions of valence (pleasantness) and arousal (Russell, 1980). Strong bodily feedback theories predict a moderating role of interoception for both arousal and valence experience, whereas hybrid accounts predict a moderating role of interoception only for arousal experience.

From an etymological perspective, one might expect that bodily feedback would relate more strongly to arousal than to valence experience, given that the definition of arousal (e.g., "intensity of peripheral physiological reactions;" Frijda, 2009, p. 268) necessarily includes bodily elements, whereas the definition of valence does not. Indeed, Frijda (2007) proposed that key aspects of valence experience are not bodily at all, and that valence reflects instead a blend of emotion components, including appraisals and action tendencies, as well as bodily arousal.

To our knowledge, the degree to which the interplay between bodily responses and bodily perception shapes arousal versus valence experience remains an open question. In Study 1, we therefore examined the degree to which bodily responses and their perception were related to subjective arousal and valence ratings of affective images. We predicted that bodily responses would be related to arousal but not valence ratings, and that interoception would moderate body-arousal coupling and not body-valence coupling (cf. hybrid models; Schachter & Singer, 1962; Frijda, 2007).

Method

Participants. Fifty-eight participants (35 female, 23 male; mean age = 45 years, *SD* = 14 years) were recruited from the Medical Research Council (MRC) Cognition and Brain Sciences Unit (CBSU) community volunteer panel. The mean estimated full-scale IQ of participants on the National Adult Reading Test (NART; Nelson, 1982) was 117 (*SD* = 8). Participants were excluded if they had a history of learning disability, psychosis, substance abuse, or neurological problems. Study 1 (as well as Study 2) was approved by local ethics committees, and volunteers gave written informed consent. Participants received approximately U.S. $7 per hour for their time.

Affective picture task. Participants viewed 25 affective images (5 positive, 5 neutral, 5 sad, 5 disgusting, and 5 fearful) selected predominantly from the International Affective Picture System (IAPS; Lang, Greenwald, Bradley, & Hamm, 1993). The images were presented for 6 s each, with a 5-s intertrial interval. Participants rated the arousal they felt to each image (e.g., feeling jittery, awake, and alert as opposed to sluggish, dull, and sleepy; rated on a 9-point visual analog scale ranging from 1, *not at all arousing*, to 9, *very arousing*). Participants also rated their level of valence (pleasantness) felt to each image (on a 9-point visual analog scale ranging from 1, *very unpleasant*; to 5, *neutral*; to 9, *very pleasant*; cf. Lang et al., 1993). Images were presented in a pseudorandom sequence, with one of each image type randomly shown in each block of five trials.

As a measure of bodily response, heart rate (HR, recorded in beats per minute, or BPM) change to each image was quantified by subtracting mean activity during a 2-s prestimulus baseline from mean activity during the picture-viewing period (cf. Dunn, Billotti, Murphy, & Dalgleish, 2009). Median response of each participant to each image type was then computed. A BIOPAC MP100 system (BIOPAC Systems, Inc., Camino Goleta, CA) recorded HR responses, acquiring data at 200 samples per second. Two disposable Ag-AgCl electrocardiogram (ECG) electrodes were placed on the dorsal forearms with clip-on shielded leads attached.[1]

Interoception task. Interoception was then assessed separately via the Schandry heartbeat-perception task (Ehlers & Breuer, 1992; Schandry, 1982). In six trials, participants counted how many heartbeats they felt over varying time intervals (two 25-s trials, two 35-s trials, two 40-s trials); responses were then compared with how many heartbeats were measured by ECG. Interoceptive accuracy was calculated by taking the modulus of the actual value minus the estimated value, dividing this by the actual value, and then multiplying by 100 to express the inaccuracy as a percentage: [(actual − estimated) ÷ actual] × 100. The inverse of this value was the measure of accuracy. We selected the mental tracking task, as we found it to be more sensitive to individual differences than tone detection alternatives in a pilot study (e.g., Whitehead, Drescher, Heiman, & Blackwell, 1977; see Section S1 in the Supplemental Material available online).

Results

Alpha was set at .05, and we carried out two-tailed statistical tests. To validate the task as an effective emotional induction, we used a repeated measures analysis of variance (ANOVA) to compare valence, arousal, and HR responses to positive, neutral, and negative (a composite of fearful, sad, and disgusting) images (see Table 1). The images significantly differed on valence ratings, $F(2, 114) = 486.03$, $p < .001$, and arousal ratings, $F(2, 114) = 164.72$, $p < .001$. Positive images were rated as the most pleasant, and negative images as the least pleasant, ps < .001, and both positive and negative images were rated as more arousing than neutral images, ps < .001. One participant's HR data were set aside because of equipment failure, and an additional 4 participants' HR data were excluded as outliers.[2] Overall, participants showed an HR deceleration when viewing the images, a finding consistent with an initial orienting response (e.g., Bradley, 2000). HR deceleration was greater for negative images than for positive and neutral images, $F(2, 51) = 3.29$, $p < .05$ (cf. Dunn et al., 2009).

In our correlational analyses, we found that less marked HR deceleration was significantly associated with higher arousal ratings, $r = .38$, $p < .01$, whereas HR response and valence ratings were not significantly related, $r = .15$, $p = .28$. Interoception was not significantly related to arousal or valence ratings or overall HR response to the images, ps > .05. To examine our key hypothesis about interoceptive awareness moderating the relationship between HR response and subjective ratings, we ran hierarchical regression analyses on the valence and arousal ratings separately (pooling across image types; cf. Baron & Kenny, 1986). Standardized scores (Z-transformed) for interoceptive accuracy and HR responses were included at the first step, and the requisite interaction term (HR Response × Interoceptive Accuracy) was added at the second step. Moderation would be indicated if the addition of the interaction term at the second step led to a significant increase in the variance in emotion experience that was explained. One further multivariate outlier was excluded from this analysis.

As predicted, interoceptive accuracy significantly moderated the relationship between HR change and arousal ratings, $\Delta F(1, 48) = 7.95$, $p < .01$, $\Delta R^2 = .12$, overall $F(3, 48) = 5.64$, $p < .01$, $R^2 = .26$. This was not the case for valence ratings, $\Delta F(1, 48) = 0.00$, $p = .98$, $\Delta R^2 = .00$, $\beta = 0.00$, overall $F(3, 48) = 1.60$, $p = .20$, $R^2 = .09$. We deconstructed these moderation effects in the standard way by recalculating the full regression equation 1 standard deviation above and 1 standard deviation below the interoception mean (Aiken & West, 1991). Using the original and revised equations, we predicted arousal (Fig. 1a) and valence (Fig. 1b) ratings at average (0 *SD*), smaller deceleration (+1 *SD*), and greater deceleration (−1 *SD*) levels of overall HR change for average (0 *SD*), better (+1 *SD*), and worse (−1 *SD*) levels of interoceptive accuracy. Greater arousal ratings were related to less negative HR responses, and this coupling grew stronger as bodily perception (interoception) increased in accuracy (Fig 1a). No such effect was observed for the valence data (Fig 1b). The magnitude of the moderation effects for valence and arousal differed significantly, $Z = 2.45$, $p < .01$. The arousal-HR interaction term remained significant when controlling for a range of potential confounds associated with the Schandry task, when treating interoception as a dichotomous variable, and when using rank-transformed data to further control for outlier effects (ps < .05). These analyses suggest that the moderating influence of interoceptive accuracy on the relationship between felt arousal and HR response is a robust result (see Section S2 in the Supplemental Material).

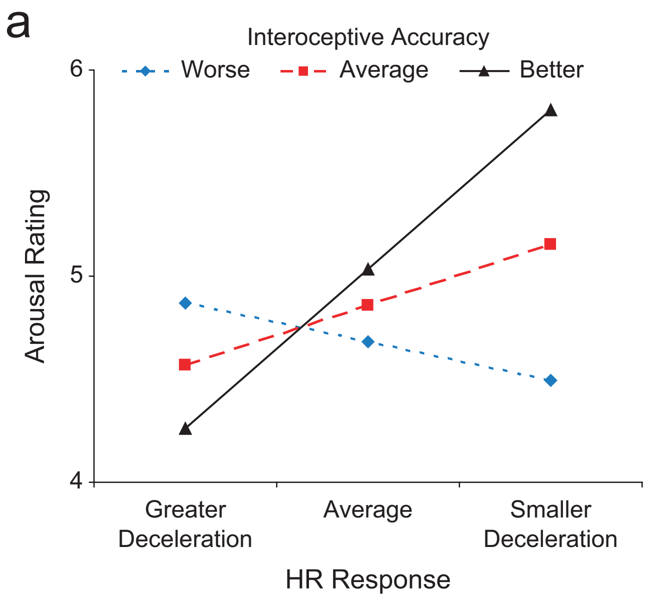
Table 1. Mean Arousal Ratings, Valence Ratings, and Heart Rate Response to Positive, Neutral, and Negative Images in Study 1

Picture valence	Arousal	Valence	HR response
Positive	5.53 (1.44)	6.94 (0.77)	−1.38 (2.96)
Neutral	2.49 (1.43)	5.04 (0.81)	−1.65 (2.32)
Negative	5.59 (1.59)	2.66 (0.92)	−2.32 (1.33)

Note: Heart rate (HR) response is mean activity (in beats per minute) during the 6-s picture-viewing period minus mean activity during a 2-s prestimulus baseline. Mean HR responses are negative, which is consistent with previous findings that viewing images results in an overall HR deceleration (e.g., Bradley, 2000). Arousal ratings are from 1 (*not at all arousing*) to 9 (*very arousing*). Valence ratings are from 1 (*very unpleasant*) to 9 (*very pleasant*), with 5 indicating a neutral response. Standard deviations are given in parentheses.

Discussion

Study 1 demonstrates that interoceptive awareness moderates the relationship between bodily changes and subjective arousal experience. In other words, the more strongly these autonomic changes are felt, the more they are associated with arousal experience. That no comparable effects were found for valence ratings suggests that bodily feedback selectively relates to particular aspects of subjective feeling postulated in the circumplex model (Russell, 1980). That increased arousal ratings are related to a less negative overall HR response may reflect individuals moving more rapidly through the "defense cascade" typically seen in response to emotional stimuli (cf. Bradley, 2000), therefore exhibiting a smaller initial HR deceleration



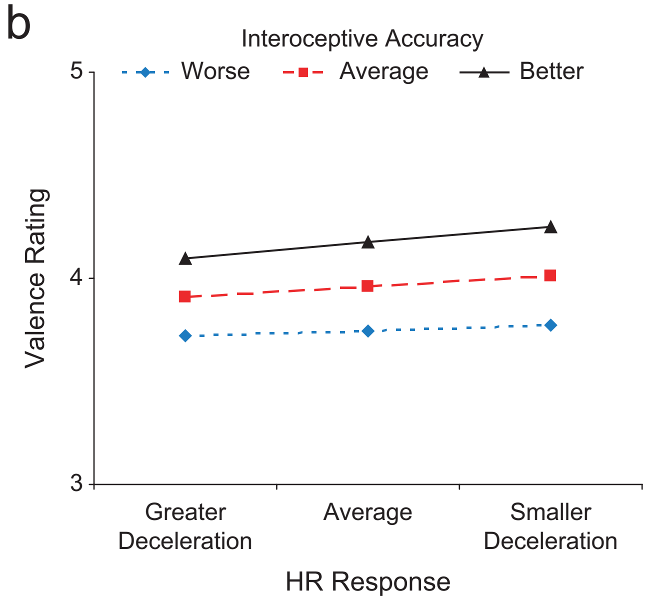


Fig. 1. Participants' ratings of felt (a) arousal and (b) valence as a function of heart rate (HR) responses to emotional images in Study 1. The lines represent the regression equations for different levels of interoceptive accuracy (better than average: 1 *SD* above the mean; worse than average: 1 *SD* below the mean).

linked to attentional orienting and a greater subsequent HR acceleration related to action preparation (see Section S2 in the Supplemental Material).

These results offer strong support for Jamesian bodily feedback theories (e.g., James, 1884), but particularly later hybrid accounts focusing on arousal experience (Schachter & Singer, 1961). To understand other, potentially more nuanced, aspects of emotion experience (e.g., valence and differentiating between basic emotion states), it may be necessary to model how individuals integrate awareness of a range of different emotion components, including affect, appraisal, and action tendency, in addition to arousal (cf. Frijda, 2009). Study 2 examined whether a similar moderating role of interoception can also account for individual differences in intuitive decision making.

Study 2

Many life domains prove challenging to navigate using cold logic alone. In many rapidly shifting social, personal, and professional situations, the complexity, uncertainty, or unavailability of the requisite information precludes extensive systematic deliberation of available response options before important choices are made. In such circumstances, key decisions are strongly shaped by intuition—automatic, emotional judgments about whether the contemplated response is a good or a bad option (Kahneman, 2003). People's ability to make effective intuitive decisions varies considerably. Consequently, intuition either can be a powerful ally, complementing logical analysis to facilitate adaptive choices, or can lead to costly and dangerous mistakes (Myers, 2002). Understanding what drives such variability in intuition is therefore important in clarifying how key decisions are made.

Accounts such as the SMH argue that intuition is partly shaped by emotional signals arising in the body (Damasio, 1994), and this bodily feedback therefore represents a potentially powerful way to account for individual differences in intuitive ability. This was the focus of Study 2. We predicted that when bodily signals offer good guidance about potential choices (i.e., favoring advantageous options), increasing interoceptive accuracy should be associated with superior intuitive decision making. However, where markers offer poor guidance (favoring disadvantageous options), then better interoceptive accuracy should actually be associated with poorer intuitive decisions. In other words, the ability to perceive the body accurately can be a mixed blessing, depending on the utility of the signals it has generated.

Method

Participants. Ninety-two participants (62 female, 30 male; mean age = 40 years, *SD* = 17 years) were recruited into Study 2 from the MRC CBSU panel, using the same exclusion criteria as in Study 1. Their mean NART estimated full-scale IQ was 117 (*SD* = 10).

Intuitive reasoning task. Participants completed a novel computerized paradigm to measure intuitive decision making (the intuitive reasoning task, IRT; see Fig 2). This task evolved out of the influential Iowa gambling task (e.g., Bechara, Damasio, Damasio, & Anderson, 1994; Bechara, Tranel, Damasio, & Damasio, 1996). To succeed on the IRT, participants had to learn—over the course of 100 trials—to choose from two profitable decks of cards and avoid two unprofitable decks of cards. Intuitive ability was defined as the degree to which participants learned this optimal behavioral strategy following the completion of all IRT trials (total profitable deck selections

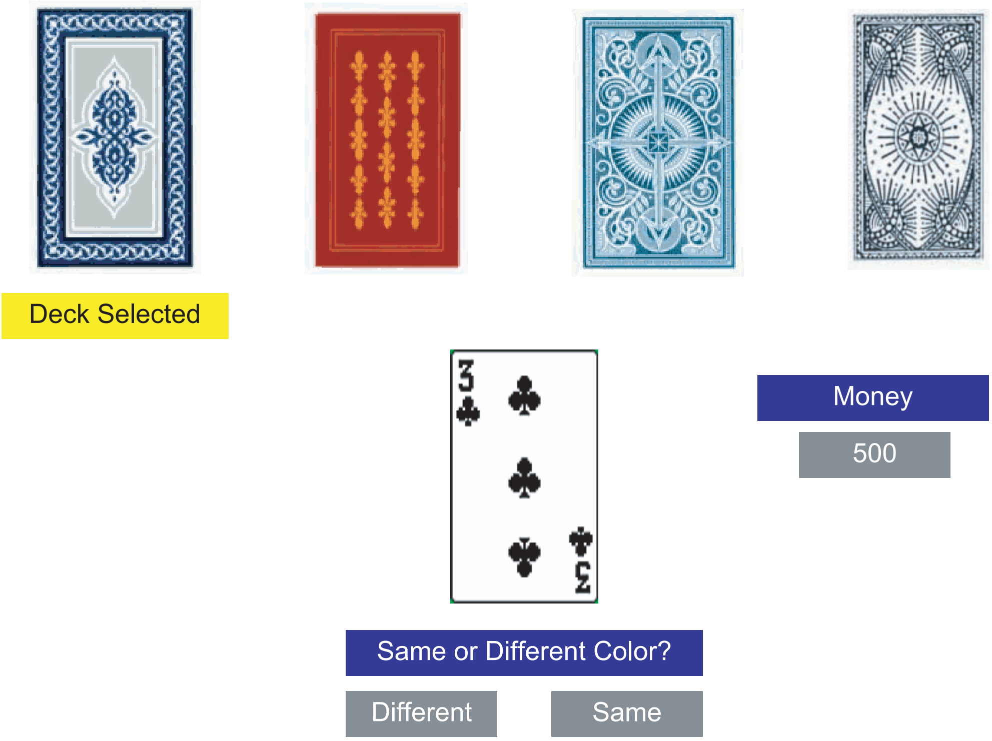


Fig. 2. Intuitive reasoning task used in Study 2. On each trial, participants chose one of four decks (top row) and then guessed if their card would be the same color as the upturned card (bottom row) or would be a different color. Increases and decreases in money won provided feedback as to whether or not guesses were correct.

minus unprofitable deck selections), with possible scores ranging from +100 (selecting entirely from profitable decks) to −100 (selecting entirely from unprofitable decks).

Figure 2 shows a typical experimental trial. On each trial, participants contemplated (for 3 s) from which of four decks they wanted to pick a card, before buttons appearing under each deck enabled them to make their choice. An upturned card was displayed in the center of the screen, and participants then guessed if the card from their chosen deck would be the same color as that central card or a different color. Feedback (3 s) about their guess was then provided: If the guess was correct, money increased, and a melodic flourish was played; if the guess was incorrect, money decreased, and a buzzer sound was played.

Unbeknownst to participants, the outcomes of each deck (A, B, C, and D) were predetermined by the computer (see Table 2 for the reinforcement schedule). Decks A and B classified participants' guesses as correct on 6 out of 10 trials, so choosing these decks led to making a profit over time. Decks C and D classified choices as correct on only 4 out of 10 trials, so choosing these decks led to a net loss over time. Decks A and C offered small-magnitude wins and losses, and Decks B and D offered large-magnitude wins and losses. However, there was no advantage in selecting more from the small-magnitude deck than from the large-magnitude deck, or vice versa. Each trial was followed by a 3-s intertrial interval.

The IRT was changed in a number of ways from the Iowa paradigm, based on our previous review (Dunn et al., 2006). First, the reinforcement schedule was altered so that the contributions of magnitude and profitability could be distinguished in a 2 × 2 design and to ensure that task acquisition did not require reversal learning. Second, the position and card back of each deck were systematically counterbalanced to control for biasing effects, and participants could select from each deck as many times as they wished to avoid exhaustion effects. Third, to increase ecological validity, we designed the task to be as much like a real-world card game as possible, and

Table 2. Reinforcement Schedule Used in the Intuitive Reasoning Task in Study 2

Deck	Magnitude of reinforcement (in pence)	Win frequency (%)	Net profit per 10 trials (in pence)
A	80–125	60	+200
B	105–180	60	+200
C	80–125	40	−200
D	105–180	40	−200

an additional financial reward of up to £5 (approximately \$7) was given to participants, based on how many points they had won by the end of the game. Fourth, by asking participants both to pick a deck and subsequently to guess the color of the card to be revealed, it was possible to isolate the physiological activity in anticipation of making a decision from the physiological activity in anticipation of receiving feedback following a decision (for a copy of the IRT instructions and the full reinforcement schedule, see Section S3 in the Supplemental Material).

To check that the reinforcement schedule on the IRT was largely hidden from participants' conscious awareness, we conducted a validation study (see Fig. 3 and Table 3). Twenty-eight participants (16 female, 12 male; mean age = 36 years, SD = 15 years; mean NART estimated full-scale IQ = 111, SD = 9) completed the IRT, and after each block of 20 trials answered questions indexing the extent of their hunch and conceptual understanding of the reinforcement schedule (cf. Maia & McClelland, 2004). Participants showed intuitive learning over the five blocks of trials, selecting more from the profitable than from the unprofitable decks, $F(1, 27) = 13.87$, $p < .01$. This preference increased over time, $F(4, 108) = 2.52$, $p < .05$; linear contrast, $F(1, 27) = 9.23$, $p < .01$, and from Block 3 onward, participants selected significantly more from profitable than from unprofitable decks, $t(27)$s > 2.20, ps < .05. Participants showed partial hunch insight in the first, fourth, and fifth blocks. Partial conceptual insight emerged only in the fifth block. In summary, participants reported minimal conscious understanding of the reinforcement schedule even at the end of the task and after intuitive learning was acquired from the third block onward. These findings indicate that the IRT learning we observed in Study 2 likely relied on intuitive reasoning (see Section S4 in the Supplemental Material for copies of the insight questions, methods, and analyses of insight data).

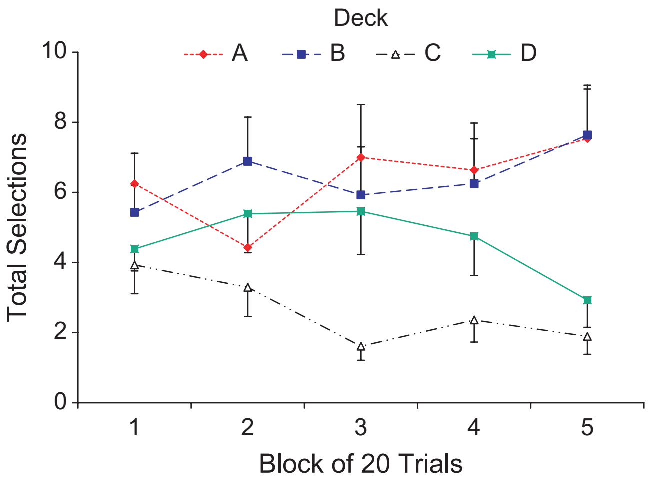


Fig. 3. Behavioral performance in the validation study of the reinforcement schedule used in the intuitive reasoning task. The number of selections from each card deck is plotted as a function of trial block. A = small-magnitude, profitable deck; B = large-magnitude, profitable deck; C = small-magnitude, unprofitable deck; D = large-magnitude, unprofitable deck. Error bars represent 1 *SEM*.

Table 3. Results of the Validation Study for the Reinforcement Schedule Used in the Intuitive Reasoning Task

	Block number				
Insight criterion	1	2	3	4	5
Hunch insight					
Chosen deck	.75*	.68†	.68†	.75*	.71*
Rated deck	.61	.43	.61	.61	.64
Conceptual insight					
Estimated net profit	.54	.39	.61	.50	.68†
Calculated net profit	.57	.54	.57	.64	.79*

Note: The table shows the proportion of participants meeting each insight criterion. Whether or not each proportion was significantly greater than chance (.05) levels was examined using binomial tests.
†$p < .10$. *$p < .05$.

Anticipatory bodily changes (somatic markers) associated with decision making on the IRT were measured by recording HR and electrodermal activity (EDA; in microsiemens) prior to each decision trial.[3] HR changes were computed by subtracting the mean activity in the 1-s baseline prior to the start of each trial from the mean activity in the period of time when participants were selecting a deck (of variable length but at least 3 s long). EDA was recorded using two grounded Ag-AgCl electrodes (TSD203 transducer, BIOPAC Systems, Inc., Camino Goleta, CA) secured ventrally on the distal index and middle finger of the nondominant hand, with BIOPAC EDA paste (with a sodium chloride concentration of 0.05M) as the electrolyte. As we had clear directional hypotheses about an increase in EDA, we subtracted mean baseline activity from maximum activity in the anticipation period. Median EDA and HR responses to each deck type were computed, with EDA responses undergoing natural log transformation prior to analysis. The interoception task, as described in Study 1, was completed after the IRT.

Results

Analysis of behavioral data from the IRT using a repeated measures ANOVA found that the participants developed good intuitive ability (see Fig. 4a), selecting more from the profitable than from the unprofitable decks, $F(1, 91) = 36.77$, $p < .001$, $\eta_p^2 = .29$. There was no significant difference in participants' preference for high-magnitude decks versus low-magnitude decks, $F < 1$. There was clear individual variation in intuitive ability ($M = 25.74$, $SD = 40.71$), with 27% of participants showing a preference for unfavorable decks (intuitive ability < 0). Analysis entering blocks of 20 trials as an additional within-subjects factor found a significant time-by-profitability interaction, $F(4, 364) = 4.22$, $p < .01$, $\eta_p^2 = .04$; linear contrast, $F(1, 91) = 10.57$, $p < .01$, $\eta_p^2 = .10$, indicating that participants' preference for the profitable decks strengthened over time.

Next, we examined anticipatory bodily responses. As expected, bodily responses differentiated between profitable

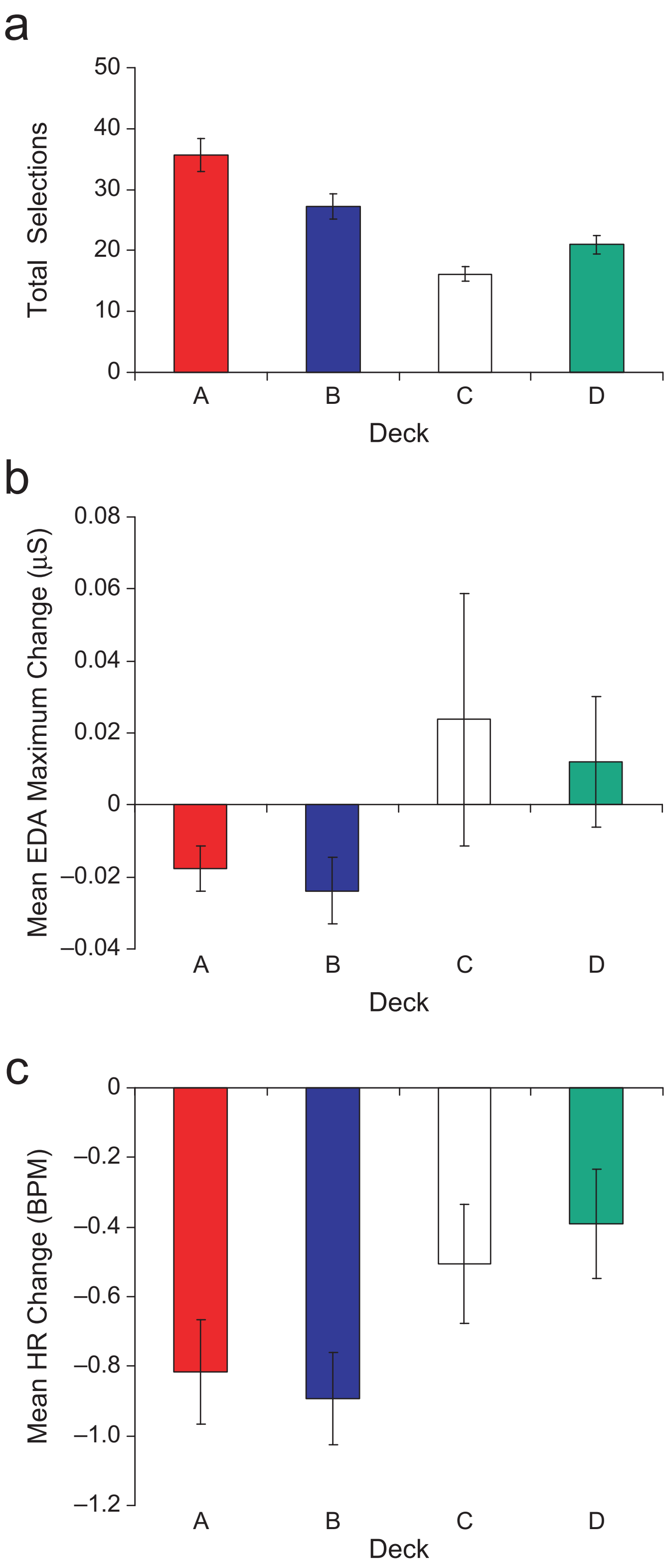


Fig. 4. Behavioral performance and the acquisition of anticipatory bodily responses on the intuitive reasoning task in Study 2, as a function of card deck: (a) total number of participant selections from each card deck; (b) mean anticipatory electrodermal (EDA) maximum change; and (c) mean anticipatory heart rate (HR) change (in beats per minute, BPM). A = small-magnitude, profitable deck; B = large-magnitude, profitable deck; C = small-magnitude, unprofitable deck; D = large-magnitude, unprofitable deck. Error bars represent 1 *SEM*.

and unprofitable deck choices. Participants showed a strong trend toward a significantly greater anticipatory EDA maximum response, $F(1, 91) = 3.89$, $p = .05$, $\eta_p^2 = .04$, and a significantly less marked anticipatory mean HR deceleration (excluding 9 outliers), $F(1, 82) = 8.92$, $p < .01$, $\eta_p^2 = .10$, for selections from unprofitable decks, relative to profitable decks (Figs. 4b and 4c). There were no significant HR or EDA differences between high- and low-magnitude decks, nor were there magnitude-by-profitability interactions, *F*s < 1. Given that bodily responses were unrelated to magnitude, in subsequent analyses we focused on comparisons between profitable and unprofitable decks.

According to the SMH, a wide array of bodily signals are centrally integrated into an overall pattern image that marks outcomes as “good” or “bad” (see Dunn et al., 2006, p. 264). This is also consistent with neural models of interoception, which propose that a spinal-thalamo-cortical pathway provides integrated bodily feedback (Craig, 2002). Therefore to assess whether IRT intuitive ability was related to anticipatory bodily responses, we computed a composite index of bodily differentiation. Mean anticipatory EDA and HR responses to unprofitable minus profitable decks were computed, *Z*-transformed, and averaged. The more positive this index, the more bodily responses favored profitable decks. Results were consistent with the SMH (Damasio, 1994), as this measure was correlated significantly and positively with IRT intuitive ability, $r = .41$, $p < .001$ (excluding 3 outliers).

Interoceptive accuracy was not significantly related to IRT intuitive ability, $r = .08$, $p = .46$, nor to bodily differentiation, $r = .07$, $p = .56$. As in Study 1, we examined the key moderating role of interoception using hierarchical regression analyses (Baron & Kenny, 1986). This time, intuitive ability was the dependent variable, and standardized interoceptive accuracy, composite bodily differentiation, and their product term were the independent variables. Indicating a moderation effect of interoception, the addition of the interaction term at the second step led to a significant increase in the variance in intuitive ability accounted for, $\Delta F(1, 76) = 8.18$, $p < .01$, $R^2 = .25$, $\Delta R^2 = .08$.

Again, we deconstructed this moderation effect by recalculating the full regression equation for values 1 standard deviation above and 1 standard deviation below the interoception mean (Aiken & West, 1991). Using the original and revised equations, we predicted intuitive ability at mean (0 *SD*), more favorable (+1 *SD*), and less favorable (−1 *SD*) levels of bodily differentiation for mean (0 *SD*), better (+1 *SD*), and worse (−1 *SD*) levels of interoceptive accuracy (Fig. 5). A more favorable value indicated a greater-than-typical EDA and HR response to unprofitable, relative to profitable, decks. A less favorable value indicated a smaller-than-typical EDA and HR responses to unprofitable, relative to profitable, decks. We found that bodily responses influenced intuitive ability more strongly as interoception ability increased. Moreover, when differential bodily responses favored adaptive choices, more accurate interoception was associated with better intuitive

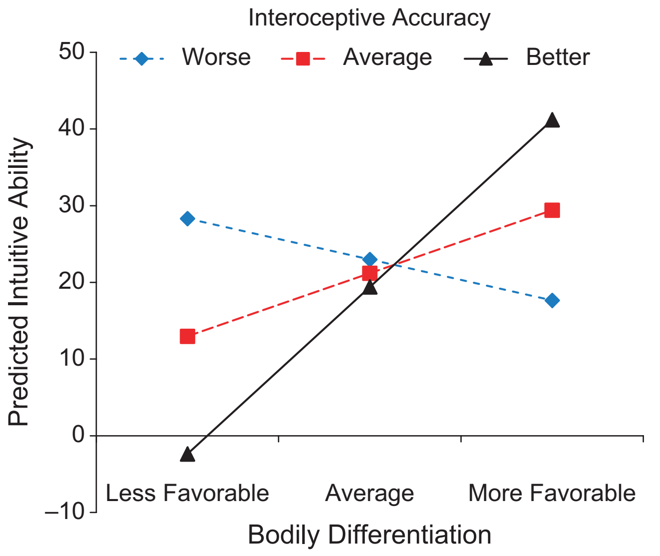


Fig. 5. Participants' predicted intuitive ability as a function of different degrees of bodily differentiation in the intuitive reasoning task in Study 2. Intuitive ability was calculated as the total number of profitable-deck selections minus the total number of unprofitable-deck selections. Bodily differentiation is standardized bodily response to unprofitable decks minus standardized bodily response to profitable decks. The lines represent the regression equations for different levels of interoceptive accuracy (better than average interoception: 1 *SD* above the mean; worse than average interoception: 1 *SD* below the mean).

decision making. In contrast, superior interoception actually hindered successful intuitive learning when somatic markers favored maladaptive choices.

This result again held when controlling for potential confounds relevant to the Schandry task, when treating interoception as a dichotomous variable, when repeating analyses using rank-transformed data to control for outlier effects, and when analyzing EDA and HR data separately, *ps* < .05. Thus, the interaction effect was robust (see Section S5 of the Supplemental Material).

Discussion

To our knowledge, the results we present in this article are the first demonstration that the interplay between individual differences in the generation of somatic marker signals and the ability to perceive subtle bodily changes of this nature (interoception) can account for significant variability in human intuition. Consequently, accurate perception of bodily information can help or hinder adaptive decision making depending on whether the anticipatory bodily signals generated favor advantageous or disadvantageous choices. This reflects the mixed blessing that intuition confers (Myers, 2002) and adds to earlier research exploring a simple relationship between interoception accuracy and decision making (Werner et al., 2009). Our findings agree with those of other studies showing that an absence of emotion following frontal head injury can in some circumstances lead to superior decision making (Shiv, Loewenstein, Bechara, Damasio, & Damasio, 2005), and with claims that elevated interoceptive awareness may maintain conditions such as anxiety (Ehlers & Breuer, 1992).

General Discussion

In the studies presented in this article, we have shown that interoceptive accuracy moderates the extent to which bodily responses are related to emotion experience and intuitive decision making. These moderation effects offer proof-of-principle support for controversial bodily feedback theories (Damasio, 1994; James, 1884). A key criticism of these frameworks is that cognitive-affective processing may be taking place via upstream mechanisms (e.g., reversal learning; see Dunn et al., 2006) and that the associated bodily responses are mere epiphenomena. If cognitive-affective processes unidirectionally shape bodily responses (as suggested by such critiques), then interoceptive accuracy should have no impact on the extent of the association found between bodily responses and how people think and feel. Consequently, the present moderation data are most parsimoniously accounted for by frameworks suggesting that bodily responses also influence aspects of emotion experience and decision making (rather than simply that emotion experience and decision making shape bodily responses).

It is important to note that in neither study was all of the variance in the outcome measures accounted for by our bodily feedback variables alone. Individuals with relatively poor interoception were nevertheless able to rate arousal, and some of these participants also made effective intuitive choices. This suggests that, although bodily feedback influences cognitive-affective processes, it may not be essential. Of course, it remains possible that these individuals used aspects of bodily feedback not measured here (e.g., somatosensory responses). However, it seems likely that there are marked individual differences in the extent to which cognitive-affective processes are embodied and that individuals with relatively poor interoceptive awareness make more use of alternative, nonbodily, mechanisms.

The individual differences approach we have adopted in our studies can in ongoing work help to reconcile a long-running controversy surrounding bodily feedback theories, suggesting that the debate should move away from evaluating whether or not cognitive-affective processes are embodied, and instead focus on when, to what extent, and for whom different mental processes are influenced by bodily feedback versus other information-processing mechanisms. This research is consistent with the idea that multiple systems support decision making and emotion experience, that none of these systems has overall primacy, and that these systems are active to varying degrees between individuals and across situations (e.g., Frijda, 2007; Knutson & Bossaerts, 2007; Laird, 2007).

Even clearer effects of bodily feedback processes may emerge when the interaction between a wider range of peripheral measures (e.g., Rainville, Bechara, Naqvi, & Damasio, 2006) is considered and, if possible, a model is developed to account for how hemispheric specialization in interoceptive awareness may relate to positive and negative affect (Craig, 2009). In summary, our findings demonstrate that emotion experience and intuition are associated with individual differences in the ability both to generate and to perceive accurately subtle changes in the body, consistent with the thesis that how one thinks and feels sometimes genuinely involves following one's heart. Knowing when to trust and when to discount such "gut feelings" may relate to the extent to which individuals regulate their emotions and make optimal choices at crucial junctures in life.

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The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

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Supplemental Material

Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

Notes

1. Two parallel image sets were developed, to ensure that effects were not specific to particular stimulus materials. Twenty-nine participants viewed each image set. Exploratory analysis found no effects of image set, so this was not included as a factor in subsequent analyses. The images are available from the corresponding author.
2. HR values more than 3 standard deviations from the mean were excluded as univariate outliers. In the psychophysiology analyses, multivariate outliers were identified and excluded on the basis of Mahalanobis distance (greater than the critical chi-square value at $p < .001$; Tabachnik & Fidell, 2001), and multivariate output was reported to minimize the effects of sphericity confounds (Vasey & Thayer, 1987).
3. We conceptualize EDA as reflecting somatic marker activity, consistent with previous work on the Iowa gambling task (e.g., Bechara et al., 1996). The source of feedback from EDA to the brain is currently unclear, however, and requires further specification.

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