

BRIEF REPORT

Interoceptive ability predicts aversion to losses

Peter Sokol-Hessner^{1†}, Catherine A. Hartley^{1†}, Jeffrey R. Hamilton¹, and Elizabeth A. Phelps^{1,2,3}

¹Department of Psychology, New York University, New York, NY, USA

²Center for Neural Science, New York University, New York, NY, USA

³Nathan Kline Institute, Orangeburg, NY, USA

Emotions have been proposed to inform risky decision-making through the influence of affective physiological responses on subjective value. The ability to perceive internal body states, or “interoception” may influence this relationship. Here, we examined whether interoception predicts participants’ degree of loss aversion, which has been previously linked to choice-related arousal responses. Participants performed both a heartbeat-detection task indexing interoception and a risky monetary decision-making task, from which loss aversion, risk attitudes and choice consistency were parametrically measured. Interoceptive ability correlated selectively with loss aversion and was unrelated to the other value parameters. This finding suggests that specific and separable component processes underlying valuation are shaped not only by our physiological responses, as shown in previous findings, but also by our interoceptive access to such signals.

Keywords: Emotion; Decision-making; Interoception; Loss aversion.

Individuals vary widely not only in their physiological reactions to emotional situations, but also in the extent to which they perceive those responses. Several prominent psychological theories have proposed that the perception of one’s own physiological emotional responses plays a central role in shaping subjective emotional experience, as well as

cognitive and behavioural reactions to external events (e.g., Damasio, 1994; Izard, 2007; Lange & James, 1922; Schachter & Singer, 1962). Consistent with these theories, individuals who show heightened “interoception”, or perception of internal physiological states, report greater subjective intensity of emotional feelings (Barrett,

Correspondence should be addressed to: Elizabeth A. Phelps, Department of Psychology and Center for Neural Science, New York University, Mailing: 6 Washington Place, New York, NY 10003, USA. Email: liz.phelps@nyu.edu

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[†]These authors contributed equally to this work.

Quigley, Bliss-Moreau, & Aronson, 2004; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Wiens, Mezzacappa, & Katkin, 2000; Zaki, Davis, & Ochsner, 2012). Heightened interoception is also proposed to play a mechanistic role in anxiety (Paulus & Stein, 2006) and addictive disorders (Koob & Volkow, 2010; Naqvi & Bechara, 2010), in which the highly intense subjective experience of physiological states of fear or craving powerfully influences behaviour. Collectively, this work suggests that interoception may critically contribute to subjective emotional experience by increasing the subjective strength of bodily responses. In this manner interoception may also influence a wide range of everyday cognitive and affective evaluations that incorporate perceived physiological information.

A growing body of work has related the physiological arousal response, a component of emotion (Scherer, 2005), to differences in risky decision-making (Bechara, Damasio, Tranel, & Damasio, 1997; Lo & Repin, 2002; van't Wout, Kahn, Sanfey, & Aleman, 2006). A recent study examining this relationship more specifically found that physiological arousal selectively predicted individual differences in "loss aversion", or the overweighting of losses relative to equal gains during risky decision-making (Sokol-Hessner et al., 2009). Participants showing greater physiological arousal responses to loss versus win outcomes also exhibited greater aversion to loss behaviourally in their choices. This finding suggests that the physiological response to loss events specifically informs the computations contributing to loss aversion (and not, for example, risk attitudes). Consistent with the notion that heightened interoception might potentiate perceived physiological responses to loss, we hypothesised that these heightened subjective responses might in turn give rise to increased loss averse behaviour. In the present study, we take an initial step towards testing this hypothesis by assessing whether individual differences in interoception selectively predict loss aversion in a risky monetary decision-making task.

METHODS

In accordance with journal policy, we certify that we report below how we determined our sample size, all data exclusions, all manipulations and all measures in the study.

Participants

We sought a final sample size of roughly 25 assuming that a possible relationship between loss aversion and interoception might be similar to that observed with physiological responses in a previous study (Sokol-Hessner et al., 2009). To attain this approximate number, 37 adults recruited from the general population gave informed consent and completed both a heartbeat-detection (HD) task and a monetary decision-making task (see details below). Participants in the HD task were asked to judge whether a set of tones triggered by their actual heartbeats were in or out of sync with their heartbeats. Ten participants were excluded from analysis because on more than 20% of out-of-sync trials, the intervals between their heartbeats were momentarily too brief to allow presentation of tones at the necessary delay of 500 ms [a proportion of participants not significantly different (chi-square with 1 degree of freedom, $p > .05$) from that reported in an exceptionally large study; Wiens & Palmer, 2001]. This short interbeat interval caused the computer to skip heartbeats during tone presentation, creating a potential source of bias in participants' judgments. Of the 27 participants remaining, 5 participants were also excluded because they exhibited more misses and false alarms than hits and correct rejections on the heartbeat-detection task, resulting in negative d' estimates (see details below). The remaining 22 participants (14 female; age 18–36, $M = 24.7$) were included in the analyses presented here. Participants received \$15 for participation. They were endowed with \$30 prior to the decision-making task and paid the actual outcomes of 18 randomly selected trials (10% of all trials).

Heartbeat-detection task

Interoception was measured with a commonly used signal-detection task in which participants indicated on each trial whether a sequence of 10 tones (800Hz, 100-ms square wave tones; Audacity software; Apple, Cupertino, CA) were perceived as in or out of sync with their heartbeat (Critchley et al., 2004; Eichler & Katkin, 1994; Katkin, Wiens, & Öhman, 2001; Khalsa et al., 2008; Schneider, Ring, & Katkin, 1998; Wiens & Palmer, 2001; Wiens et al., 2000). Participants' heartbeats were recorded from chest electrodes using AcqKnowledge software (Biopac Systems, Goleta, CA). The software detected the R-wave, indicating the peak of ventricular depolarization and triggered tone presentations at delays of 200 ms or 500 ms (delay was constant within-trial). Tones at a 200 ms delay are typically perceived as in sync with the heartbeat, whereas a 500 ms delay is perceived as out of sync (Wiens et al., 2000). Participants were instructed to attend to their heartbeats without manually feeling for their pulse. Labelled practice trials (two synchronous and two asynchronous) were completed first, followed by 25 trials of each type in the actual task. Interoception was indexed by the difference between participants' normalised hit rate and normalised false alarm rate ($z(\text{Hits}) - z(\text{False Alarms})$), yielding a d' -prime (d') signal-detection performance measure. Five participants had negative d' values, all between -1 and 0 . Though it is possible their response pattern may have resulted from poor ability to perform the task, the negative values also raised the possibility that they did not understand the task and/or the button mappings. Because of the inherent difficulty in interpreting these negative d' values, we therefore excluded those participants from subsequent analyses unless otherwise indicated.

Choice task

We measured participants' choice behaviour in a risky monetary decision-making task (Sokol-Hessner, Camerer, & Phelps, 2013; Sokol-Hessner et al., 2009). After endowment (see above),

participants were thoroughly instructed, quizzed and practiced on the task before beginning, as in prior studies (Sokol-Hessner et al., 2009, 2013).

Each decision (2-s view window, followed by a 2s-or-less response window) was followed 1 s later by its outcome (1 s), before the next trial began 1–3 s later. Choices were made in 5 blocks of 36 trials, separated by 45 s breaks during which participants rated their feelings in the previous block using analog scales.

Participants made 180 choices between a risky gamble (two options, each with probability of .5) and a guaranteed alternative. 150 choices were between a mixed valence gamble (positive and negative possible outcomes) and \$0 guaranteed, and 30 choices were between gain-only gambles (positive and zero possible outcomes) and a smaller positive guaranteed alternative. For the exact monetary amounts, see Table S1 and Figure S1. Monetary amounts were selected to enable separate individual estimates of loss aversion (λ), risk attitudes (ρ) and consistency over choices (μ) using a standard maximum likelihood estimation procedure in MATLAB v7.14 (MathWorks, Natick, MA). The details of estimation, including utility, softmax and likelihood functions were identical to that used in prior work (Sokol-Hessner et al., 2009, 2013).

RESULTS

Participants varied in interoceptive ability (d' : range: $0-2.9$; $M = 0.83$, $SE = 0.16$). Because d' estimates were non-normally distributed (Shapiro-Wilk test, $W = .85$, $p = .004$), we performed a square-root transform (as the log of a d' of 0 would be infinite), resulting in a normalised distribution of d' ($W = .97$, $p = .60$) with no outliers (all points within two standard deviations; mean $\text{sqrt}(d') = 0.79$, corresponding to $d' = 0.63$). Estimates of loss aversion (λ ; $M = 1.38$, $SE = 0.21$), risk attitudes (ρ ; $M = 0.91$, $SE = 0.07$), and consistency over choices (μ ; $M = 2.51$, $SE = 0.76$) were consistent with previous observations (Sokol-Hessner et al., 2009, 2013). Because loss aversion coefficients (λ) are generally positively skewed, a log transformation

produces a more normally distributed value ($\log(\lambda)$ $M = 0.11$, $SE = 0.14$); corresponding to $\lambda = 1.12$). Only risk attitudes (ρ) and consistency (μ) were marginally correlated with each other, $r(20) = -.41$, $p = .06$ (all other p s $> .49$), however, this finding should be interpreted cautiously as μ is non-normally distributed and no correlations were observed in previous studies (Sokol-Hessner et al., 2009, 2013).

To examine the connection between interoception and decision-making, we correlated individuals' d' values with their loss aversion, risk attitudes and choice consistency. Interoception correlated only with loss aversion ($\log(\lambda)$ and $\text{sqrt}(d')$; $r(20) = .57$, $p = .006$; see Figure 1) and not with risk attitudes (ρ and $\text{sqrt}(d')$; $r(20) = -.36$, $p = .10$) or choice consistency (μ and $\text{sqrt}(d')$; $r(20) = .17$, $p = .44$). Using Fisher's r -to- z transformation, we tested the correlations against one another, and found the correlation with loss aversion was significantly greater than that with risk attitudes ($z = 3.16$ $p = .002$), though it was not significantly different from that with choice consistency ($z = 1.47$ $p = .14$). The correlations with risk attitudes and with consistency were marginally different ($z = 1.69$, $p = .09$).

The same pattern of selective correlation between loss aversion and interoception holds when we include the five participants excluded based on negative d' values (median behavioural

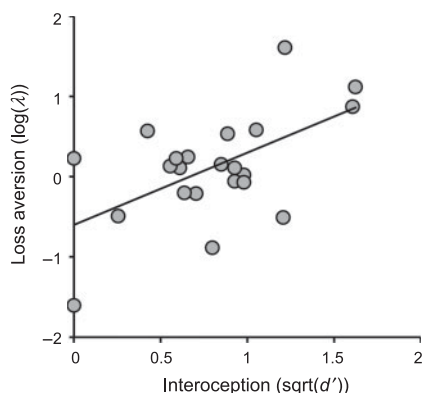


Figure 1. Individuals' interoceptive sensitivity (d') in a heart-beat-detection task was correlated with their loss aversion in a risky monetary choice task ($r(20) = .57$, $p = .006$).

parameters of $\lambda = 1.90$, $\rho = 0.88$ and $\mu = 0.44$). Though we believe their inclusion to be problematic due to the inherent difficulties in interpreting and analyzing negative d' values, we replicated the above analyses using the absolute value of d' (which would reflect participants' interoceptive ability if, for example, they had failed to note the correct response keys). In analyzing all 27 participants, we find that $\text{sqrt}(|d'|)$ is significantly correlated with $\log(\lambda)$ ($r(25) = .37$, $p = .05$), but not with ρ ($r(25) = -.20$, $p = .31$) or μ ($r(25) = .16$, $p = .43$), and that the correlation of $\text{sqrt}(|d'|)$ with $\log(\lambda)$ is significantly greater than that with ρ (Fisher's r -to- z , $z = 2.08$, $p = .04$), though not with μ ($z = 0.80$, $p = .42$). There was no significant difference between the correlations with ρ and with μ ($z = 1.27$, $p = .20$). Despite replicating the effects observed in participants with positive d' values, we consider the initial analyses that exclude negative d' participants to be conservative in that we only include participants demonstrating successful performance of the tasks at a clear and objective level.

DISCUSSION

Here, we show that interoceptive sensitivity to physiological signals selectively predicts aversion to loss in one's choices but is unrelated to risk attitudes and choice consistency. Individuals who are better able to perceive their bodily states are also most loss averse. This result complements a previous finding that greater physiological responses to losses compared to gains also predicts loss aversion (Sokol-Hessner et al., 2009), as well as extensive evidence that interoception leads to more intense emotional experiences (Barrett et al., 2004; Critchley et al., 2004; Wiens et al., 2000; Zaki et al., 2012). Our finding, in the context of this body of research, suggests that heightened interoception may magnify the relative weight placed on losses during decision-making by increasing the subjective intensity of choice-relevant emotional signals.

While previous studies have suggested a general relationship between interoception and decision-making under risk (Dunn et al., 2010; Werner,

Jung, Duschek, & Schandry, 2009), we extend these findings by identifying a specific choice process affected by interoception. This specificity is achieved through the use of a quantitative model of monetary decision-making from behavioural economics that enables the precise resolution of distinct component processes underlying an individual's evaluation of risky choices. In teasing apart these separable components of risky decision-making, we have revealed that interoception is related to the relative weighting of gains and losses but not to attitudes towards risk. We note that while these two processes can have similar apparent effects on choices, their mechanisms are very different. Heightened risk aversion causes one to accept fewer gambles because the value of the larger, risky option is discounted—losses and gains are treated no differently. While loss aversion also results in fewer gambles being accepted, this stems instead from the greater weight placed on potential losses relative to gains. Without a properly designed task and model, risk and loss aversion can be behaviourally conflated since their effects on choice are coarsely similar—fewer gambles are accepted. Only by separately quantifying the processes underlying valuation in this monetary decision-making task were we able to identify the specific relationship between interoceptive ability and aversion to loss.

Our study did not directly assess the role of physiological responses in this association between interoception and choice behaviour. However, recent work has shown that larger physiological responses to losses versus gains predicts increased loss aversion, suggesting that individuals who experience losses more intensely avoid them more in their choices (Sokol-Hessner et al., 2009). Our present finding suggests that increased interoception may exert a similar influence upon choice by intensifying the subjective experience of such signals. In other words, there may be two mechanisms that can lead to the heightened subjective experience of loss that contributes to loss aversion: substantially larger physiological responses to losses versus gains or increased sensitivity to a differential response of average magnitude. As an analogy, one may subjectively experience a light as

very bright either because the light is in fact objectively intense or because one's eyes are very sensitive. Thus, physiological responses and increased interoception, through their similar effects on subjective experience, might both influence decision-making processes that incorporate perceived bodily information.

Although physiological reactivity and interoception could in theory be independent of one another, they might also interact in a number of possible ways. Some previous findings suggest that good interoceptors may have greater physiological responses (Eichler & Katkin, 1994), suggesting a possible feedback loop in which sensitivity to physiological responses subsequently leads to an amplification of the bodily signal itself, which is then perceived even more intensely. Alternatively, interoception and physiological responses may statistically interact (Dunn, Evans, Makarova, White, & Clark, 2012) such that responses drive behaviour only for good interoceptors who can accurately perceive those responses. Future research directly assessing the relationship between physiological responses, interoception and loss aversion may further refine our understanding of the interaction between these variables.

Beyond the limitations discussed above with respect to specifying the interplay between interoception, physiological responses and choice behaviour, our study is also limited by a relatively small sample size (22 or 27, depending on participant exclusion), and the inability of several participants to satisfactorily complete the interoception task (see Methods section). Nevertheless, the robustness of our results across analyses and their consistency with prior studies lend validity to the present findings and suggest that they might be replicated in future work.

The neural link between loss aversion and interoception may involve the anterior insula. The insula receives afferent viscerosensory input about the physiological state of the body (Craig, 2009) and is implicated in the interoceptive awareness of such bodily information (Critchley et al., 2004; Khalsa, Rudrauf, Feinstein, & Tranel, 2009). In addition, both lesion and functional neuroimaging data implicate the insula in the anticipation and

avoidance of loss (Palminteri et al., 2012; Samanez-Larkin, Hollon, Carstensen, & Knutson, 2008). These data suggest that the insula may play a critical role in connecting interoceptive information to value-related processes that shape choice. As further evidence, dysregulated insula activity is also proposed to contribute to the aetiology of anxiety (Paulus & Stein, 2006), consistent with reports that anxious individuals exhibit both increased interoceptive sensitivity (Critchley et al., 2004) and excessive avoidance of potentially negative situations (Hartley & Phelps, 2012). Our present finding links these symptoms of anxiety, suggesting that heightened interoception may mechanistically increase loss aversion and in turn motivate avoidance behaviour.

Contrary to the centuries-old conventional distinction between thoughts and feelings, contemporary theories view cognition and emotion as inextricably intertwined. Appraisal theories of emotion propose that emotional responses arise through cognitive evaluations of both salient external events and their resulting internal physiological responses (Schachter & Singer, 1962; Scherer, 2005; Smith & Kirby, 2009). Heterogeneity in such appraisal processes is proposed to give rise to individual variability in the subjective feelings and behavioural responses elicited by emotional events. The findings in the present study are compatible with this view, highlighting interoception as a specific appraisal process underlying the subjective evaluation of monetary options, and therefore the decisions we make. More broadly, the link observed in this study between interoception and loss aversion provides further evidence of a naturally integrated role for affective processes in decision-making, demonstrating that not only objective emotional signals, but also our subjective experiences of them, play specific and powerful roles in shaping our choices.

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Supplementary material

Supplementary material (Figure S1 and Table S1) is available via the ‘Supplementary’ tab on the article’s online page. (<http://dx.doi.org/10.1080/02699931.2014.925426>).

REFERENCES

- Barrett, L. F., Quigley, K. S., Bliss-Moreau, E., & Aronson, K. R. (2004). Interoceptive sensitivity and self-reports of emotional experience. *JPSP*, *87*, 684–697. doi:10.1037/0022-3514.87.5.684
- Bechara, A., Damasio, H., Tranel, D., & Damasio, A. R. (1997). Deciding advantageously before knowing the advantageous strategy. *Science*, *275*, 1293–1295. doi:10.1126/science.275.5304.1293
- Craig, A. D. B. (2009). How do you feel – now? The anterior insula and human awareness. *Nature Reviews Neuroscience*, *10*, 59–70. doi:10.1038/nrn2555
- Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, *7*, 189–195. doi:10.1038/nn1176
- Damasio, A. R. (1994). *Descartes’ error: Emotion, reason, and the human brain*. New York, NY: Grosset/ Putnam.
- Dunn, B., Evans, D., Makarova, D., White, J., & Clark, L. (2012). Gut feelings and the reaction to perceived inequity: The interplay between bodily responses, regulation, and perception shapes the rejection of unfair offers on the ultimatum game. *Cognitive, Affective, & Behavioral Neuroscience*, *12*, 419–429. doi:10.3758/s13415-012-0092-z
- Dunn, B., Galton, H., Morgan, R., Evans, D., Oliver, C., Meyer, M., ... Dalgleish, T. (2010). Listening to your heart: How interoception shapes emotion experience and intuitive decision making. *Psychological Science*, *21*, 1835–1844. doi:10.1177/0956797610389191
- Eichler, S., & Katkin, E. S. (1994). The relationship between cardiovascular reactivity and heartbeat detection. *Psychophysiology*, *31*, 229–234. doi:10.1111/j.1469-8986.1994.tb02211.x
- Hartley, C. A., & Phelps, E. A. (2012). Anxiety and decision-making. *Biological Psychiatry*, *72*, 113–118. doi:10.1016/j.biopsych.2011.12.027
- Izard, C. E. (2007). Basic emotions, natural kinds, emotion schemas, and a new paradigm. *Perspectives*

- on *Psychological Science*, 2, 260–280. doi:10.1111/j.1745-6916.2007.00044.x
- Katkin, E. S., Wiens, S., & Öhman, A. (2001). Nonconscious fear conditioning, visceral perception, and the development of gut feelings. *Psychological Science*, 12, 366–370. doi:10.1111/1467-9280.00368
- Khalsa, S. S., Rudrauf, D., Damasio, A. R., Davidson, R. J., Lutz, A., & Tranel, D. (2008). Interoceptive awareness in experienced meditators. *Psychophysiology*, 45, 671–677. doi:10.1111/j.1469-8986.2008.00666.x
- Khalsa, S. S., Rudrauf, D., Feinstein, J. S., & Tranel, D. (2009). The pathways of interoceptive awareness. *Nature Neuroscience*, 12, 1494–1496. doi:10.1038/nn.2411
- Koob, G. F., & Volkow, N. D. (2010). Neurocircuitry of addiction. *Neuropsychopharmacology*, 35, 217–238. doi:10.1038/npp.2009.110
- Lange, C. G., & James, W. (1922). *The emotions* (Vol. 4). Baltimore, MD: Williams & Wilkins.
- Lo, A. W., & Repin, D. V. (2002). The psychophysiology of real-time financial risk processing. *Journal of Cognitive Neuroscience*, 14, 323–339. doi:10.1162/089892902317361877
- Naqvi, N. H., & Bechara, A. (2010). The insula and drug addiction: An interoceptive view of pleasure, urges, and decision-making. *Brain Structure and Function*, 214, 435–450. doi:10.1007/s00429-010-0268-7
- Palminteri, S., Justo, D., Jauffret, C., Pavlicek, B., Dauta, A., Delmaire, C., ... Pessiglione, M. (2012). Critical roles for anterior insula and dorsal striatum in punishment-based avoidance learning. *Neuron*, 76, 998–1009. doi:10.1016/j.neuron.2012.10.017
- Paulus, M. P., & Stein, M. B. (2006). An insular view of anxiety. *Biological Psychiatry*, 60, 383–387. doi:10.1016/j.biopsych.2006.03.042
- Samanez-Larkin, G., Hollon, N., Carstensen, L., & Knutson, B. (2008). Individual differences in insular sensitivity during loss anticipation predict avoidance learning. *Psychological Science*, 19, 320–323. doi:10.1111/j.1467-9280.2008.02087.x
- Schachter, S., & Singer, J. E. (1962). Cognitive, social and physiological determinants of emotional state. *Psychological Review*, 69, 379–399. doi:10.1037/h0046234
- Scherer, K. R. (2005). What are emotions? And how can they be measured? *Social Science Information*, 44, 695–729. doi:10.1177/0539018405058216
- Schneider, T. R., Ring, C., & Katkin, E. S. (1998). A test of the validity of the method of constant stimuli as an index of heartbeat detection. *Psychophysiology*, 35, 86–89. doi:10.1111/1469-8986.3510086
- Smith, C. A., & Kirby, L. D. (2009). Putting appraisal in context: Toward a relational model of appraisal and emotion. *Cognition & Emotion*, 23, 1352–1372. doi:10.1080/02699930902860386
- Sokol-Hessner, P., Camerer, C. F., & Phelps, E. A. (2013). Emotion regulation reduces loss aversion and decreases amygdala responses to losses. *Social Cognitive and Affective Neuroscience*, 8, 341–350. doi:10.1093/scan/nss002
- Sokol-Hessner, P., Hsu, M., Curley, N. G., Delgado, M. R., Camerer, C. F., & Phelps, E. A. (2009). Thinking like a trader selectively reduces individuals' loss aversion. *PNAS*, 106, 5035–5040. doi:10.1073/pnas.0806761106
- van't Wout, M., Kahn, R., Sanfey, A. G., & Aleman, A. (2006). Affective state and decision-making in the ultimatum game. *Experimental Brain Research*, 169, 564–568. doi:10.1007/s00221-006-0346-5
- Werner, N., Jung, K., Duschek, S., & Schandry, R. (2009). Enhanced cardiac perception is associated with benefits in decision-making. *Psychophysiology*, 46, 1123–1129. doi:10.1111/j.1469-8986.2009.00855.x
- Wiens, S., Mezzacappa, E., & Katkin, E. (2000). Heartbeat detection and the experience of emotions. *Cognition & Emotion*, 14, 417–427. doi:10.1080/026999300378905
- Wiens, S., & Palmer, S. N. (2001). Quadratic trend analysis and heartbeat detection. *Biological Psychology*, 58, 159–175. doi:10.1016/S0301-0511(01)00110-7
- Zaki, J., Davis, J. I., & Ochsner, K. N. (2012). Overlapping activity in anterior insula during interoception and emotional experience. *NeuroImage*, 62, 493–499. doi:10.1016/j.neuroimage.2012.05.012

Supplementary Materials

Title: Interoceptive ability predicts aversion to losses

Authors: Sokol-Hessner, P., Hartley, C.A., Hamilton, J.R., Phelps, E.A.

Heartbeat detection task details

Electrodes were attached to participants' chests to record the electrocardiogram signal (ECG), and AcqKnowledge BIOPAC Systems (Biopac Systems, Goleta, CA) software detected R-waves, indicating the peak of ventricular depolarization. Participants were instructed to attend to their heartbeats without manually feeling for their pulse. On each trial, a tone (800 Hz, 100-ms square-wave tones generated using Audacity software; Apple, Cupertino, CA) was played at a delay of 200ms or 500ms after each of ten consecutive R-waves (delay was constant within-trial). Participants indicated whether the tones were in or out of sync with their heartbeats via a key press. A tone presented at a 200 ms delay is typically perceived as being in sync with the heartbeat, whereas it is perceived as out of sync at a delay of 500 ms (Wiens, Mezzacappa, & Katkin, 2000). In order to present delayed tones, participants' interbeat intervals must be 550ms or greater. Interbeat intervals (IBI) shorter than that cause the computer program to skip a tone presentation, creating an external source of information that might bias a participant's judgment. Thus, individuals whose IBI exceeded this level on more than 20% of out-of-sync trials were excluded from analysis. Excluded participants had an IBI shorter than the cutoff on an average of 17 trials (ranging from 9 to 24

trials), suggesting that elevated heart rates posed a technical obstacle to the presentation of out of sync trials for these individuals.

Participants completed four practice trials before beginning the task and were informed beforehand of each trial type (two synchronous, two asynchronous). The actual task consisted of 25 trials of each type. We estimated a heartbeat detection index (d') as a measure of interoceptive ability, computing the normalized difference between the number of times the participant correctly judged the in-sync tones to be synchronous with their heartbeats and the number of times they incorrectly judged out-of-sync tones to be synchronous with their heartbeat ($z\text{-scoreHITS} - z\text{-scoreFALSE ALARMS}$).

Monetary decision-making task details

After consent and endowment, the experimenter read instructions out loud with the participant. Participants then took a brief comprehension quiz and did 12 practice trials. Each decision (2s view, ≤ 2 s response window) was followed 1s later by its outcome (1s), before the next trial began 1-3s later. Choices were made in five blocks of 36 trials, separated by 45s breaks during which participants rated their feelings in the previous block using analog scales.

Behavioral estimation procedure

The estimation procedure was almost identical to that used in previous related studies (Sokol-Hessner, Camerer, & Phelps, 2012; Sokol-Hessner, Hsu, Curley

et al., 2009). Briefly, participants' utility functions over gains and losses was modeled with an exponential (Tversky & Kahneman, 1992). The utility functions were as follows:

$$u(x) = \begin{cases} x^\rho & \text{if } x \geq 0 \\ -\lambda \cdot (-x)^\rho & \text{if } x < 0 \end{cases} \quad (1)$$

The exponential function captures risk attitudes and diminishing sensitivity. Lower values of ρ indicate more diminishing sensitivity and therefore increasing risk aversion in the gain domain and risk seeking in the loss domain. Conversely, higher values of ρ indicate less risk aversion for gains, and less risk seeking for losses. A ρ of 1 indicates a linear value function, and therefore risk-neutrality and an absence of diminishing sensitivity.

The loss aversion coefficient (λ), represents the multiplicative weight on losses relative to gains. Higher values of λ indicate a greater weight on losses relative to gains. A λ of 1 means that participants weight gains and losses equally.

The probability of choosing the gamble instead of the guaranteed amount was given by the logit (softmax) function F :

$$F(p, x_1, x_2, c) = \left(1 + \exp \left\{ -\mu \left(U(p, x_1, x_2) - u(c) \right) \right\} \right)^{-1} \quad (2)$$

$$U(p, x_1, x_2) = p \cdot u(x_1) + p \cdot u(x_2) \quad (3)$$

where p is the probability of winning the gamble (always 0.5 in our study), x_1 and x_2 are the outcomes in the gamble, c is the value of the guaranteed alternative, and U is the expected utility of the gamble. The parameter μ in the logit function captures the consistency of participants' choices. Low (high) estimates of μ indicate less (more) consistency over choices.

Denoting the choice of the participant in trial i as y_i , where $y_i = 1$ if the participant chose the gamble, and 0 if the guaranteed alternative, we fit the data using maximum likelihood, with the log likelihood function:

$$\sum_{i=1}^{180} y_i \log(F(p, x_1, x_2, c)) + (1 - y_i) \log(1 - F(p, x_1, x_2, c)) \quad (4)$$

Estimation was performed in MATLAB v7.14 (Mathworks, Natick, MA) using the interior-point algorithm as implemented in the minimizing function `fmincon`.

Standard errors were calculated using the square root of the diagonal terms in the inverse of the Hessian matrix evaluated at the estimated parameter values. The Hessian matrix contains the second partial derivatives of the log likelihood function, and its inverse is a standard estimator for covariance of the parameter estimates. The square root of the diagonal variance terms yields the standard

error estimates. The intuition is that the Hessian is an indication of the relative steepness (flatness) of the likelihood surface near the parameter estimates, which thereby indicates more (less) precise parameter estimates.

Significance Tests

Likelihood ratio test (LRTs; Greene, 2003) were used on individual participants' data to assess overall model fit. The test compares the likelihood of the observed choices given the "full model" (least constrained, most parameters) against the reduced model (more constrained, fewer parameters). The likelihood ratio statistic, expressed in log, is $-2(\log(L(Q_0)) - \log(L(Q)))$, where L is the likelihood function evaluated at the vector of parameters Q . That statistic is asymptotically distributed as a Chi-squared distribution with k degrees of freedom, where k is the number of parameter restrictions on the model.

In assessing overall model fit, the comparison was between the full model and a null model in which ρ , λ , and μ were constrained to 0 (a random choice model) yielding three degrees of freedom.

Monetary Choice Amounts

For the exact monetary amounts, see Table S1. For the mixed-valence trials (choices between a gamble with a positive and a negative possible outcome, and a guaranteed amount of \$0), gain values were from the set {\$2, \$4, \$5, \$6, \$8, \$9, \$10, \$12}. Loss values were derived by multiplying each gain value by

factors from -2 to -1/4 in steps of 1/8. This yielded 120 mixed-valence gambles. Thirty (30) of those trials were repeated to enhance our ability to detect inconsistencies in decision-making (see Figure S1) yielding a total of 150 mixed-valence trials. The thirty gain-only trials consisted of choices between a gamble with positive and \$0 possible outcomes, and a positive guaranteed amount.

Supplemental analyses

Five participants with negative d' values were excluded from the final analysis. Their median behavioral parameter estimates were as follows: loss aversion (1.90), risk attitudes (0.88), and consistency over choices (0.44). A negative d' value suggests that a participant is able to detect their heartbeat to some degree (i.e. differentiate between in-sync and out-of-sync tone/heartbeat trials), but provides the opposite response than the one instructed (despite instruction and practice to the contrary). Thus, both the interpretation of their true ability and the correct approach to analyzing their data is inherently difficult. However, we also tested whether we observe the same general pattern of results if we assume that the absolute value of d' represents the true ability of these participants in the task (as would be the case if these five participants somehow failed to note the correct response keys). Performing this analysis on all 27 participants, we find that d' shows a trend level positive correlation with $\log(\lambda)$ at the two-tailed level ($r(25) = .35$, $p = .069$), but no correlation with risk attitudes (ρ and d' ; $r(25) = -0.13$, $p = 0.53$) or choice consistency (μ and d' ; $r(25) = 0.077$, $p = 0.70$), replicating the same selective pattern of correlation reported in the main text. The

differences between the correlations also largely replicate the pattern reported in the main text, with the correlation of $|d'|$ with $\log(\lambda)$ marginally greater than that with ρ (Fisher's r-to-z, $z = 1.73$, $p = 0.08$), though not significantly different from that with μ ($z = 1.02$, $p = 0.31$). Despite replicating the effect shown in the main manuscript, we believe that inclusion of these negative d' participants is inherently problematic, due to the unavoidable difficulty in quantifying their performance in the heartbeat detection task. Therefore, in the manuscript we took the conservative approach of only including those participants who demonstrated successful performance of the experimental tasks at a clear and objective level.

REFERENCES

- Greene, W. H. (2003). *Econometric Analysis*. Upper Saddle River, NJ: Prentice Hall.
- Sokol-Hessner, P., Camerer, C. F., & Phelps, E. A. (2012). Emotion Regulation Reduces Loss Aversion and Decreases Amygdala Responses to Losses. *Social Cognitive and Affective Neuroscience*, 1-54.
- Sokol-Hessner, P., Hsu, M., Curley, N. G., Delgado, M. R., Camerer, C. F., & Phelps, E. A. (2009). Thinking like a trader selectively reduces individuals' loss aversion. *PNAS*, 106, 5035-5040.
- Tversky, A., & Kahneman, D. (1992). Advances in Prospect-Theory - Cumulative Representation of Uncertainty. *Journal of Risk and Uncertainty*, 5, 297-323.
- Wiens, S., Mezzacappa, E., & Katkin, E. (2000). Heartbeat detection and the experience of emotions. [10.1080/026999300378905]. *Cognition & Emotion*, 14, 417-427.

Table S1: Monetary Choice Amounts (*Repeated trial)

<u>Gamble Values</u>			<u>Guar.</u>	<u>Gamble Values</u>			<u>Guar.</u>	<u>Gamble Values</u>			<u>Guar.</u>
<u>Gain</u>	<u>Loss</u>	<u>Alt.</u>		<u>Gain</u>	<u>Loss</u>	<u>Alt.</u>		<u>Gain</u>	<u>Loss</u>	<u>Alt.</u>	
\$2.00	-\$0.50	\$0.00*		\$6.00	-\$5.25	\$0.00		\$10.00	-\$15.00	\$0.00*	
\$2.00	-\$0.75	\$0.00		\$6.00	-\$6.00	\$0.00		\$10.00	-\$16.25	\$0.00	
\$2.00	-\$1.00	\$0.00		\$6.00	-\$6.75	\$0.00*		\$10.00	-\$17.50	\$0.00	
\$2.00	-\$1.25	\$0.00		\$6.00	-\$7.50	\$0.00		\$10.00	-\$18.75	\$0.00	
\$2.00	-\$1.50	\$0.00*		\$6.00	-\$8.25	\$0.00		\$10.00	-\$20.00	\$0.00*	
\$2.00	-\$1.75	\$0.00		\$6.00	-\$9.00	\$0.00		\$12.00	-\$3.00	\$0.00	
\$2.00	-\$2.00	\$0.00		\$6.00	-\$9.75	\$0.00*		\$12.00	-\$4.50	\$0.00	
\$2.00	-\$2.25	\$0.00		\$6.00	-\$10.50	\$0.00		\$12.00	-\$6.00	\$0.00	
\$2.00	-\$2.50	\$0.00*		\$6.00	-\$11.25	\$0.00		\$12.00	-\$7.50	\$0.00*	
\$2.00	-\$2.75	\$0.00		\$6.00	-\$12.00	\$0.00		\$12.00	-\$9.00	\$0.00	
\$2.00	-\$3.00	\$0.00		\$8.00	-\$2.00	\$0.00*		\$12.00	-\$10.50	\$0.00	
\$2.00	-\$3.25	\$0.00		\$8.00	-\$3.00	\$0.00		\$12.00	-\$12.00	\$0.00	
\$2.00	-\$3.50	\$0.00*		\$8.00	-\$4.00	\$0.00		\$12.00	-\$13.50	\$0.00*	
\$2.00	-\$3.75	\$0.00		\$8.00	-\$5.00	\$0.00		\$12.00	-\$15.00	\$0.00	
\$2.00	-\$4.00	\$0.00		\$8.00	-\$6.00	\$0.00*		\$12.00	-\$16.50	\$0.00	
\$4.00	-\$1.00	\$0.00		\$8.00	-\$7.00	\$0.00		\$12.00	-\$18.00	\$0.00	
\$4.00	-\$1.50	\$0.00*		\$8.00	-\$8.00	\$0.00		\$12.00	-\$19.50	\$0.00*	
\$4.00	-\$2.00	\$0.00		\$8.00	-\$9.00	\$0.00		\$12.00	-\$21.00	\$0.00	
\$4.00	-\$2.50	\$0.00		\$8.00	-\$10.00	\$0.00*		\$12.00	-\$22.50	\$0.00	
\$4.00	-\$3.00	\$0.00		\$8.00	-\$11.00	\$0.00		\$12.00	-\$24.00	\$0.00	
\$4.00	-\$3.50	\$0.00*		\$8.00	-\$12.00	\$0.00		\$4.00	\$0.00	\$2.00	
\$4.00	-\$4.00	\$0.00		\$8.00	-\$13.00	\$0.00		\$8.00	\$0.00	\$4.00	
\$4.00	-\$4.50	\$0.00		\$8.00	-\$14.00	\$0.00*		\$12.00	\$0.00	\$6.00	
\$4.00	-\$5.00	\$0.00		\$8.00	-\$15.00	\$0.00		\$18.00	\$0.00	\$9.00	
\$4.00	-\$5.50	\$0.00*		\$8.00	-\$16.00	\$0.00		\$24.00	\$0.00	\$12.00	
\$4.00	-\$6.00	\$0.00		\$9.00	-\$2.25	\$0.00		\$5.00	\$0.00	\$3.00	
\$4.00	-\$6.50	\$0.00		\$9.00	-\$3.38	\$0.00*		\$7.00	\$0.00	\$4.00	
\$4.00	-\$7.00	\$0.00		\$9.00	-\$4.50	\$0.00		\$10.00	\$0.00	\$6.00	
\$4.00	-\$7.50	\$0.00*		\$9.00	-\$5.63	\$0.00		\$17.00	\$0.00	\$10.00	
\$4.00	-\$8.00	\$0.00		\$9.00	-\$6.75	\$0.00		\$22.00	\$0.00	\$13.00	
\$5.00	-\$1.25	\$0.00		\$9.00	-\$7.88	\$0.00*		\$28.00	\$0.00	\$13.00	
\$5.00	-\$1.88	\$0.00		\$9.00	-\$9.00	\$0.00		\$5.00	\$0.00	\$2.00	
\$5.00	-\$2.50	\$0.00*		\$9.00	-\$10.13	\$0.00		\$26.00	\$0.00	\$10.00	
\$5.00	-\$3.13	\$0.00		\$9.00	-\$11.25	\$0.00		\$7.00	\$0.00	\$3.00	
\$5.00	-\$3.75	\$0.00		\$9.00	-\$12.38	\$0.00*		\$13.00	\$0.00	\$5.00	
\$5.00	-\$4.38	\$0.00		\$9.00	-\$13.50	\$0.00		\$12.00	\$0.00	\$6.00	
\$5.00	-\$5.00	\$0.00*		\$9.00	-\$14.63	\$0.00		\$25.00	\$0.00	\$10.00	
\$5.00	-\$5.63	\$0.00		\$9.00	-\$15.75	\$0.00		\$4.00	\$0.00	\$2.00	
\$5.00	-\$6.25	\$0.00		\$9.00	-\$16.88	\$0.00*		\$3.00	\$0.00	\$1.00	
\$5.00	-\$6.88	\$0.00		\$9.00	-\$18.00	\$0.00		\$25.00	\$0.00	\$9.00	
\$5.00	-\$7.50	\$0.00*		\$10.00	-\$2.50	\$0.00		\$13.00	\$0.00	\$6.00	
\$5.00	-\$8.13	\$0.00		\$10.00	-\$3.75	\$0.00		\$22.00	\$0.00	\$10.00	
\$5.00	-\$8.75	\$0.00		\$10.00	-\$5.00	\$0.00*		\$12.00	\$0.00	\$5.00	
\$5.00	-\$9.38	\$0.00		\$10.00	-\$6.25	\$0.00		\$2.00	\$0.00	\$1.00	
\$5.00	-\$10.00	\$0.00*		\$10.00	-\$7.50	\$0.00		\$8.00	\$0.00	\$3.00	
\$6.00	-\$1.50	\$0.00		\$10.00	-\$8.75	\$0.00		\$19.00	\$0.00	\$8.00	
\$6.00	-\$2.25	\$0.00		\$10.00	-\$10.00	\$0.00*		\$26.00	\$0.00	\$12.00	
\$6.00	-\$3.00	\$0.00		\$10.00	-\$11.25	\$0.00		\$30.00	\$0.00	\$12.00	
\$6.00	-\$3.75	\$0.00*		\$10.00	-\$12.50	\$0.00		\$23.00	\$0.00	\$10.00	
\$6.00	-\$4.50	\$0.00		\$10.00	-\$13.75	\$0.00		\$12.00	\$0.00	\$4.00	

Figure S1. Mixed Valence Gamble Values.

