Biasing predictive processing of interoceptive information affects implicit spirituality and religiosity

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Summary

In the predictive processing framework, religiosity and spirituality (R&S) have been linked to increased reliance on prior beliefs and decreased prediction error monitoring. In addition, R&S might be differentially related to processing exteroceptive and interoceptive information. The study manipulated different components of the predictive processing model in interoception, and evaluated the resulting changes in implicit R&S. In a variant of the heartbeat discrimination task sham TMS was used to induce prior beliefs about changes of heartbeat frequency (Experiment 1). Prediction error monitoring was modulated by manipulating error feedback reliability (Experiment 2). Results showed that the decision criterion tended to shift towards the direction of the induced prior, while the sensitivity decreased with unreliable error feedback. Crucially, implicit R&S increased following the prior beliefs induction and decreased following the unreliable error feedback. The results support the predictive coding account of R&S and demonstrate the role of bodily signals in R&S experiences.

Keywords: predictive coding; religiosity and spirituality; interoception; heartbeat discrimination task; implicit associations test.

Introduction

Neurocognitive bases of religiosity and spirituality (R&S) are gaining increasing interest as a field of study. Indeed, within the emerging neuroscience of religion, experimental data on the neural correlates of the R&S is growing [1]. However, at present, there is no consensus on the R&S neurocognitive mechanisms, partially due to a large variability of methods and measures that often contradict each other [2].

One promising theoretical account of R&S is the recently proposed model of R&S within the predictive coding theory [2]. According to this theory, perceptual experiences are based on the incoming sensorial information that is interpreted in the context of predictions about upcoming sensorial events (a priori knowledge and beliefs). Whenever a discrepancy between the predictions and the sensory information occurs, a prediction error is generated; predictions are then dynamically updated in order to minimize the prediction error [3,4]. In relation to the R&S, these experiences might be underpinned by a differential weighting of prior beliefs and prediction error in perceptual processing [2]. In detail, religious and spiritual experiences might be rooted in a stronger reliance on prior beliefs compared to the sensorial evidence, in combination with reduced prediction error monitoring.

Individual differences in the relative weighing of predictions vs sensorial information have been shown to reflect predictive strategies during visual perception in healthy participants [5]. Furthermore, it is possible that these differences are related to the prevalence of autistic or schizotypal personality traits because, at the extreme levels, autism spectrum disorder (ASD) and schizophrenic spectrum disorder (SSD) present opposing patterns of this imbalance: in ASD, the role of sensory information and prediction errors is overestimated compared to the predictions, while in SSD, the reliance on pre-existing models is prioritized over sensorial information [6-9]. From this perspective, differences in the weighting of predictions and sensorial information might reflect also the individual differences in R&S. Indeed, higher reliance on prior beliefs in individuals with higher R&S is consistent with the fact that R&S positively correlate with schizotypal personality traits and negatively correlate with autistic traits [10]. In a similar vein, reduction of prediction error monitoring in relation to R&S experiences might explain both lower-level perceptual phenomena, such as visions, and higher-level predictions that are at the basis of complex belief systems [2]. Attenuated prediction error monitoring reduces the effects of prediction error signals when sensorial information contradicts the prediction, which further reinforces the prior beliefs and the reliance on them [2,11].

However, different predictive coding strategies may affect not only the perception of external events, but also the perception of one's own internal states, namely interoception. Interestingly, despite being subserved by the same predictive processing model, R&S might be dissociated in the weighting of perceived information about external events and bodily signals. This lies in the fact that religiosity typically concerns more institutionalized aspects of belief, such as traditions and rituals of religious communities, namely the ritualistic and cognitive dimensions of the multidimensional model of religious commitment [12]. In turn, spirituality is based on the experiential dimension of the same model, as it represents the emotional component of religious commitment, the experience of a transcendent reality, and a related blurring of the boundaries between the self and others [13]. Based on this, it is possible to hypothesize that spirituality might be more related to the processing of internal states built upon interoceptive information than religiosity[2,14].

To summarize, R&S could be interpreted within the predictive coding theory, which suggests an increased weighting of prior beliefs over sensorial evidence and reduced prediction error monitoring. Together with that, spirituality might be more related to the processing of interoceptive signals compared to religiosity. However, to date, these two assumptions have not been tested directly and within a single experimental paradigm. To fill this gap, the present study aimed to investigate the changes in the levels of implicit R&S following an experimental manipulation of either prior beliefs or prediction error related to interoception. In Experiment 1, prior beliefs about the frequency of participants' heartbeat were induced via sham transcranial magnetic stimulation (TMS) combined with instructions about the direction of the cardiac change (decreased/increased heart rate) in a variant of the classic heartbeat discrimination task (HDT). In Experiment 2, prediction error was manipulated by introducing, in the same task, reliable or unreliable error feedback about participants' performance. In both experiments, implicit R&S were measured after the HDT and compared between control and experimental conditions (Experiment 1: no stimulation vs sham TMS; Experiment 2: reliable vs unreliable error feedback). The effectiveness of the prior and error feedback manipulation was evaluated by comparing, between the control and experimental conditions, psychophysics parameters that reflect decision making and sensitivity within psychometric function (i.e., point of subjective equality, PSE; just noticeable difference, JND) and signal detection theory (i.e., d-prime, d'; and decision criterion, *c*) models. Lastly, by considering the impact of individual differences in weighting of predictions vs sensorial information, autistic and schizotypal personality traits were evaluated as variables that could influence the individual susceptibility to the manipulations. We hypothesized that: 1) Inducing prior beliefs about the effects of sham TMS on the heartbeat perception would shift PSE and *c* in the direction of the prior, without affecting sensitivity, and it would increase implicit spirituality but not religiosity; 2) Decreasing the reliability of error feedback about one's heartbeat perception with unreliable error feedback would decrease sensitivity in the heartbeat perception task, without affecting PSE and *c*, and it would decrease implicit spirituality but not religiosity; 3) In both experiments, higher prevalence of schizotypal traits would be related to stronger effects of prior, while higher prevalence of autistic traits would be related to higher susceptibility to the feedback manipulations of heartbeat discrimination.

Experiment 1 – Prior beliefs manipulation

Methods

Participants

Forty-six healthy adult volunteers without history of neurologic and psychiatric diseases gave written informed consent to participate in the study. All participants were students at the University of Udine (Italy); they were naïve about the study aims and procedures, and fulfilled the inclusion criteria (absence of diagnosed cardiac conditions). Participants received course credits for completing the experiment.

Fifteen participants were excluded due to: technical problems with the equipment (n = 7), dropping out before completing both sessions of the study (n = 3), not following the instructions of the HDT correctly, as indicated by the task performance and/or subjective feedback (n = 4), and having a cardiac condition not reported during the recruitment (n = 1).

The final sample included thirty-one participants (23 F, 8 M, mean age ± SD = 25.8±7.5 years, self-reported handedness: 31 right-handed; self-reported religiosity: 17 catholic Christians, 14 non-religious). The sample size was not estimated a priori due to the fact that the current experiment was performed as a behavioral pilot study for the pre-registered EEG experiment. A sensitivity power analysis performed in G*Power [15] confirmed that this sample size, with alpha level = 0.05 and power = 0.80 in a 2x2x2 mixed-effects ANOVA, was sufficient to detect a medium effect size (f = 0.26).

The study was approved by the local ethics committee (*Institutional Review Board*, Department of Languages and Literatures, Communication, Education and Society, University of Udine; protocol number CGPER-2022-12-22-02) and carried out in accordance with the ethical standards of the 2013 Declaration of Helsinki.

Pre-registration of experiments

The method and analysis plan were pre-registered on the Open Science Framework (OSF) prior to data collection (https://doi.org/10.17605/OSF.IO/NG75F). Experiment 1 of the present study followed the experimental design, procedures and analysis plan of the behavioral data of the EEG Study 2 of the pre-registration.

Setup and procedure

Experimental design

The study consisted of two experimental sessions that lasted 2.5-3 hours each and were administered at least two days apart. The sessions had an identical structure (see Fig. 1) and differed only in the presence/absence of the prior belief induction via sham-TMS, according to the experimental condition (stimulation and baseline, respectively). In each session, after completing initial questionnaires (Multidimensional Assessment of Interoceptive Awareness, MAIA, and/or State-Trait Anxiety Inventory, STAI, depending on the session), participants performed two blocks of the HDT; after each block, they completed one of the implicit associations tests (R-IAT or S-IAT, depending on the randomization sequence). In addition, questionnaires evaluating personality traits (Autism-spectrum Quotient, AQ, and Schizotypal Personality Questionnaire, SPQ) and religiosity and spirituality (Brief Multidimensional Measure of Religiousness/Spirituality, BMMRS, and Baylor Religion Survey, BRS) were administered at the end of the second session. All experimental tasks and measures are described in detail below.
The study followed a 2x2x2 within-between design with Prior type ("decrease", "increase") as a between-subject factor, and Stimulation (baseline, stimulation) and Block of HDT (block 1, block 2) as within-subject factors.

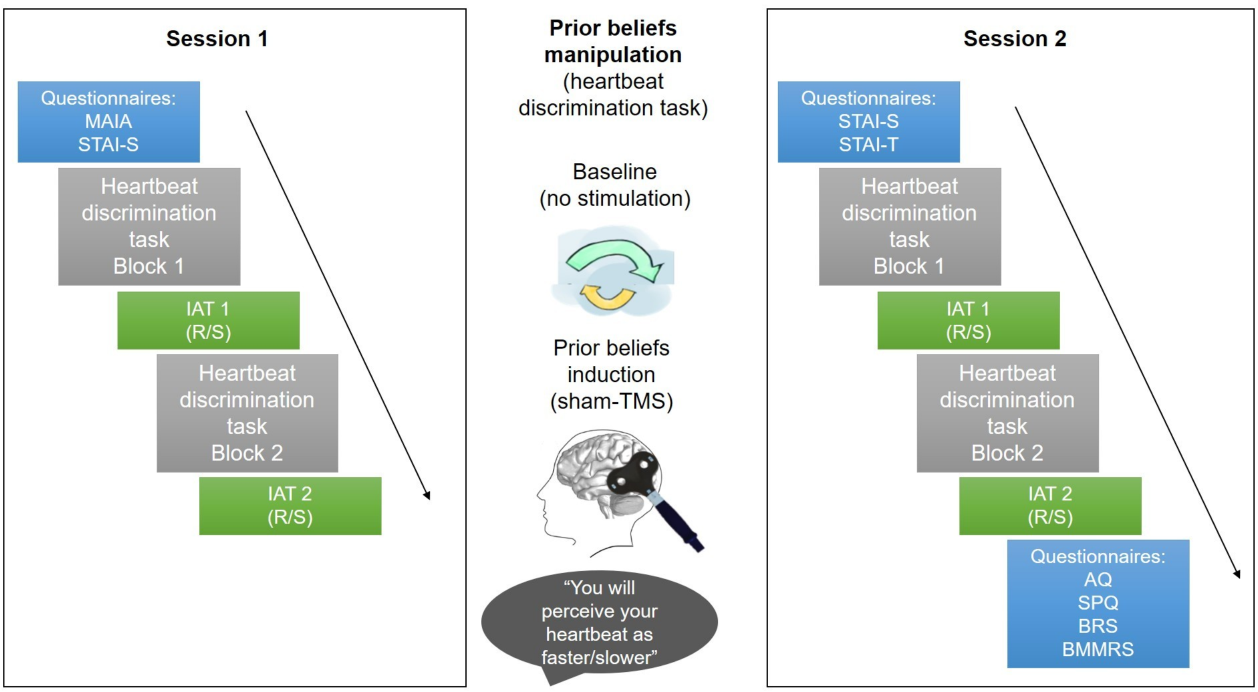

Figure 1. Experiment 1 – experimental design, procedures and timeline.

Heartbeat discrimination task

The present study employed a variant of the HDT, which is a well-known paradigm providing a measure of interoceptive accuracy that typically requires participants to judge whether presented audio or visual signals are synchronous or asynchronous with their heartbeat [16,17]. In combination with psychophysics measures, it allows evaluating perceptual sensitivity independently from non-perceptual factors [18].

In the present study, the HDT was modified in order to allow inducing directional prior beliefs about one's own heart rate (i.e., beliefs that the heartbeats will be perceived as slower or faster than the actual heart rate; see details below). It was a two-alternative forced choice task that consisted of comparing one's own perceived heart rate with short audios of heart rate of different frequencies and reporting whether the own heart rate was slower or faster than the one in the audio. The frequencies were parametrically modified online based on the registered own heart rate.

The task was administered on a laptop PC (Lenovo ThinkPad with Windows 11, screen resolution – 1920 x 1200 pixels), working in battery supply mode, via a custom code that used the Psychophysics Toolbox extensions [19-21] in MATLAB. Participant's heart rate was recorded with an AD8232 ECG module connected to an Arduino Uno microcontroller (https://www.arduino.cc/). Three lead cables were connected to participants' chest via adhesive electrodes placed under the ribcage on the left and under each of the collarbones. The ECG recording was calibrated at the beginning of each experimental session using a custom script for the microcontroller that allowed setting an individual threshold of peak amplitude to in order to define the ECG peaks (R waves) that passed through and were consecutively considered in the heart rate calculation. After the threshold was determined, the heart rate was recorded for 60 s prior to the beginning of the task. Participants wore on-ear headphones (Harman International Industries, Inc.) for the entire duration of the task, and the sound volume was set at a comfortable level that was not changed throughout the session.

The task consisted of multiple 9-trial runs, where in the beginning of each run participants were instructed to perceive their own heartbeat for 20 seconds. During this phase, participants were asked to remain still and relaxed, and to focus on their heartbeat in the present moment without using any “strategies”, such as imagining a pre-determined rhythm, or touching their wrist or neck to feel their pulse. This phase was followed by a sequence of short audios of heartbeats (duration of each audio was random within the interval of 3-7 s). After each audio, participants were prompted to reply whether their own heart rate was slower or faster with respect to the one in the audio. Responses were made via pressing the “S” and “K” keys on the keyboard, corresponding to “slower” and “faster”, respectively. The response time was not limited but participants were instructed to reply as fast as possible. After 9 trials (audio + response), the following trial run started (see Fig. 2A for the task timeline).

The audios of the heartbeats were created online during each trial run based on the participant’s heart rate recorded throughout the “own heartbeat perception” phase, which occurred every two runs. In detail, the heart rate was recorded prior to the beginning of the task and entered manually in the main task code at the beginning of the task in order to create the audio stimuli for the first two trial runs of the task. After that, it was recorded at the beginning of every two trial runs. The audios of the heartbeats were created from an audio file of a single heartbeat, namely a normal heartbeat recording from The Michigan Heart Sound and Murmur database (https://www.med.umich.edu/lr) that was programmed to be presented with a determined frequency (beats per minute, BPM). The frequency included nine levels: level 0 corresponded to participant’s own heart rate (e.g., 75 BPM), and the other eight levels were created with a step of 3 BPM, so that four levels had slower (e.g., 72, 69, 66, 63 BPM) and the other four had faster heartbeats (e.g., 78, 81, 84, 87 BPM) compared to one’s own (i.e., own heart rate +3, +6, +9, +12, and -3, -6, -9, -12 BPM). The audio stimuli were changed according to the newly recorded heart rate every 2 trial runs, i.e., every 18 trials, where each level of the heartbeat was presented twice in random order.

The task included 16 trial runs, i.e., 144 trials, during which each level of the heartbeats in the audios was presented 16 times. In each session, the task was repeated twice (this is referred to as block 1 and block 2 in the statistical analyses), amounting to a total of 288 trials and 32 trials/level per condition. In the beginning of the first half of the task (block 1), a short training was administered that consisted of 18 trials. At the end of the task, participants were asked to rate the perceived difficulty and the perceived accuracy (performance) on a 0-100 visual analogue scale (VAS).

Prior belief manipulation. During the Stimulation condition, participants' beliefs about their heart rate perception were manipulated using sham transcranial magnetic stimulation (TMS) with instructions that were aimed at inducing prior beliefs towards a certain direction. In detail, sham single-pulse TMS was administered with a figure-of-eight coil and a Magstim Rapid stimulator (https://www.magstim.com/). The coil was placed laterally on the right fronto-temporal area of participant's head, with the right-wing edge touching the scalp, ensuring that no current was expected to reach the brain; the stimulation intensity was set at 100% of stimulator output. The single pulses were delivered once in every "own heartbeat perception" phase at the beginning of each block of trials (i.e., 16 times/task block and 32 times/condition). Before the task started, participants were presented with standardized instructions about the purpose of the stimulation. The instructions served to induce prior beliefs about the stimulation and provided a false statement about the possible effects of the TMS on the heartbeat perception. They were the following:

"Spirituality and religiosity have been related to interoception, which refers to our capability of perceiving our internal body sensations. Here, we will study the neural bases of interoception. In particular we will study a brain area that is involved in the perception of heartbeat frequency, and that is called the insula. This is important because, as you know, there are conditions in which people perceive their heart beating faster than what is their actual heartbeat frequency, for example, during panic attacks. There are also conditions in which people perceive their heart beating slower than it really is, for example, when people do not realize that their heartbeat is too fast, as during tachycardia."

For the “Decrease” prior group: “*In this case, during the task you will receive a stimulation to the insula that will lead you to perceive your heartbeat as slower.”*

For the “Increase” prior group: “*In this case, during the task you will receive a stimulation to the insula that will lead you to perceive that your heartbeat as faster.”*

In the Baseline condition, no stimulation nor related instructions were present. Participants were blindly allocated to one of the prior-type groups (i.e., decrease or increase) following a randomization matrix created before the data collection. The order of conditions (Baseline, Stimulation) was counterbalanced across participants.

Interoceptive accuracy was indexed by fitting of the psychometric function and the resulting measures of the point of subjective equality (PSE) and the just noticeable difference (JND), and by estimating the signal detection theory measures of d-prime (d’) and decision criterion (*c*). PSE and JND were computed for each participant, condition and task block using the MixedPsy package for R [22]. The PSE refers to the intensity level at which a stimulus is perceived as equivalent to another stimulus of different magnitude in 50% of trials; the JND is a minimal difference in stimulus intensity that is required to discriminate between two stimuli in 50% of trials. They represent response accuracy and sensitivity, respectively [23]. The d’ similarly represents sensitivity, while the *c* indicates a presence of choice bias in the responses [24]. Both these measures are calculated based on a proportion of hits and false alarms. In particular, the hits were identified as responses “slower” at the levels where participant’s own heartbeat was slower than the presented heartbeats, whereas false alarms were considered as responses “slower” when participant’s own heartbeat was faster than the presented heartbeats. The audios with the heartbeat frequency equal to participants’ own (stimuli of level 0) were excluded from the calculation of hits and false alarms. Hence, negative *c* values pointed to a tendency to report slower response (i.e. own heart is beating more slowly than the audio recordings), while positive *c* values hinted to a tendency to report faster responses (i.e., own heart is beating faster).

Religious and Spiritual IAT

Implicit R&S were measured with religious and spiritual Implicit Association Tests (R-IAT and S-IAT, respectively). We used the stimuli and procedure that were previously adapted and validated for the Italian population [14].

The task was administered with E-Prime 2 software (Psychology Software Tools, Inc., Pittsburgh) on a desktop computer with Windows 7. Participants were seated in front of a computer screen (Philips 196VL, resolution 1366 x 768 pixels) at a distance of approximately 50 cm. Throughout the task, in each trial, a single word was presented at the center of the screen, and the labels of the categories (one or two at a time) were displayed in top left- and right corners of the screen. Participants were instructed to identify whether the presented word belonged to the category on the left or on the right by pressing a left or a right key on the keyboard ("E" and "I", respectively). In addition, they were required to respond as fast and as accurately as possible.

The *stimuli* included 10 words associated with the religious/spiritual dimension and 10 words associated with the non-religious/non-spiritual dimension in R-IAT/S-IAT, respectively. In addition, 12 stimuli associated with the Self-Other pronoun dimension were used in both IATs.

The *procedure* was identical in both IATs and followed the standard IAT structure [25], see Fig. 2B for the task timeline. In detail, after the instructions that also listed all stimuli and categories, the task included 7 blocks containing 3 familiarization blocks (blocks 1, 2 and 5) and 4 test blocks with congruent and incongruent mapping of categories (blocks 3-4 and 6-7, respectively). The categories were mapped as congruent when the response key for the category of Self-pronouns was the same as the one for the categories Religious/Spiritual, and the other response key was used for the Other-pronouns and the categories Non-religious/Non-spiritual. Conversely, in the incongruent blocks, the same response key was expected for the Self-pronouns and the category Non-religious/Non-spiritual, and the other one for the Other-pronouns and the Religious/Spiritual words. The order of congruent/incongruent test blocks was counterbalanced across participants, as for half of the participants, blocks 1, 3 and 4 were switched with blocks 4, 5 and 7. Throughout the task, the stimuli and the categories labels were presented until a response was given; in case of an erroneous response, a red "X" appeared on the screen and participant was required to correct the response. The intertrial interval was set at 500 ms from the moment of the correct response to the presentation of the following stimulus. Blocks 1, 2, 3 and 6 consisted of 20 trials; blocks 4, 5 and 7 included 40 trials. The entire duration of each IAT was approximately 7 minutes. The order of the two IATs was counterbalanced across participants and was kept constant in both sessions of the experiment.

Implicit R&S were quantified as D scores, an index that reflects the difference between congruent and incongruent trials and factors in both the accuracy and the reaction times (RTs) [25]. Higher D scores indicate higher implicit preference for the congruent categories; in this case, stronger association between the self and the R&S. In addition, accuracy and RTs were considered separately due to the fact that they represent different aspects of the IAT performance, namely the strength of the implicit associations and the cognitive control involved in overcoming implicit biases [14,26,27], and, therefore, they might be differentially affected by the experimental manipulation. In order to control for the individual differences, we computed standardized indices of the error rate (1 – proportion of accuracy) and RTs by dividing the difference between the incongruent and the congruent condition by their sum. As a result, both for the standardized error rate and the standardized RTs, higher and more positive values indicated higher implicit R&S.

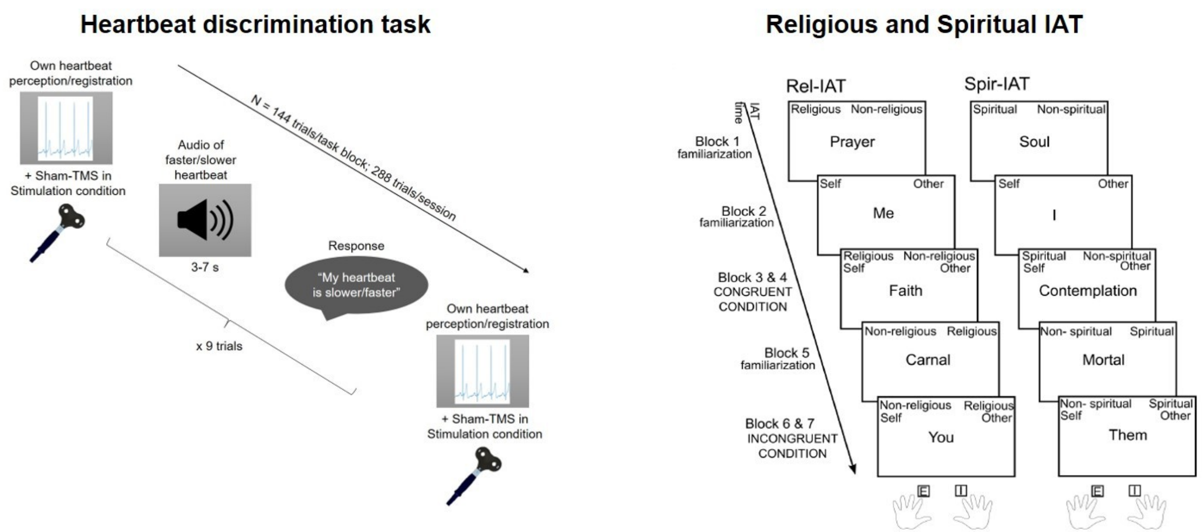

Figure 2. Experiment 1 – timeline of the heartbeat discrimination task and the R- and S-IATs

Questionnaires

Multidimensional Assessment of Interoceptive Awareness (MAIA) was used in its Italian version to assess individual levels of interoceptive awareness in our sample. The questionnaire consists of 32 items that measure eight facets of interoceptive (body) awareness: 1) Noticing: awareness of uncomfortable, comfortable, and neutral body sensations; 2) Not-distracting: tendency to ignore or distract oneself from sensations of pain or discomfort; 3) Not-worrying: emotional distress or worry with sensations of pain or discomfort; 4) Attention regulation: ability to sustain and control attention to body sensation; 5) Emotional Awareness: awareness of the connection between body sensations and emotional states; 6) Self-regulation: ability to regulate psychological distress by attention to body sensations, 7) Body listening: actively listens to the body for insight, and 8) Trusting: experiences one own's body as safe and trustworthy [28,29]. Each statement of the questionnaire is rated on a scale from 0 (never) to 5 (always). The ratings are averaged for each subscale (facet), and higher scores on each subscale indicate higher interoceptive awareness.

State-Trait Anxiety Inventory (STAI) was used to evaluate the levels of anxiety [30,31]. The questionnaire includes 40 items (20 for state- and 20 for trait anxiety) that are rated on a scale from 1 to 4. In case of STAI-S, the scale refers to the level of agreement with the statements (1 = not at all, 4 = very much so), and in case of STAI-T, it indicates the frequency (1 = almost never, 4 = almost always). Higher scores reflect higher levels of anxiety.

Autism-spectrum Quotient (AQ) questionnaire [32] was employed to test the presence of autistic personality traits in the sample. The questionnaire consists of 50 items that are rated on a scale from 1 (completely agree) to 4 (completely disagree), and the score above 32 indicates the possible presence of autistic traits.

Schizotypal Personality Questionnaire (SPQ) was used to evaluate schizotypal personality traits in the sample [33]. The questionnaire includes 74 items that follow a dichotomous response scale (“Yes/No”). A total score is computed, as well as scores on 9 subscales that reflect the features of the schizotypal personality disorder (Ideas of Reference, Excessive Social Anxiety, Odd Beliefs or Magical Thinking, Unusual Perceptual Experiences, Odd or Eccentric Behavior, No Close Friends, Odd Speech, Constricted Affect, Suspiciousness). Higher scores suggest higher prevalence of schizotypal traits.

Baylor Religion Survey (BRS) and Brief Multidimensional Measure of Religiousness/Spirituality (BMMRS) were administered in order to assess the explicit levels of participants’ religiosity and spirituality, and to obtain sample characteristics regarding religious/spiritual attitudes and practices. *BRS Wave VI* [34,35] was translated in Italian; the items concerning the demographic characteristics of the sample were not included because they would require country-specific adaptation of the original survey and because that information was beyond the scope of the present study. Original items 47-70 were included in final version of the adapted questionnaire. As in the BRS codebook, for each question, we computed the percentage of the sample for each response option. Italian version of the *BMMRS* [36-38] included ten subscales: Daily Spiritual Experiences, Values/Beliefs, Forgiveness, Private Religious Practice, Religious/Spiritual Coping, Religious Support, Religious/Spiritual History, Commitment, Organizational Religiousness, and Overall Self-Ranking. The scores were computed for each scale and then standardized in order to obtain a total score, and lower total score represented higher religiosity/spirituality.

MAIA, STAI, AQ and SPQ were administered in E-prime 2, and BMMRS and BRS were administered online via Qualtrics Online Survey software (https://www.qualtrics.com). MAIA was administered at the beginning of the first session. STAI-S was administered at the beginning of both sessions, and STAI-T only at the beginning of the second session. AQ, SPQ, BMMRS and

BRS were administered at the end of the second session in counterbalanced order.

Statistical analysis

Data preprocessing and visualization for the HDT and the IATs were performed with R software in R Studio [39]. Statistical analyses were performed with JASP [40]. The effect size was estimated as partial eta squared (η^2_p) for ANOVA (small: 0.01, medium: 0.06, large: 0.14), and as Cohen's *d* for pairwise comparisons (small: 0.2, medium: 0.5, large: 0.8), or point-biserial correlation coefficient r in case of non-parametric pairwise comparisons (small: 0.1 to 0.3 or -0.3 to -0.1, medium: 0.3 to 0.5 or -0.5 to -0.3, large: 0.5 or -5). A significance threshold of $p = 0.05$ was set for all statistical analyses. Tukey HSD correction was applied to post-hoc paired comparisons when they were performed.

Subjective ratings of the perceived difficulty and performance (VAS) in the HDT were compared between the experimental conditions with a paired-sample t test (two tailed). *Psychophysics* indexes at the HDT, namely JND, PSE, d', and *c*, were separately entered in 2x2x2 mixed-effects ANOVAs with Prior type ("decrease", "increase") as between-subject factor, and Condition (baseline, stimulation) and Block (block 1, block 2) as within-subject factors. D scores, standardized error rate and standardized RTs at the Religious and Spiritual IATs were analyzed with 2x2 repeated-measures ANOVAs with IAT type (religious, spiritual) and Condition (baseline, stimulation) as within-subject factors.

For each of the parameters, the main analyses were followed up by 2x2 ANOVAs performed with the addition of the total scores of AQ and SPQ, respectively, as continuous predictors, to test whether the effects were modulated personality traits.

The scores on the STAI-S were compared between the two experimental conditions (baseline vs stimulation) with a Wilcoxon signed-ranked test. Other questionnaires are presented in a descriptive manner to provide a characterization of the sample.

Finally, as a validation of the present variant of the HDT, exploratory Spearman correlations were performed between the psychophysics parameters at baseline averaged for the two task blocks, subjective performance and difficulty, and the questionnaires (MAIA, STAI-T and STAI-S at baseline).

Data and code availability

All tasks scripts and analyses code and files, as well as all raw and processed data of the HDT, the IATs and the questionnaires are publicly available in the OSF repository (https://osf.io/4jvsp/?view_only=c83dbc455aff4c1593902cb34faa5d0c).

Results

All descriptive statistics are presented in Supplementary Table 1.

Sample characterization at questionnaires

STAI-T scores suggested that participants had high levels of trait anxiety. State anxiety (STAI-S) was moderate and did not differ significantly between the two experimental conditions ($W = 239.00$, $p = 0.65$, $r = 0.09$).
The scores on eight MAIA subscales were over and around the middle of the 0-5 scale for all subscales, except for higher scores on the subscales Noticing (awareness of bodily sensations) and Emotional awareness (awareness of the connection between bodily sensations and emotional states).
Participants' religiosity and spirituality, according to the *BRS*, can be summarized as follows. 25% consider themselves slightly religious; 20.8% reported being moderately religious; 45.8% not religious; 8.3% replied “do not know”. 41.6% are slightly spiritual; 33.3% are moderately spiritual; 16.7% are very spiritual; 4.2% are not spiritual; 4.2% replied “do not know”. In the past ten years, 62.5% have become less religious; 4.2% have become more religious; 25% remained the same; 8.3% never were religious. Of the participants that reported being religious, 70.8% identify as Roman Catholic; 4.2% as Evangelic Christian; 25% are non-religious.

In the *BMMRS*, the average score ± SD was 65.92±18.48, suggesting a below-average level of religiosity and spirituality in the sample (see Supplementary Table 1 for the scores on all subscales).

Heartbeat discrimination task

Neither the *perceived task difficulty*, nor the *perceived performance* (perceived accuracy) in the HDT were significantly different between the baseline and the stimulation conditions (difficulty: $t(30) = 0.40$, $p = 0.69$, $d = 0.08$; performance: $t(30) = 0.90$, $p = 0.38$, $d = 0.17$). This suggests that the induced prior beliefs about the effects of sham stimulation on the interoceptive performance did not influence the subjective perception of the task.

As regards the *psychophysics* results of the HDT, firstly, a significantly decreased sensitivity (JND and d') was observed in the second block of the task compared to the first one, independently of the stimulation condition and prior group.

In detail, a 2x2x2 mixed effects ANOVA for the JND showed a significant main effect of Block [$F(1, 1, 29) = 5.53$, $p = 0.03$, $\eta_p^2 = 0.16$], with lower JND in block 1 compared to block 2 (see Fig. 3C); in addition, there was a significant main effect of Prior [$F(1, 29) = 4.20$, $p = 0.049$, $\eta_p^2 = 0.13$] that indicated that the "decrease" prior group had lower JND than the "increase" prior group. There was no significant main effect of Stimulation, nor any significant interactions (see Supplementary Table 2 for full results).

Similarly, a 2x2x2 mixed effects ANOVA for the d' showed a significant main effect of Block [$F(1, 1, 29) = 7.33$, $p = 0.01$, $\eta_p^2 = 0.20$] demonstrating that the d' was higher in block 1 than in block 2 (see Fig. 3D). No other significant main effects or interactions were present (see Supplementary Table 2 for full results).

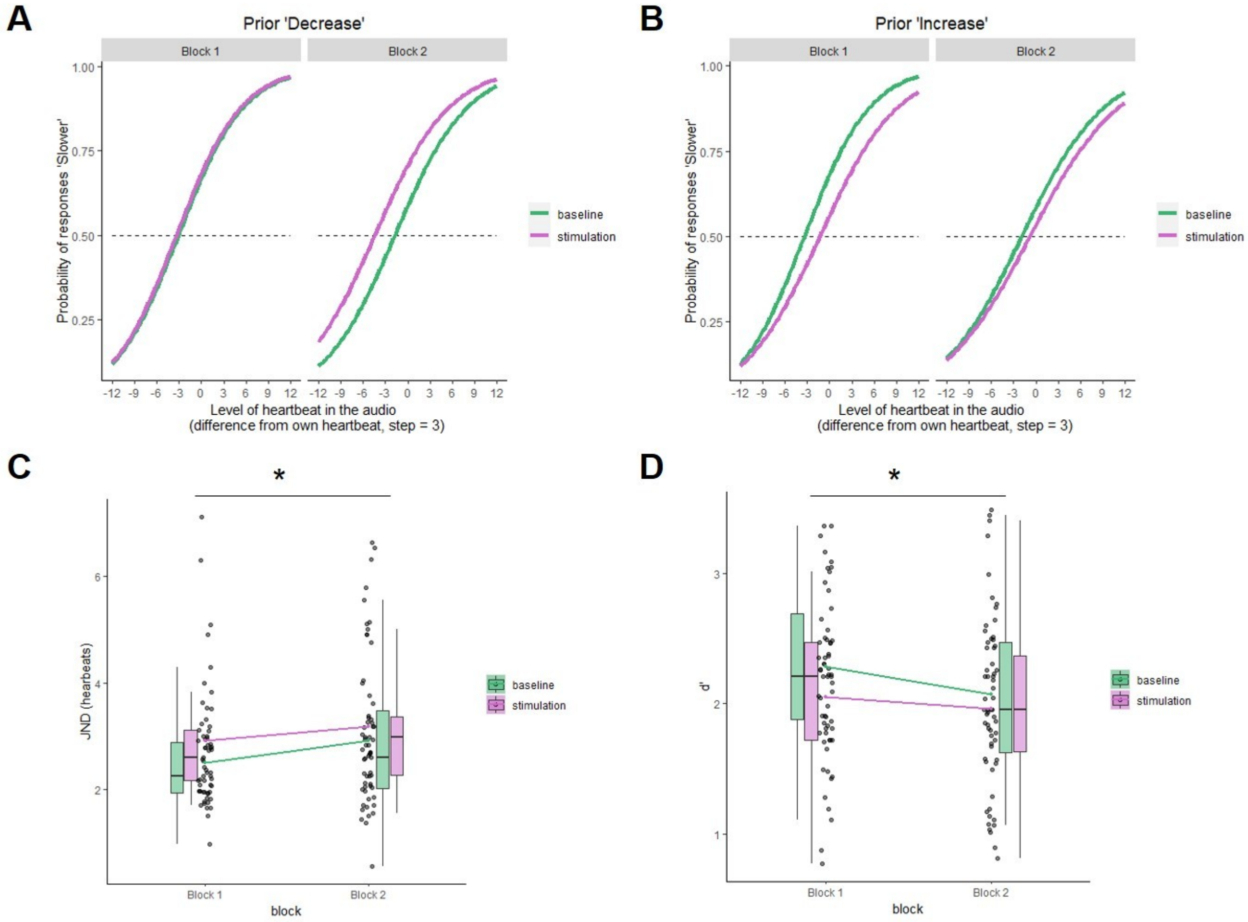

Figure 3. **A.** Psychometric function in the baseline and stimulation conditions of the heartbeat discrimination task plotted by task block in the "decrease" prior group; **B.** Psychometric function in the baseline and stimulation conditions of the heartbeat discrimination task plotted by task block in the "increase" prior group; **C.** The just noticeable difference (JND) values per condition and task block; **D.** The d-prime (d') values per condition and task block. For **C-D**, in the boxplot, hinges of the box represent the first and the third quartile, with the line in the middle of the box representing the median and the bottom and top whiskers representing the smallest and the largest value no further than 1.5*IQR from the lower and the upper hinges, respectively. The colored lines show the trend per task block. * = significant difference.

Crucially, a significant effect of Stimulation, in the interaction with task Block, was observed for both the PSE and the *c*. In case of the PSE, when the significant interaction of Stimulation x Block [$F(1, 1, 29) = 4.80$, $p = 0.04$, η_p^2

= 0.14] was followed up with post-hoc paired comparisons, none of the comparisons with Tukey HSD correction resulted to be significant. However, there was a trend of the PSE shifting in the direction of the induced prior in the stimulation condition compared to the baseline, in particular, in block 2 for the “decrease” group and in both blocks for the “increase” group (see Fig. 4A-B). In case of the *c*, the significant interaction of Stimulation x Block [F(1, 1, 29) = 7.89, p = 0.009, $\eta_p^2 = 0.21$] was driven by the significantly more negative *c* in block 1, compared to block 2, at baseline ($p_{corr.} = 0.02$), but not after sham stimulation ($p_{corr} = 0.99$). Similarly to the PSE, however, as a trend, the *c* shifted in the direction of the prior in the stimulation condition, which was evident in block 2 for the “decrease” group and in both blocks for the “increase” group (see Fig. 4C-D). No other significant effects or interactions were present in either of the analyses (PSE and *c*); see Supplementary Table 2 for full results.

Furthermore, considering AQ and SPQ scores as continuous predictors in the analyses of each of the analyzed parameters did not yield any significant effects of personality scores.

Exploratory correlations between the HDT measures and the subjective performance and difficulty of the task showed that higher perceived task difficulty was significantly correlated with more positive PSE (r = 0.50, p = 0.007) and *c* (r = 0.54, p = 0.003), that is with a tendency to respond “faster” more often. The perceived difficulty was negatively correlated with the d’ (r = -0.39, p = 0.04), suggesting that the subjective difficulty was inversely related to the sensitivity. Subjective task performance was significantly negatively correlated with the PSE (r = -0.41, p = 0.03). As for the correlations with MAIA and STAI, there was a significant positive correlation between STAI-T and PSE (r = 0.40, p = 0.03) and *c* (r = 0.40, p = 0.03). MAIA subscales Noticing, Attention Regulation and Body Listening were correlated negatively with the PSE (r = -0.45, p = 0.01; r = -0.45, p = 0.01; r = -0.42, p = 0.02, respectively); Noticing and Attention Regulation were correlated negatively with the *c* (r = -0.37, p = 0.04; r = -0.43, p = 0.02, respectively). Trusting subscale was correlated negatively with JND (r = -0.37, p = 0.04); Not Distracting subscale was correlated positively with the d’ (r = 0.40, p = 0.03). Full results are presented in Supplementary Table 4.

To summarize, in the HDT, there was a significant effect of prior belief induction (stimulation) in the interaction with task block. At baseline, there was a strong bias in the first block of the task for replying “slower” more often; this bias reduced in the second block of the baseline, suggesting learning effects. Possibly, such big differences between the blocks at baseline did not allow revealing significant differences between the baseline and stimulation conditions. However, there was a trend of PSE and *c* shifting in the direction of the prior. In addition, we observed a significant reduction of sensitivity over time (i.e., increased JND and decreased d’) independently of the stimulation condition, suggesting possible effects of fatigue in the second half of the task.

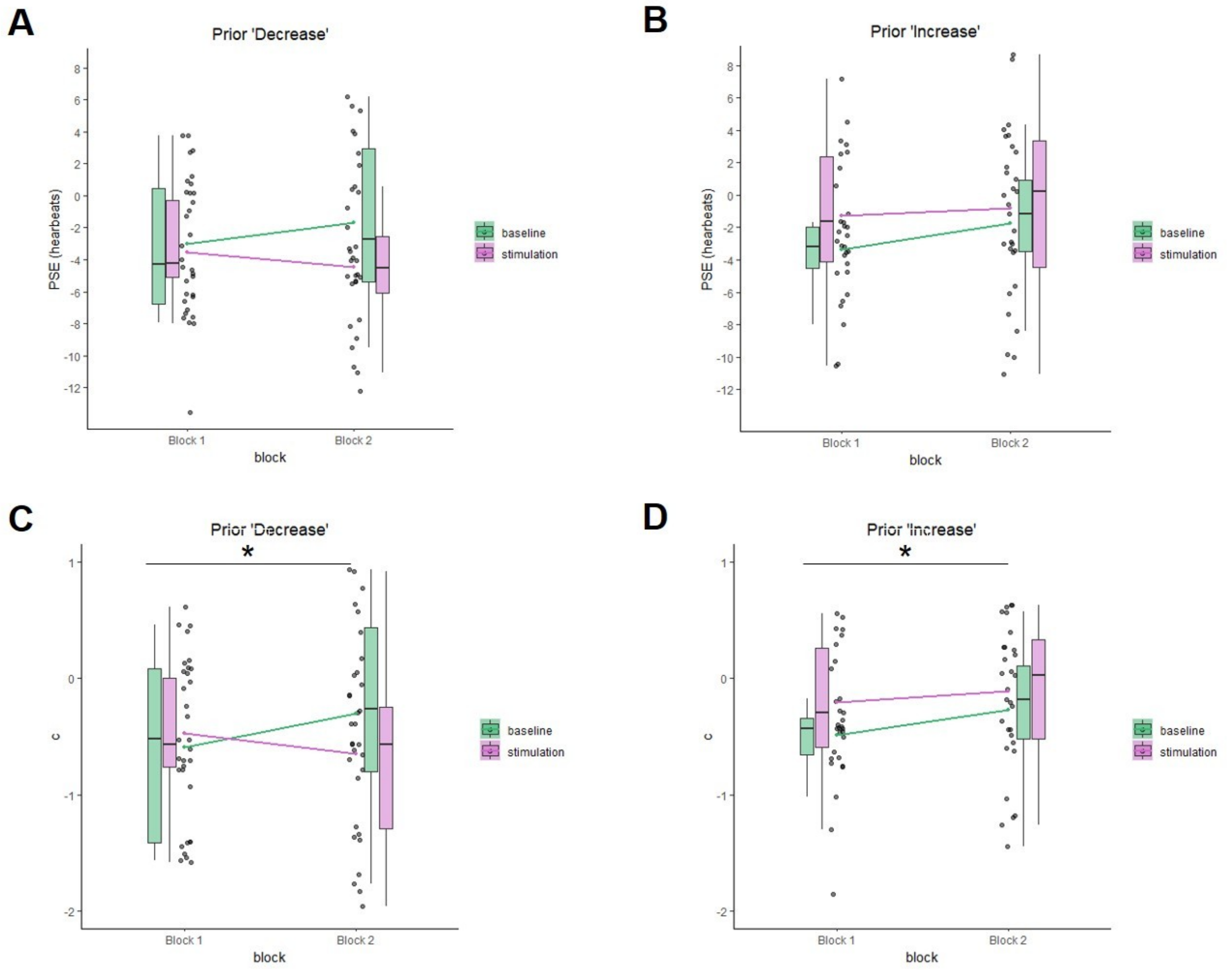

Figure 4. **A.** The point of subjective equality (PSE) values per condition and task block in the “decrease” prior group; **B.** The point of subjective equality (PSE) values per condition and task block in the “increase” prior group; **C.** The decision criterion (*c*) values per condition and task block in the

“decrease” prior group; **D.** The decision criterion (*c*) values per condition and task block in the “increase” prior group. In all panels, in the boxplot, hinges of the box represent the first and the third quartile, with the line in the middle of the box representing the median and the bottom and top whiskers representing the smallest and the largest value no further than 1.5*IQR from the lower and the upper hinges, respectively. The colored lines show the trend per task block. * = significant difference.

Religious and Spiritual Implicit Associations Tests

A 2x2 repeated-measures ANOVA for IAT type x Stimulation for the *standardized error rate* (accuracy) showed a significant main effect of Stimulation [$F(1, 30) = 4.90$, $p = 0.04$, $\eta_p^2 = 0.14$], with higher standardized error rate in the stimulation condition compared to the baseline in both IATs (see Fig. 5). There was no significant main effect of IAT type [$F(1, 30) = 1.51$, $p = 0.23$, $\eta_p^2 = 0.05$], nor of the interaction IAT type x Stimulation [$F(1, 30) = 2.55$, $p = 0.12$, $\eta_p^2 = 0.08$].

No significant effects or interactions were found for the D scores or the standardized reaction times; moreover, there were no significant effects of personality traits (AQ and SPQ) considered as a continuous predictor. See Supplementary Table 3 for full results.

In summary, implicit spirituality and religiosity increased after the prior belief induction in the cardiac interoception task. Despite a visible trend suggesting that spirituality increased more than religiosity, there was no significant effect of IAT type; finally, the effect of prior beliefs induction was not modulated by autistic and schizotypal personality traits.

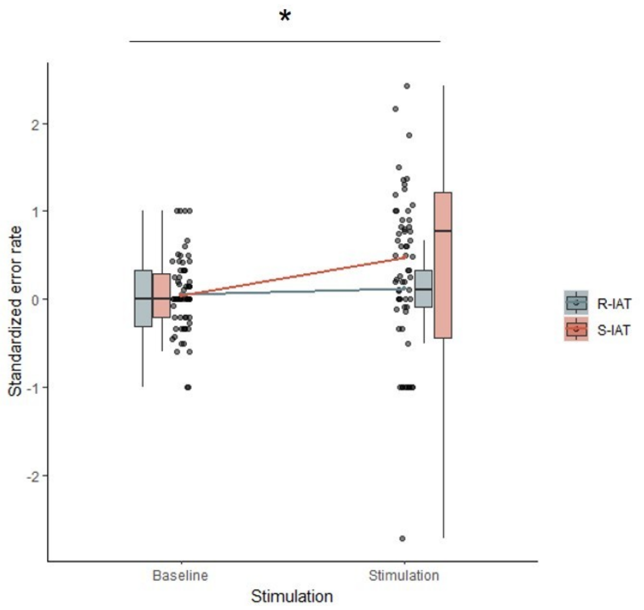

Figure 5. The standardized error rate (accuracy) per IAT type and stimulation condition. In the boxplot, hinges of the box represent the first and the third quartile, with the line in the middle of the box representing the median and the bottom and top whiskers representing the smallest and the largest value no further than 1.5*IQR from the lower and the upper hinges, respectively. The colored lines show the trend per feedback type. * = significant difference; “R-IAT” = Religious IAT; “S-IAT” = “Spiritual IAT”.

Experiment 2 – Prediction error manipulation

Methods

Participants

Twenty-seven healthy adult volunteers without history of neurologic and psychiatric diseases gave written informed consent to participate in the study. All participants were students at the University of Udine (Italy); none of them participated in Experiment 1. They were naïve about the study aims and procedures and fulfilled the inclusion criteria (namely absence of diagnosed cardiac conditions). Participants received course credits for completing the experiment.

Three participants were excluded due to: technical problems with the heartbeat recording in session 1 (n = 1), not following the instructions of the IAT correctly (n = 1), or dropping out before completing the second session (n =1).

The final sample included twenty-four participants (19 F, 5 M, mean age ± SD = 24.1±6.8 years, self-reported handedness: 20 right-handed, 4 left-handed; self-reported religiosity: 13 catholic Christians, 1 evangelic Christian, 10 non-religious). The sample size was not estimated a priori since the current experiment was performed as a behavioral pilot study for the pre-registered EEG experiment. A sensitivity power analysis performed in G*Power [15] confirmed that this sample size, with alpha level = 0.05 and power = 0.80 in a 2x2 repeated-measures ANOVA, was sufficient to detect a medium-to-large effect size (f = 0.30).

The study was approved by the local ethics committee (*Institutional Review Board*, Department of Languages and Literatures, Communication, Education and Society, University of Udine; protocol number CGPER-2022-12-22-02) and carried out in accordance with the ethical standards of the 2013 Declaration of Helsinki.

Pre-registration of experiments

The method and analysis plan were pre-registered on the Open Science Framework (OSF) prior to data collection (https://doi.org/10.17605/OSF.IO/NG75F). Experiment 2 of the present study followed the experimental design, procedures and analysis plan of the behavioral data of the EEG Study 4 of the pre-registration.

Setup and procedure

The study had similar design and procedures to Experiment 1, consisting of two sessions of 2.5-3 hours each that were administered at least 2 days apart. The session structure was identical (see Fig. 6), except for the absence of any prior manipulation and the presence of error feedback manipulation (true/false error feedback) in the HDT. The stimuli, setup, procedures and

counterbalancing of the R&S IATs and all questionnaires (MAIA, STAI-S, STAI-T, AQ, SPQ, BMMRS and BRS) were identical to Experiment 1.
The study followed a 2x2 within-subject design with Feedback type (true, false) and Block of HDT (block 1, block 2) as within-subject factors.

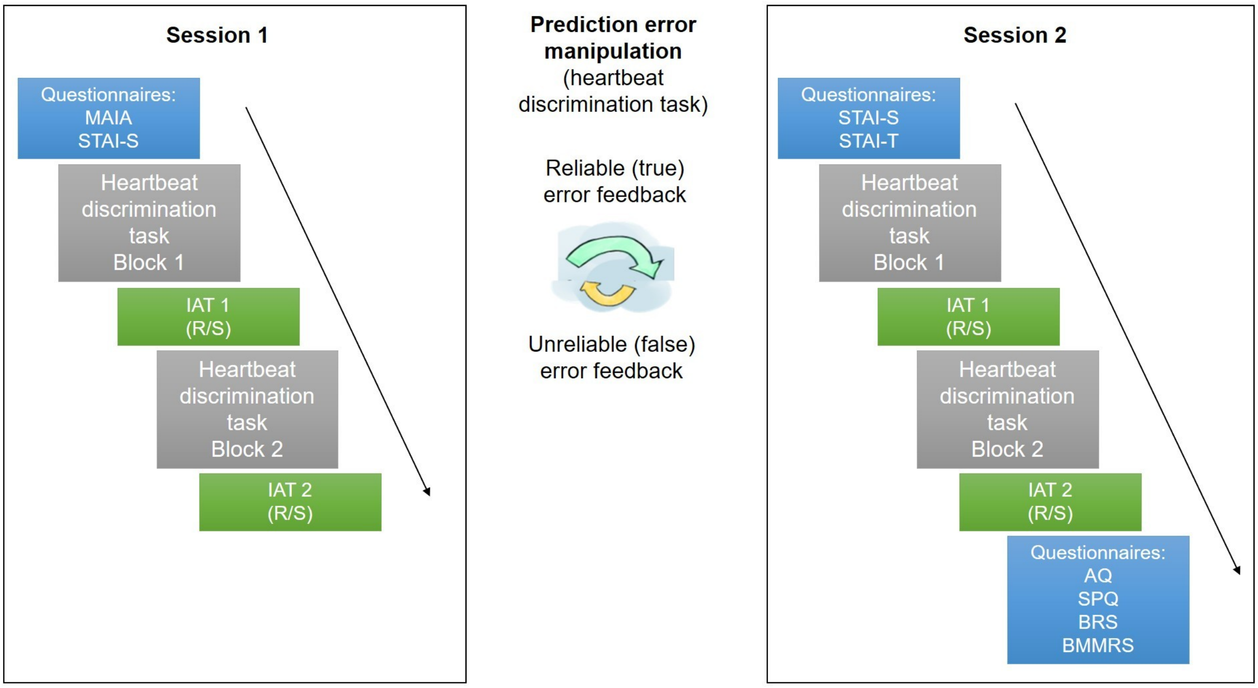

Figure 6. Experiment 2 – experimental design, procedures and timeline.

The stimuli, procedure and duration of the HDT were identical to Experiment 1. The only difference was the presence of response feedback after participant's responses in each trial. In particular, a black tick mark was presented to indicate a correct response, and a black "X" mark of the same size was presented to indicate an error. The feedback was presented for 1 s, after which the following trial began (see Fig. 7, left panel, for trial and task timeline).
Error feedback manipulation was achieved the following way: in the true feedback condition, the feedback was reliable, as it indicated "correct" when the given response was correct and "wrong" when the response was erroneous. The exception was made for the stimuli of level 0, namely the heartbeats with frequency equal to participant's own, because in that case, there was no correct response, since there was no option to reply "my heartbeat is equal to the one in the audio". For these stimuli, the

“correct”/“wrong” feedback was presented with a 50/50% probability, assuring that throughout the task there was an equal number of “correct” and “wrong” feedback occurrences for the stimuli of level 0. In the false feedback condition, the same 50/50% feedback presentation was used for the level 0, and the feedback was always true (reliable) in the extreme levels (i.e., -12, -9, 9 and 12). The latter was done in order not to make the feedback manipulation too obvious for the participants, and to manipulate it only at the levels where the heartbeat discrimination was more difficult. Therefore, in the four intermediate levels (-6, -3, 3 and 6), the feedback was rendered unreliable. Within each of these levels, this was done by presenting valid/invalid feedback with a 50/50% probability, thus making it reliable only in 50% of trials of each level. The order of feedback conditions (sessions) was counterbalanced across participants.

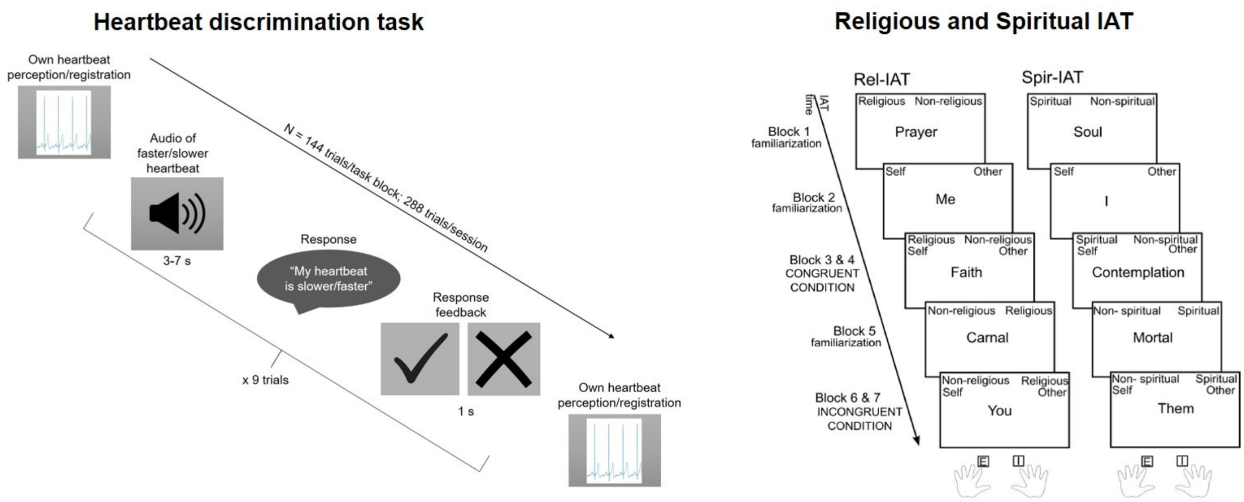

Figure 7. Experiment 2 – timeline of the heartbeat discrimination task and the religious and spiritual IATs.

Statistical analysis

Data preprocessing, visualization and analysis approach for the HDT and the IATs were as in Experiment 1.
Subjective ratings of the perceived difficulty and performance (VAS) in the HDT were compared between the experimental conditions with a paired-sample t test (two-tailed). Each of the psychophysics parameters in the HDT

was entered in a 2x2 repeated-measures ANOVA with Feedback type (true, false) and Block (block 1, block 2) as within-subject factors.

D scores, standardized error rate and standardized RTs in the religious and spiritual IATs were analyzed with 2x2 repeated-measures ANOVAs with IAT type (religious, spiritual) and Feedback (true, false) as within-subject factors. For each of the parameters, post-hoc 2x2 ANOVAs were performed with the addition of the total scores of AQ and SPQ, respectively, as continuous predictors. For all analyses, Tukey HSD correction was applied to post-hoc paired comparisons when they were performed.

The scores on the STAI-S were compared between the two experimental conditions (true vs false feedback) with a Wilcoxon signed-ranked test. Other questionnaires are presented in a descriptive manner as the sample characterization.

Finally, as a validation of the present variant of the HDT, exploratory Spearman correlations were performed between the psychophysics parameters in the true feedback condition averaged for the two task blocks, subjective performance and difficulty, and the questionnaires (MAIA, STAI-T and STAI-S in the true feedback condition).

Data and code availability

All tasks scripts and analyses code and files, as well as all raw and processed data of the HDT, the IATs and the questionnaires are publicly available in the OSF repository (https://osf.io/4jvsp/?view_only=c83dbc455aff4c1593902cb34faa5d0c).

Results

All descriptive statistics are presented in Supplementary table 5.

Sample characteristics

STAI-T scores indicated that participants, on average, had high levels of trait anxiety.

State anxiety (STAI-S) was moderate and did not differ significantly between the two experimental conditions ($W = 143.50$, $p = 0.16$, $r = 0.15$).
Similarly to the sample in Experiment 1, the scores on eight MAIA subscales were around the middle of the 0-5 scale for all subscales, except for slightly higher scores on the subscales Noticing (awareness of bodily sensations) and Emotional awareness (awareness of the connection between bodily sensations and emotional states).
Participants' religiosity and spirituality, according to the *BRS*, can be summarized as follows. 23.3% consider themselves slightly or moderately religious, respectively; 3.3% reported being very religious; 43.3% not religious; 3.3% replied "do not know". 23.3% are slightly spiritual; 36.7% are moderately spiritual; 30% are very spiritual; 10% are not spiritual. In the past ten years, 43.3% have become less religious; 30% became more religious; 10% remained the same; 16.7% never were religious. Of the participants that reported being religious, 36.7% identify as Roman Catholic; 6.7% as Buddhist (despite having indicated in the general demographic data that they either were raised Catholic, or non-religious); 30% are non-religious; 20% replied "do not know".
In the *BMMRS*, the average score ± SD was 71.28±18.26, suggesting a below-average level of religiosity and spirituality in the sample (see Supplementary Table 5 for the scores on all subscales).

Heartbeat discrimination task

Subjective ratings of the *perceived task difficulty* indicated that the false feedback condition was perceived as significantly more difficult than the true feedback condition ($t(23) = -4.90$, $p < 0.001$, $d = -1.00$). The ratings of the *perceived performance* (perceived accuracy) were significantly lower in the false feedback condition compared to the true feedback one ($t(23) = 5.95$, $p < 0.001$, $d = 1.22$). Together, this suggests that, even though the feedback manipulation was not explicitly noticed by the participants, it successfully induced differences in the subjective perception of the seemingly identical task.

As regards the *psychophysics* results of the HDT, a 2x2 repeated-measures ANOVA performed on the JND showed a significant interaction of Feedback x Block [$F(1, 23) = 7.17$, $p = 0.01$, $\eta_p^2 = 0.24$], which was driven by a significantly larger JND in the false feedback condition compared to the true feedback condition in block 2 of the task ($p_{corr} = 0.03$; see Fig. 8). No significant main effects of Feedback [$F(1, 23) = 2.69$, $p = 0.12$, $\eta_p^2 = 0.11$] or Block [$F(1, 23) = 0.16$, $p = 0.69$, $\eta_p^2 = 0.007$] were present.
The 2x2 repeated-measures ANOVAs performed on the other analyzed parameters (PSE, d' and *c*) showed no significant effects or interactions (see Supplementary Table 6 for full results). Furthermore, considering AQ or SPQ scores as a continuous predictor did not yield any significant effects of personality traits.

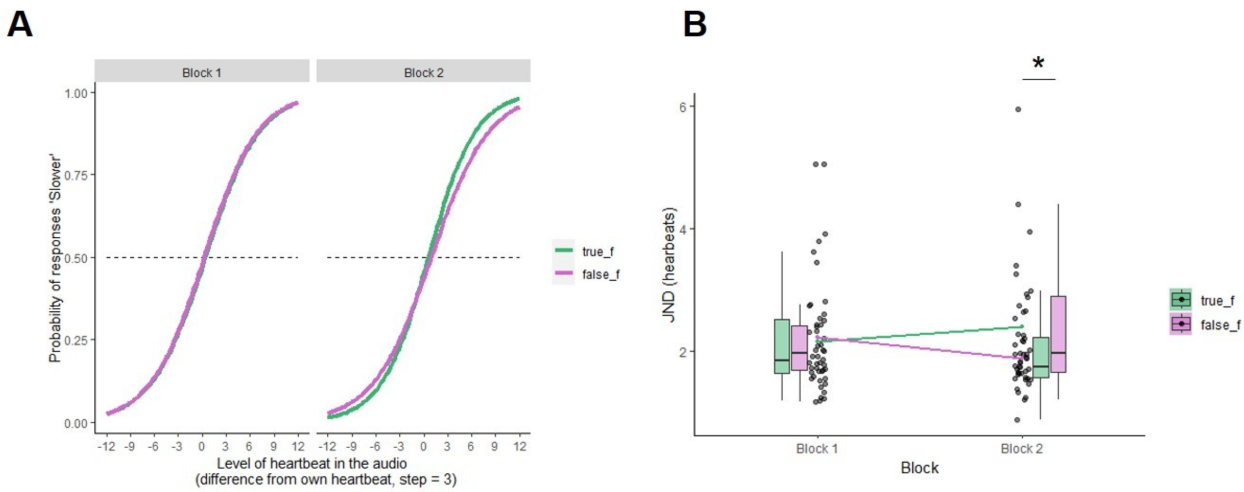

Figure 8. **A**. Psychometric function in the true- and false feedback conditions of the heartbeat discrimination task plotted by task block; **B.** The just noticeable difference (JND) values per feedback type and task block. In the boxplot, hinges of the box represent the first and the third quartile, with the line in the middle of the box representing the median and the bottom and top whiskers representing the smallest and the largest value no further than 1.5*IQR from the lower and the upper hinges, respectively. The colored lines show the trend per feedback type. * = significant difference; "true_f" = true feedback condition, "false_f" = false feedback condition.

Exploratory correlations between the HDT measures and the subjective performance and difficulty of the task showed that higher perceived task

difficulty was significantly correlated with more positive JND ($r = 0.49$, $p = 0.02$); subjective task performance was correlated negatively with JND ($r = -0.41$, $p = 0.04$). As regards STAI and MAIA, higher STAI-T scores were positively correlated with JND ($r = 0.47$, $p = 0.02$); MAIA subscale Noticing was positively correlated with the PSE ($r = 0.60$, $p = 0.002$). Full results are presented in Supplementary Table 9.
To summarize, false error feedback resulted in reduced sensitivity (JND) compared to the true error feedback, and this was modulated by learning effects, since the difference between the feedback types was observed only in the second block of the task, but not by autistic or schizotypal personality traits.

Religious and Spiritual Implicit Associations Tests

No significant effects or interactions were observed for the D scores, standardized error rate and reaction times (see Supplementary Table 7 for full results). However, with AQ as a continuous predictor, a 2x2 repeated-measures ANOVA for IAT type x Feedback showed a significant main effect of Feedback [$F(1, 1, 22) = 4.61$, $p = 0.04$, $\eta_p^2 = 0.17$], indicating that the D scores in both R- and S-IAT were significantly lower after the false feedback condition in the HDT compared to the true feedback condition, see Fig. 9A. The main effect of IAT type was not significant [$F(1, 1, 22) = 0.038$, $p = 0.85$, $\eta_p^2 = 0.002$], nor the main effect of the covariate [AQ score, $F(1, 22) = 3.27$, $p = 0.08$], nor any of the interactions: IAT type x Feedback [$F(1, 1, 22) = 0.05$, $p = 0.83$, $\eta_p^2 = 0.002$], IAT type x AQ [$F(1, 1, 22) < 0.001$, $p = 0.99$, $\eta_p^2 < 0.001$], Feedback x AQ [$F(1, 1, 22) = 3.93$, $p = 0.06$, $\eta_p^2 = 0.15$], IAT type x Feedback x AQ [$F(1, 1, 22) = 0.12$, $p = 0.73$, $\eta_p^2 = 0.005$].
To further investigate the role of AQ in the observed significant effect of Feedback, exploratory Pearson correlations were performed for the total AQ score and the D scores in true and false feedback conditions in both IATs. Significant negative correlation was present between the AQ and the D scores in the true feedback condition in both IATs (S-IAT: $r = -0.45$, $p = 0.027$; R-IAT: $r = -0.45$, $p = 0.026$); see Fig. 9B. No significant correlations were present for

the D scores in the false feedback condition, nor for a difference between false and true feedback conditions (see Supplementary Table 8).

Similarly considering AQ as a continuous predictor in the analyses of the standardized error rate and RTs did not yield any significant effects or interactions. SPQ as continuous predictor did not affect the analyses of any of the parameters.

Summarizing, implicit religiosity and spirituality decreased following the false feedback condition in the interoception task, with the prevalence of autistic personality traits potentially influencing this effect via low levels of R&S in the control condition (true feedback).

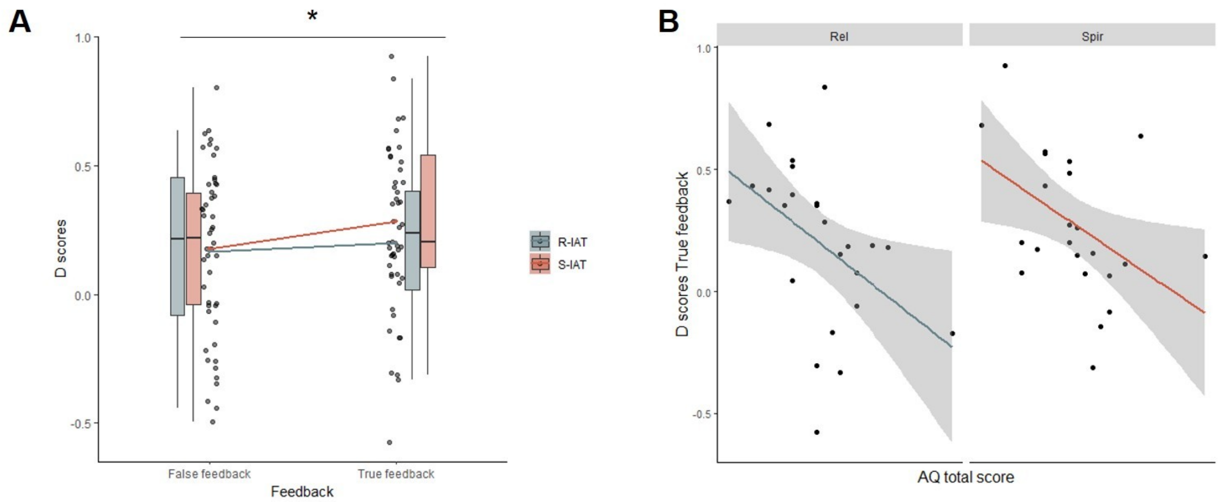

Figure 9. **A**. D scores per IAT type and feedback condition. In the boxplot, hinges of the box represent the first and the third quartile, with the line in the middle of the box representing the median and the bottom and top whiskers representing the smallest and the largest value no further than 1.5*IQR from the lower and the upper hinges, respectively. The colored lines show the trend per feedback type. * = significant difference; **B**. Correlations between the D scores in the true feedback condition and the AQ total scores; “R-IAT” = Religious IAT; “S-IAT” = Spiritual IAT”; “Rel” = Religious IAT; “Spir” = Spiritual IAT.

Discussion

In the present study, we manipulated prior beliefs and prediction error related to cardiac interoception (i.e., heartbeat discrimination), and investigated the effects of those manipulations on the levels of implicit religiosity and spirituality (R&S). In summary, in keeping with the hypotheses, inducing prior beliefs about changes in the heartbeat perception via sham brain stimulation resulted in increased R&S compared to a baseline condition (Experiment 1). Instead, decreasing reliability of error feedback in the same HDT led to decreased sensitivity in the heartbeat discrimination and decreased implicit R&S (Experiment 2). Contrary to the hypothesis, autistic and schizotypal personality traits did not affect the susceptibility to the experimental manipulations, or the corresponding changes in the R&S levels.

Validity of the Heartbeat discrimination task

Using a valid and sensitive measure of interoceptive accuracy has been a major challenge in psychological research [41,42], and several types of measures have been proposed [43]. The variant of the HDT employed in the present study was developed in order to allow inducing directional effects of prior beliefs manipulation, namely beliefs about perceiving the heartbeat as slower or faster, depending on the assigned experimental group. To this end, the task required the participants to judge whether the heartbeats they heard as audios were slower or faster than their own heartbeat, rather than evaluating the synchronicity of their heartbeat with an external stimulus, as in the classical HDT [16,17]. Similarly to the classical task, the variant adopted in the present study was still subjectively perceived as difficult (mean = 66.8/100 in the baseline condition of Experiment 1). However, the classical HDT often proves to be too difficult [majority of participants have d' < 0.75, i.e., reply below chance level; [44]], while in the present study, the performance was good (lowest mean d' at baseline in Experiment 1 = 1.88±0.64). Crucially, in Experiment 1, i.e., without error feedback, the performance worsened significantly over time (i.e., d' decreased and JND increased in block 2 of each condition), independently of the experimental condition, which suggests that the duration of the task was too long for its difficulty. Instead, adding error feedback (Experiment 2) made the task subjectively easier (mean subjective difficulty = 44.29/100 in the condition with reliable feedback), which corresponded to better performance that did not decrease over time but, rather, was affected by learning effects related to feedback reliability (see details below). Such facilitatory effect of error feedback is consistent with previous studies on error feedback in various contexts (for example, [45,46]). Furthermore, when considering the correlations between the psychophysics and the metacognitive results in both experiments, they were coherent: in both experiments, lower sensitivity (d' or JND) was associated with higher subjective difficulty; in Experiment 2, higher sensitivity (JND) was related to higher perceived performance. In addition, only in Experiment 1, the tendency to perceive the own heart rate as faster was (more positive PSE and *c*) was related to higher perceived difficulty and worse performance. This latter result might suggest that people that perceive their heart rate as faster have lower interoceptive sensibility and accuracy, which might be rooted in lower interoceptive awareness and/or higher anxiety. Indeed, correlations between the psychophysics results and MAIA and STAI seem to confirm this: higher state anxiety was positively correlated both with the tendency to perceive the own heart rate as faster (Experiment 1) and with lower sensitivity (Experiment 2). Anxiety has been often linked to altered interoceptive accuracy, although different studies showed the opposite directions of this alteration and a recent meta-analysis showed no significant relationship between anxiety and interoceptive accuracy [47]. Nevertheless, perceiving the own heart as beating faster when anxiety levels are higher is consistent with increased perception of somatic sensations in the anxious state [48], and the results of the present study are in line with that. As regards the MAIA, the tendency to perceive the own heart rate as faster was related to lower scores on the subscales Noticing and Attention Regulation, while lower sensitivity was related to lower scores on the subscales Trusting and Not-Distracting in Experiment 1. This suggests that, in the more difficult variation of the HDT, lower interoceptive accuracy was observed in individuals that are more prone to distracting themselves from the body sensations and trust their bodies less; in addition, individuals that tended to perceive their heart rate as faster were less able to direct and maintain attention towards their body and were less aware of their body sensations of any modality. This is partially consistent with the existing literature that showed a link between interoceptive accuracy and awareness [29] and further contributes to the discussion on the complex nature of the relationship between different facets of interoception [49].

To summarize, the newly developed variant of the HDT could be considered appropriate in terms of the task difficulty, psychometric properties and relationship with metacognitive interoceptive judgments and interoceptive awareness.

Predictive coding manipulation of the heartbeat discrimination task

As regards the main results of the study, in Experiment 1, the hypotheses were partially confirmed, as we observed a trend of the heartbeat discrimination shifting in the direction of the induced prior, which was represented by the PSE and the *c*. However, for both these psychometric parameters, the effect of the prior induction was significant only in the interaction with the task block, and the follow-up analyses showed that the only significant difference was present for the *c* at baseline (block 1 < block 2). Indeed, both PSE and *c* were considerably more negative in the first block of the baseline condition than in the second, which could have driven the opposite pattern of results in the two blocks for the “decrease” prior group. In detail, the “decrease” group received the instructions that, in the stimulation condition, they would perceive their heartbeat as slower; however, in the first block of the baseline, they already had a bias towards replying “slower” much more than “faster”. As a result, the sham stimulation instructions did not further strengthen this effect. The “increase” prior group had the same bias in the first block of the baseline, but the sham stimulation instructions shifted the proportion of their responses towards more responses “faster”, as hypothesized. This tendency to underestimate one’s own heart rate has been previously demonstrated [50]; moreover, the mean underestimation has been shown to be around -7 BPM, which is larger than the one in the present sample (mean PSE in block 1 of baseline was around -3 BPM). Interestingly, in the present study, this bias decreased in the second block of the baseline, possibly due to the learning effects. In summary, despite the fact that the prior belief manipulation shifted the PSE and the *c* in the direction of the prior, a baseline bias towards underestimating one’s heart rate possibly created large discrepancies in the baseline vs stimulation differences between the task blocks and the prior groups, thus affecting the overall results.

However, at a trend level, such placebo manipulation of prior beliefs about cardiac interoception proved efficient.

In Experiment 2, introducing reliable vs unreliable error feedback allowed manipulating the weight of the prediction error. In line with the hypothesis, unreliable error feedback decreased the sensitivity (i.e., increased the JND) because unreliable feedback is generally misleading and, therefore, it impairs learning and has negative effects on the decision making [e.g., [51,52]]. In terms of the predictive coding theory, unreliable error feedback would provide false information for the consequent updating of the prediction model, which would lead to increasingly false judgments about the sensorial information that would follow. These unreliable judgments about the sensorial information, in turn, would increase the reliance on the error feedback in an attempt to correct the errors and make the prediction model fit better with the information. Moreover, the detrimental effects of the unreliable feedback were present only in the second block of the task, suggesting that learning reinforces the effects of feedback reliability over time, in line with [53]. Overall, in the present HDT, the error feedback manipulation acted as hypothesized.

Taken together, the results of the two experiments confirmed that interoceptive processes, in this case, cardiac interoception, might be explained by the predictive coding theory and predictive processing models [54,55]. By selectively modulating the two components of the predictive coding model – the prior beliefs and the prediction error – we showed how the differential weighting of these components affects cardiac interoception.

It is worth pointing out that, contrary to the hypothesis, in either of the experiments, the individual susceptibility to the experimental manipulations was not mediated by autistic or schizotypal personality traits. In particular, considering that autistic traits are related to a stronger reliance on sensorial evidence, and schizotypal traits are linked to a higher weighting of predictions [5], we expected that individuals with higher prevalence of autistic traits would be less susceptible to the prior beliefs manipulation and more susceptible to the prediction error manipulation, while those with higher prevalence of schizotypal traits would exhibit the opposite pattern. The fact that it was not the case could be related to the lack of large individual variability of prevalent personality traits in our sample; potentially, testing a more diverse sample (e.g., with very high/low AQ and SPQ scores) could yield different results. Another explanation might lie in the type of data that were considered, i.e., the behavioral data, while the studies that described the differences in predictive strategies related to the personality traits were based on neurophysiological data, and in particular, on neural oscillations [5,9].

Effects of predictive coding manipulation on implicit religiosity and spirituality

The central question of the present study was whether manipulating different components of the predictive processing model of interoception would affect R&S. Based on the existing theoretical accounts of the R&S [2], we hypothesized that R&S would increase after a relative boost of prior beliefs/predictions, and decrease when more weight would be given to the prediction error monitoring. In addition, we hypothesized that these effects would be selective, namely that spirituality, but not religiosity, would be affected by the manipulation of interoceptive predictive processing. The former hypothesis was confirmed: boosting prior beliefs about cardiac interoception increased the implicit R&S, while boosting the reliance on error feedback decreased them. However, there was no dissociation between religiosity and spirituality, as they were similarly affected, which contradicts the latter hypothesis.

The fact that R&S respectively increased or decreased in correspondence with the increased weighting of prior beliefs or prediction error monitoring confirms the predictive coding account as the fundamental mechanism of R&S, as previously suggested by van Elk and Aleman [2]. Moreover, our results provide direct evidence that R&S rely on the increased weighting of prior beliefs, together with decreased prediction error monitoring. Crucially, the changes in the R&S were observed even though the predictive coding model was manipulated in relation to interoception, rather than during the measurement of the R&S. This further supports the idea that the R&S experiences are rooted in the perception of bodily signals and experiences [2], to the extent that altering the processing of these signals is able to change the R&S [14,27,56].

The lack of dissociation between the R&S in terms of their changes following the modulation of interoceptive processing might be explained by the complexity of both phenomena, which cannot be measured fully independently from each other. Theoretical accounts of the R&S define religiosity as the cognitive and the ritualistic dimensions of the religious commitment, and spirituality as its experiential dimension [12], and the R- and S-IATs employed in the present study were validated to reflect that dissociation [14]. Based on this, it is reasonable to assume that religious experiences should revolve more around the perception of the external world, and spiritual experiences should be rooted primarily in the bodily experiences. Indeed, it has been recently demonstrated that stimulating the vagus nerve decreased spirituality but not religiosity, possibly through boosting interoception but not exteroception [14]. However, it is possible that, beyond such direct manipulations, both R&S are related to the processing of both internal and external signals, although the internal and external information might be weighted differently within them. In fact, even the ritualistic component of religiosity commonly involves body-related practices and experiences, such as movements, postures, and alteration of bodily states, for example fasting [57]. Therefore, both R&S might be subserved, at least in part, by the predictive processing of interoceptive information, and either the present experimental manipulations of interoception, or the measures of the implicit R&S were not able to capture a clear dissociation between them. In addition, the HDT requires to focus not only on the internal sensations from the heart but also on the external stimuli (audios of the heartbeats). Therefore, it involves both interoception and exteroception, which might partially explain its effects on both R&S.
Notably, similarly to the results of the HDT, the observed changes in the R&S were not influenced by the individual differences in the prevalence of autistic and schizotypal personality traits. The only instance in which autistic personality traits explained part of the results was the reduction of the R&S following the unreliable error feedback compared to the reliable one. There, higher prevalence of autistic personality traits was negatively correlated with both R&S at baseline (i.e., in the reliable feedback condition), which is in line with the literature [10]. Possibly, individuals with higher AQ scores had very low levels of R&S already at baseline, and therefore, their R&S did not decrease

further following the error feedback manipulation. Apart from that, however, the personality traits did not affect the susceptibility to the experimental manipulations of the R&S. Possibly, as in the case of the HDT, our behavioral data did not reflect the connection between the personality traits and the individual predictive strategies that has been previously shown for the neural oscillations [5].

Conclusions

The present study manipulated the weighting of different components of the predictive processing within cardiac interoception in order to influence implicit R&S. In a variant of the HDT, we were able to induce changes in the heartbeat discrimination that corresponded with the induction of prior beliefs, or with the manipulation of error feedback reliability. As a consequence, R&S increased following the increased weighting of prior beliefs and decreased following the boosted reliance on prediction error monitoring. Together, these results shed light on the mechanisms that underlie the predictive coding account of the R&S, and in particular, they suggest that R&S experiences and phenomena rely more on predictions and less on prediction error monitoring. Future studies might focus on investigating the neural/neurophysiological indices of the observed behavioral changes in the cardiac interoception and the R&S following the predictive processing modulations. In particular, brain oscillations of certain frequencies have been linked to the distinct components of the predictive coding model: prior beliefs may be reflected in the neuronal activity in alpha and beta frequencies, while prediction error is related to the activity in the gamma frequency [58-60]. Furthermore, as mentioned above, recent studies suggested that individual predictive strategies, which might be related to the personality traits, are reflected in the balance of prior-related alpha activity and stimulus-related theta activity [5,9]. From this perspective, adding neurophysiological data to the behavioral results of the present study might provide further insights into the predictive coding mechanisms of the R&S and interoception.

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Data availability statement

All raw and processed data collected and analyzed in the study are publicly available in the OSF repository (https://osf.io/4jvsp/?view_only=c83dbc455aff4c1593902cb34faa5d0c).

Competing Interests

The authors declare that they have no competing interests.