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# Biasing predictive processing of interoceptive information affects implicit spirituality but not religiosity

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ABSTRACT

In a predictive processing framework, religiosity and spirituality (R&S) have been linked to increased reliance on prior knowledge and decreased prediction error monitoring. In addition, R&S might be differentially related to processing exteroceptive and interoceptive information. The present study aimed at manipulating different components of the predictive processing model (prior and prediction error monitoring) in interoception, and evaluating the resulting changes in implicit R&S. In a variant of the heartbeat discrimination task (HDT), we used a sham transcranial magnetic stimulation protocol with verbal suggestions to induce priors about a perceived decrease or increase of the heartbeat frequency (Experiment 1). Prediction error monitoring was modulated by manipulating error feedback reliability in an identical HDT (Experiment 2). Results showed that the point of subjective equality shifted towards the direction of the induced prior compared to the baseline condition only in the direction of decreased heartbeat frequency (Experiment 1), while the sensitivity (just noticeable difference) decreased with unreliable error feedback (Experiment 2). Crucially, implicit spirituality, but not religiosity, increased following the prior induction in the HDT in the "decrease" prior group, and this effect was gauged by the prevalence of autistic personality traits. No significant change in R&S was observed after the unreliable error feedback. An increase of implicit spirituality following the successful induction of priors in the interoceptive processing highlights the role of predictive processing in R&S and the stronger relation of interoception with spirituality than with religiosity, supporting the predictive coding account of R&S.

## 1. Introduction

Neurocognitive bases of religiosity and spirituality (R&S) are gaining increasing interest as a field of study. Indeed, within the emerging neuroscience of religious cognition, the amount of experimental data on the neural correlates of R&S is growing (Grafman et al., 2020). However, at present, there is no consensus on the neurocognitive mechanisms of R&S, partially due to a large variability of methods and measures that often contradict each other (van Elk & Aleman, 2017).

Even though, at present, there is no single definition of these constructs [for discussion, see (Paloutzian & Park, 2005)], religiosity is typically defined as a set of formal institutionalized beliefs, practices and traditions. In turn, spirituality is considered as more experience-related and transcendent, concerning one's beliefs and values "in regard to self, others, nature, life, and whatever one considers to be the Ultimate (Elkins et al., 1988). Therefore, R&S might be considered as distinct facets of a multidimensional phenomenon (Hill et al., 2000).

One promising theoretical approach to R&S is the recently proposed framework of R&S (van Elk & Aleman, 2017) that capitalizes on the predictive brain account (Friston et al., 2006). According to this account, perceptual experiences are based on the incoming sensory information that is interpreted in the context of predictions (priors) about upcoming sensory events (prior knowledge and beliefs). Whenever a discrepancy between the priors and the sensory information occurs, a prediction error is generated; priors are then dynamically updated in order to minimize the prediction error (Apps & Tsakiris, 2014; Friston

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et al., 2006). In relation to R&S, these experiences might be underpinned by a differential weighting of priors and prediction error in perceptual processing (van Elk & Aleman, 2017). In detail, religious and spiritual experiences might be rooted in a particular processing of sensory information that consists in stronger reliance on priors compared to the sensory evidence, in combination with reduced prediction error monitoring. In other words, according to the proposed framework, the acceptance and maintenance of religious and spiritual beliefs and experiences rely on the lack of updating of the complex pre-existing beliefs via reduced prediction error monitoring during the processing of exteroceptive and interoceptive information. The reduction of prediction error monitoring, and thus the maintenance of the R&S beliefs, might explain both lower-level perceptual phenomena, such as visions, and higher-level predictions that are at the basis of complex belief systems (van Elk & Aleman, 2017). Attenuated prediction error monitoring reduces the effects of prediction error signals when sensory information contradicts the priors, which further reinforces the pre-existing beliefs and the reliance on them (Schjoedt et al., 2013; van Elk & Aleman, 2017).

The individual differences in the relative weighing of priors and sensory information, which might underlie the differences in the R&S beliefs, might be related to the prevalence of certain personality traits. In particular, it has been shown that individual predictive strategies are related to the prevalence of autistic or schizotypal personality traits in the general population. Accordingly, 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 priors, while in SSD, the reliance on pre-existing models is prioritized over sensory information (Corlett et al., 2019; Sinha et al., 2014; Sterzer et al., 2018; Tarasi et al., 2023; Tarasi, Trajkovic, et al., 2022). From this perspective, differences in the weighting of priors and sensory information might reflect also the individual differences in R&S. Indeed, higher reliance on priors 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 (Crespi et al., 2019).

Moreover, another aspect highlighted by the predictive coding theoretical framework of R&S is the fact that the prediction error signals concern both exteroceptive and interoceptive information, as both these modalities are crucial for R&S (van Elk & Aleman, 2017). Interestingly, however, R&S might be dissociated in the weighting of the incoming perceived information about external events and bodily signals. This lies in the fact that, as described above, religiosity typically concerns more institutionalized aspects of beliefs, such as traditions and rituals of religious communities, namely the ritualistic and cognitive dimensions of the multidimensional model of religious commitment (Glock, 1962). In turn, spirituality is based on the experience-related 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 (Hood & Chen, 2005). 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, and vice versa, religiosity is based more on exteroceptive information (van Elk & Aleman, 2017). Indeed, a recent study (Finisguerra et al., 2019) provided support to this hypothesis by demonstrating that implicit spirituality, but not religiosity, decreased when brain areas involved in interoception (Critchley & Harrison, 2013) were stimulated via the auricular branch of the vagus nerve, which plays a prominent role in conveying interoceptive signals to the brain. To summarize, R&S could be interpreted within the predictive coding account, which suggests an increased weighting of priors over sensory 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 considerations remain theoretical and have not been tested directly as components of a single model.

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 priors or prediction error related to interoception. We capitalized on the fact that R&S, while being extremely complex and multifaceted, are also plastic and can rapidly change, for example, following non-invasive brain stimulation of brain regions like the right inferior parietal cortex (Crescentini et al., 2014; Crescentini et al., 2015), or following transcutaneous vagus nerve stimulation (Finisguerra et al., 2019). Therefore, we aimed to induce rapid changes in the implicit R&S representations following the changes in the weighting of the priors and the prediction error monitoring. Rather than searching for a correlation between individual levels of R&S and the susceptibility to the manipulation of priori beliefs or prediction error, here we aimed at a causal pathway evidence, investigating whether and at what extent inducing a change in the weighting of prior or prediction error affects R&S. To test the second aspect of the theoretical model, that is the dissociation between religiosity and spirituality in terms of their reliance on exteroceptive and interoceptive processing, respectively, we focused on manipulating the interoceptive processing but not the exteroceptive, expecting a greater influence on spirituality than religiosity.

In Experiment 1, priors about the frequency of participants' heartbeat were induced via a placebo sham transcranial magnetic stimulation (TMS) combined with verbal suggestions about the direction of the cardiac change (decreased/increased heart rate) in a variant of the 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, the HDT was administered over two blocks (halves) in each condition, and either implicit religiosity or implicit spirituality was measured in each block (counterbalancing across participants) and compared between control and experimental conditions (Experiment 1: no stimulation vs sham TMS with verbal suggestions; 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 the psychometric function model, namely, point of subjective equality, PSE, and just noticeable difference, JND. Finally, by considering the impact of individual differences in weighting predictions vs sensory information, autistic and schizotypal personality traits were evaluated as variables that could influence the individual susceptibility to the manipulations.

We hypothesized that: 1) in Experiment 1, inducing priors about the effects of sham TMS on the heartbeat perception would a) shift the PSE in the direction of the prior, without affecting the sensitivity (JND), and b) it would increase implicit spirituality but not religiosity; 2) in Experiment 2, decreasing the reliability of error feedback about one's heartbeat perception with unreliable error feedback would a) decrease the sensitivity (i.e., increase the JND) in the HDT, without affecting the PSE since no directional manipulation of the error feedback was implemented, and b) it would decrease implicit spirituality but not religiosity; 3) in both experiments, learning effects might occur in the HDT, thus increasing the effects of the experimental manipulations from block 1 to block 2; 4) higher prevalence of schizotypal traits and lower prevalence of autistic traits would be related to a) stronger effects of prior induction, and therefore, higher increase of spirituality, in Experiment 1, and b) lower susceptibility to the feedback manipulations and the resulting lower decrease of spirituality in Experiment 2. Finally, in both experiments, we administered two questionnaires to measure the subjective R&S of the sample, a questionnaire to measure subjective levels of interoceptive awareness and a questionnaire assessing perceived levels of state and trait anxiety. The two latter questionnaires were included in an exploratory correlation analysis for the performance indices of the HDT, as a proxy of interoceptive accuracy, and the subjective components of interoception.

## 2. Experiment 1 – prior manipulation

### 2.1. Methods

#### 2.1.1. 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 and absence of the exclusion criteria for TMS (Rossi et al., 2009)]. Participants received course credits for completing the experiment. 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 1964 Declaration of Helsinki and its revisions. Participants were informed that they were involved in studies of R&S and interoception, but no explicit mention was made about the relation between the two dimensions. Information about the experimental hypotheses was provided only at the end of the experimental sessions.

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 (Faul et al., 2007) confirmed that this sample size, with alpha level = 0.05 and power = 0.80 in a 2 × 2 × 2 mixed-effects ANOVA, was sufficient to detect a medium effect size ($f = 0.26$).

#### 2.1.2. Pre-registration of experiments

The method and analysis plan were pre-registered on the Open Science Framework (OSF) prior to data collection (https://osf.io/ng75f/overview). 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.

#### 2.1.3. Setup and procedure

*2.1.3.1. Experimental design.* The study consisted of two experimental sessions that lasted 2.5–3 h each and were administered at least two days apart (*Mean* ± *SD* = 7.00 ± 6.41 days). The sessions had an identical structure (see Fig. 1) and differed only in the presence/absence of the prior induction via sham-TMS, according to the experimental condition (stimulation and baseline, respectively). The order of conditions (Stimulation, Baseline) was counterbalanced across participants. 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 association tests (R-IAT or S-IAT, depending on the counterbalanced 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. These questionnaires were all administered at the end of the second session to avoid any unwanted effects of exposing participants to information that could hint at the nature of the study, apart from the instructions to the main experimental tasks. 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 variables.

*2.1.3.2. Heartbeat discrimination task.* The present study employed a

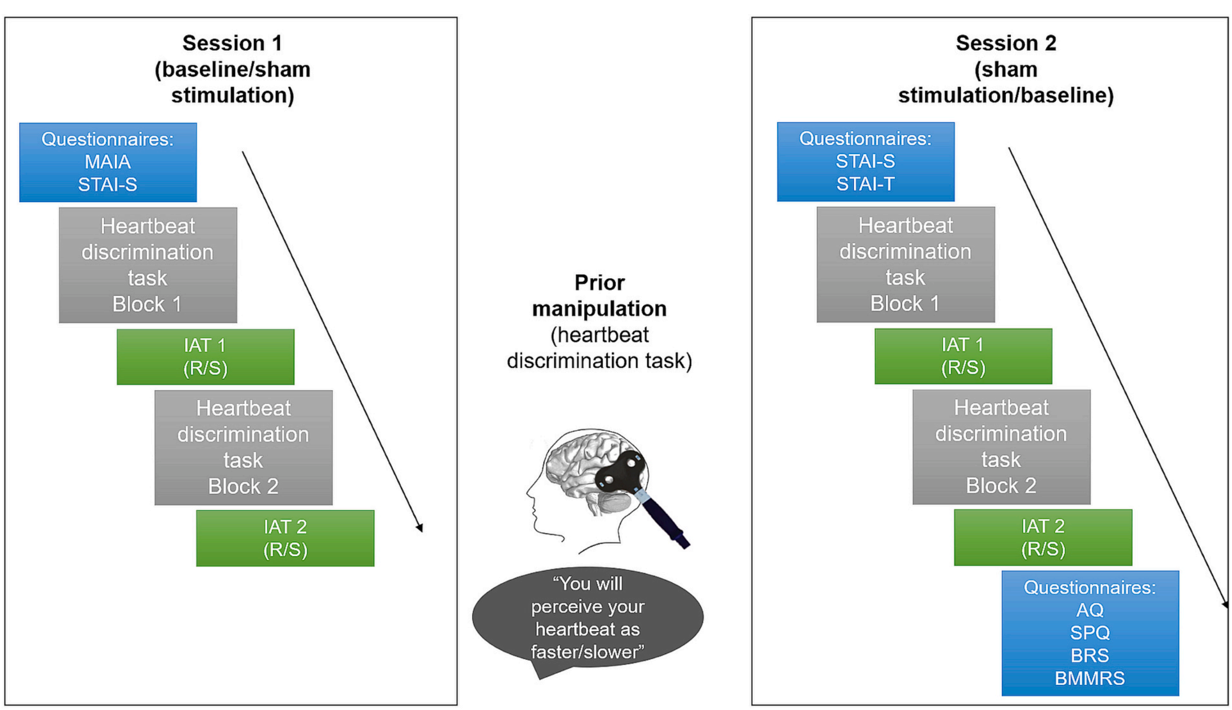


**Fig. 1.** Experiment 1 – experimental design, procedures and timeline.

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 (Khalsa & Lapidus, 2016; Whitehead et al., 1977). In combination with psychophysics measures, it allows evaluating perceptual sensitivity independently from non-perceptual factors (Rominger et al., 2021).

In the present study, the HDT was modified in order to allow inducing directional priors 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 × 1200 pixels), working in battery supply mode, via a custom code that used the Psychophysics Toolbox extensions (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997) 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 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 runs with identical structure. In the beginning of each run participants were instructed to perceive their own heartbeat for 20 s. 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 addition, 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 performance on a 0–100 visual analogue scale (VAS).

*Prior manipulation.* During the Stimulation condition, participants' beliefs about their heart rate perception were manipulated using a placebo manipulation where sham single-pulse TMS was delivered together with instructions that were aimed at inducing priors towards a certain

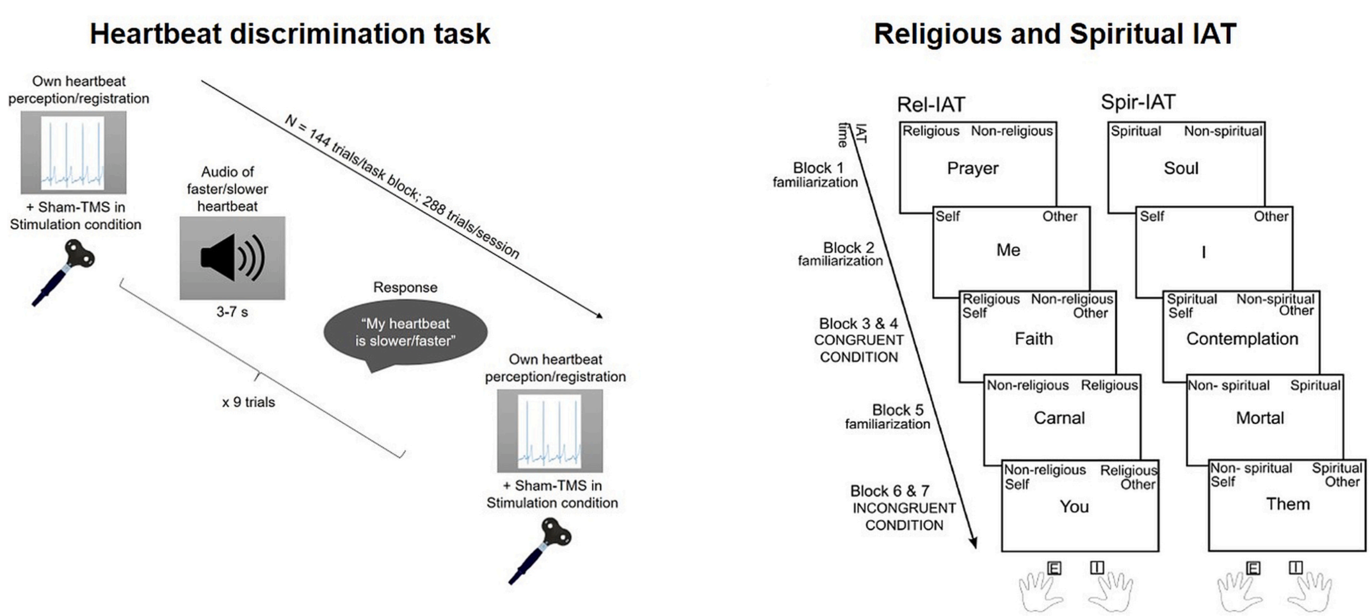


**Fig. 2.** Experiment 1 – timeline of the heartbeat discrimination task and the R- and S-IATs.

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. A single-pulse TMS was 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 verbal suggestion served to induce priors about the stimulation and provided a false statement about the possible effects of TMS on the heartbeat perception. The instructions 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 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 performance in the task was indexed by fitting of the psychometric function and the resulting measures of PSE and JND were computed for each participant, condition and task block using the MixedPsy package for R (Priscilla et al., 2022). 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 (Kingdom, 2016). In this case, negative PSE indicates a tendency to underestimate the own heart rate frequency with respect to the audios, and vice versa for the positive PSE. Smaller JND represents higher sensitivity. While we initially preregistered the analyses of the HDT also according to Signal Detection Theory (i.e., sensitivity and criterion), here we focused on the psychophysics indexes of PSE and JND since they allow considering the level 0 (i.e., where the frequency of the heartbeats in the audios was equal to participant's heart rate frequency), where the induction manipulation is likely to exert more effects.

*2.1.3.3. 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 (Finisguerra et al., 2019).

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 × 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 R&S dimension (for example, "prayer" for the religious category and "soul" for the spiritual category) and 10 words associated with the non-R&S dimension in R-IAT/S-IAT (for example, "concreteness" for the non-religious category and "mortal" for the non-spiritual category). In addition, 12 stimuli associated with the Self-Other pronoun dimension (such as "I", "mine", "you", "your") were used in both IATs. The full list of stimuli for each category is presented in Supplementary table 1.

The *procedure* was identical in both IATs and followed the standard IAT structure (Greenwald et al., 2003), 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 R&S categories, and the other response key was used for the Other-pronouns and the non-R&S categories. Conversely, in the incongruent blocks, the same response key was expected for the Self-pronouns and the non-R&S categories, and the other one for the Other-pronouns and the R&S categories. 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 min. 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) (Greenwald et al., 2003). Higher D scores indicate higher implicit preference for the congruent categories; in this case, stronger association between the self and R&S. In addition, error rate 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, respectively (Crescentini et al., 2014; Crescentini et al., 2015; Finisguerra et al., 2019), 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 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.

*2.1.3.4. Questionnaires.* We administered the AQ and SPQ questionnaires to assess the prevalence of autistic and schizotypal personality traits, respectively. As described in the introduction, these indices were considered as factors that could influence the susceptibility to the experimental manipulation in the HDT. Furthermore, we administered MAIA to characterize the subjective component of interoception, and the STAI to measure state (STAI-S) and trait (STAI-T) anxiety. The scores of these questionnaires were used in the exploratory correlation analysis between the objective (HDT) and subjective facets of interoception. Finally, subjective R&S of the sample was characterized via the BMMRS and BRS. The detailed description of the questionnaires is presented in the Supplementary materials.

MAIA, STAI, AQ and SPQ were administered in *E*-prime 2, and

BMMRS and BRS were administered online (on the same laboratory PC as the other questionnaires) 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.

### 2.1.4. Statistical analysis

Data preprocessing and visualization for the HDT and the IATs were performed with R software in R Studio (R Core Team, 2020). Statistical analyses were performed with JASP (JASP Team, 2024). The effect size was estimated as partial eta squared ($\eta_p^2$) for ANOVA (small: 0.01, medium: 0.06, large: 0.14) for main effects and interactions, as Cohen's $d$ for pairwise comparisons (small: 0.2, medium: 0.5, large: 0.8), or point-biserial correlation coefficient r for 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). To test the hypotheses about the effects of the prior induction in the HDT (hypotheses 1a and 3), *psychophysics* indexes at the HDT, namely the PSE and the JND, were separately entered in 2 × 2 × 2 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 variables.

To test the hypothesis about the effects of the prior manipulation in the HDT on the R&S (hypothesis 1b), D scores, standardized error rate and standardized RTs at the R- and S-IATs were analyzed with 2 × 2 repeated-measures ANOVAs with IAT type (religious, spiritual) and Condition (baseline, stimulation) as within-subject variables.

To test the hypothesis about modulation of the effects by personality traits (hypothesis 4a), for each of the parameters, the main analyses were followed up by ANOVAs performed with the addition of the total scores of AQ and SPQ, respectively, as continuous predictors. Whenever significant interactions of AQ or SPQ with other factors were present, follow-up correlation analyses were performed to explore the role of the personality traits in those interactions.

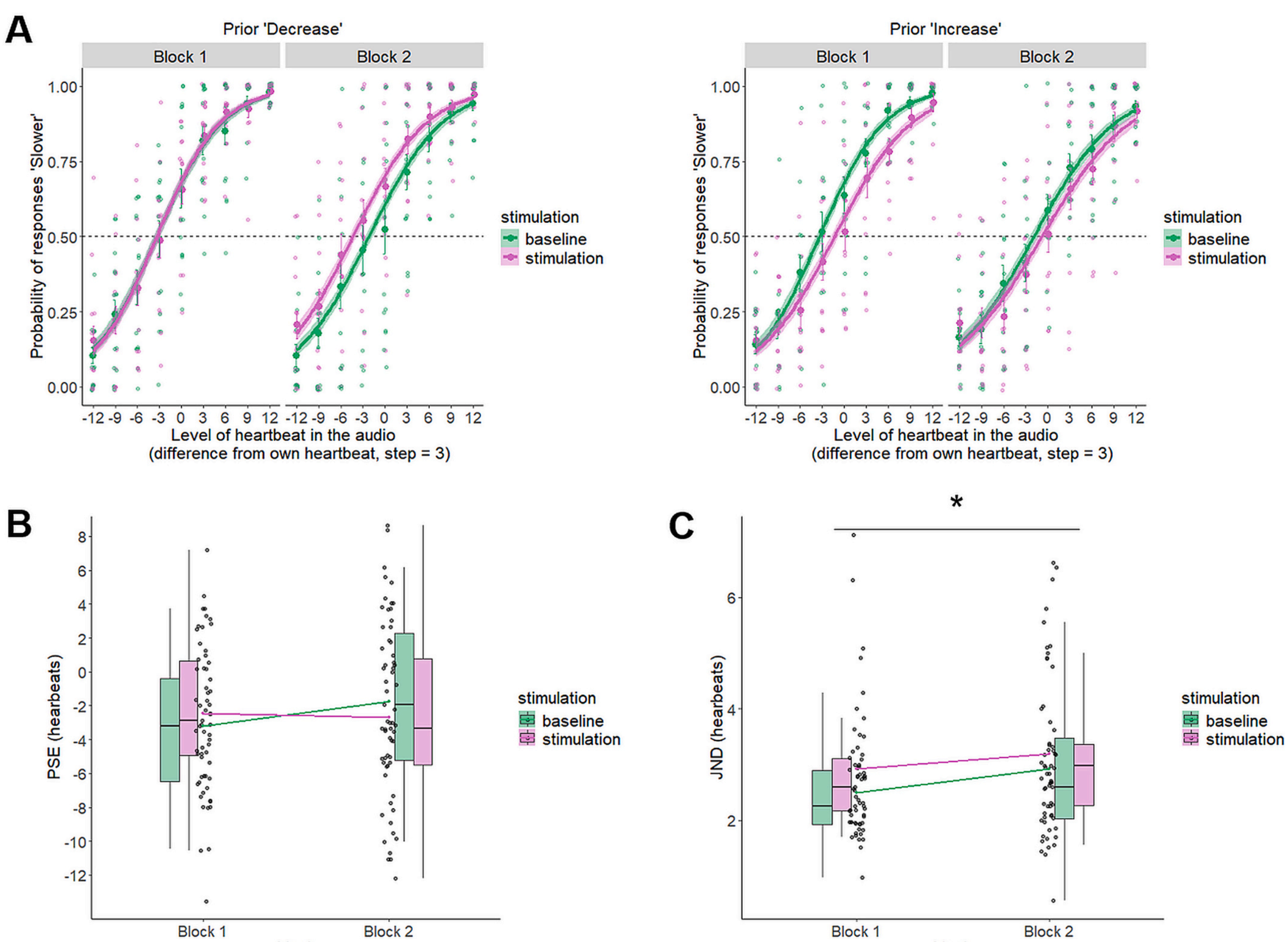


**Fig. 3.** **A.** Psychometric function in the baseline and stimulation conditions of the heartbeat discrimination task plotted by task block in the "decrease" (left) and "increase" (right) prior group. In each plot, the sample mean is represented by the solid line, and the shaded area around it represents the standard error; the bigger dots represent the mean at each level and the whiskers represent the standard error; the smaller dots represent individual participants' values; **B.** The PSE values plotted for the interaction of condition x task block; **C.** The JND plotted for the interaction of condition x task block. For **B**—**C**, 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 dots represent individual participants' values. The colored lines show the trend per task block. * = significant difference.

#### 2.1.5. Data and code availability

All task 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=98dc29387d6b465399fdfe456e2ce2a0).

### 2.2. Results

All descriptive statistics and full output of all statistical analyses are presented in the Supplementary materials. The sample characterization at questionnaires and the exploratory correlation analysis are presented in the Supplementary materials.

#### 2.2.1. 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 priors about the effects of sham stimulation on the interoceptive performance did not influence the subjective perception of the task.

Regarding the *psychophysics* results of the HDT, while visual inspection of the psychometric functions (Fig. 3A) would suggest a tendency of the decrease and increase groups to provide, respectively, more or less "slower" responses in the stimulation than in the baseline session, thus following the prior induction manipulation, the main effect of Prior group and its interactions were all non-significant in the analysis of PSE (all $F < 2.85$; $p > 0.1$; see Supplementary table 3). The analysis of the PSE yielded only a significant interaction between Stimulation and Block [$F(1, 29) = 4.80$, $p = 0.04$, $\eta_p^2 = 0.14$]. However, none of the post-hoc paired comparisons with Tukey HSD correction resulted to be significant (see Fig. 3B).

In a similar vein, a significantly decreased sensitivity (JND) 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 [$F(1, 29) = 5.53$, $p = 0.03$, $\eta_p^2 = 0.16$], 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 3 for full results).

The follow-up analyses to test the possible modulation effects of the personality traits on the HDT indicated that the results concerning the PSE were significantly modulated by the total AQ score, but not by the total SPQ score. In particular, when the AQ was added as a continuous predictor in the 2x2x2 mixed effects ANOVA for the PSE, we observed a significant main effect of Stimulation [$F(1, 27) = 7.93$, $p = 0.009$, $\eta_p^2 = 0.23$], with more negative PSE in Stimulation compared to Baseline. In addition, this effect, and the interaction of Stimulation x Prior type, interacted significantly with the AQ score: Stimulation x AQ score [$F(1, 27) = 9.57$, $p = 0.005$, $\eta_p^2 = 0.26$], and Stimulation x Prior type x AQ score [$F(1, 27) = 7.27$, $p = 0.01$, $\eta_p^2 = 0.21$]. No other significant effects or interactions were present; see Supplementary table 4 for full results.

The effects of the significant interaction of stimulation condition and prior group with the AQ score were followed up by the analyses performed on two groups of participants that were divided by prior type (decrease and increase group), considering the hypothesized differences in the direction of the stimulation effect on the PSE in the two groups. For each group, we performed a $2 \times 2$ mixed effects ANOVA (Stimulation x Block) with AQ score as a continuous predictor.

In the *"decrease"* prior group, there was a significant main effect of Stimulation [$F(1, 14) = 15.38$, $p = 0.002$, $\eta_p^2 = 0.52$], with significantly more negative PSE in the stimulation condition compared to the baseline. Furthermore, there was a significant interaction of Stimulation x AQ score [$F(1, 14) = 20.33$, $p < 0.001$, $\eta_p^2 = 0.59$]. No other significant effects or interactions were present; see Fig. 4A and Supplementary table 5 for full results. The significant Stimulation x AQ interaction was further explored by computing Pearson correlation coefficient between the index of PSE change (stimulation minus baseline averaged for the two blocks of the task) and the AQ scores. There was a significant negative correlation between the two parameters ($r = -0.77$, $p < 0.001$, *Fischer's* $z = -1.02$), suggesting that higher prevalence of autistic traits was associated with a larger shift of the PSE in the direction of the induced prior in the stimulation condition; see Fig. 4B. To further investigate the observed negative correlation between the PSE shift and the AQ scores, in an exploratory analysis, we explored the possible differences between the prevalence of autistic traits and HDT performance, in case the observed effects were related to the differences at baseline. In particular, it is possible that lower reliance on priors and higher reliance on sensory information in people with higher prevalence of autistic traits (Tarasi, di Pellegrino, & Romei, 2022) might result in less biased (more correct) cardiac interoception. To this end, we computed Pearson correlation coefficient between the PSE at baseline (averaged for the two blocks of the task) and the AQ scores, and observed a significant positive correlation between the two parameters ($r = 0.64$, $p = 0.008$, *Fischer's* $z = 0.75$). This suggests that people with higher prevalence of autistic traits tended to underestimate less their heart rate frequency at baseline.

In the *"increase"* prior group, no significant effects or interactions were present, suggesting that the prior induction did not influence the PSE in the stimulation condition, and the prevalence of autistic traits did not modulate this pattern of results; see Fig. 4A and Supplementary table 6 for full results.

To summarize, in the HDT, there was a significant effect of prior induction (sham stimulation) in the interaction with task block, which, however, was not explained by post-hoc paired comparisons. Therefore, despite the trend of the PSE shifting in the direction of the induced prior in the second block of the task, the pairwise comparison was not significant in the whole group. The observed pattern of results was significantly modulated by prevalence of autistic personality traits, and this effect was different for the two prior groups. In detail, in the "decrease" prior group, the PSE shifted in the direction of the induced prior, and this effect was stronger for people with higher prevalence of autistic personality traits, who also tended to be more precise in perceiving their heart rate frequency at baseline. On the other hand, no significant effects were observed in the "increase" prior group. In addition, in the entire sample, the sensitivity decreased in the second block of the task regardless of the stimulation condition or prior group.

#### 2.2.2. Religious and spiritual implicit associations tests

A $2 \times 2$ 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 regardless of the IAT type [baseline mean $\pm$ SE $= 0.05 \pm 0.06$, stimulation mean $\pm$ SE $= 0.30 \pm 0.11$; $t(30) = -2.21$, $p = 0.04$, $d = -0.40$]. 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 RTs (See Supplementary table 7 for full results).

In the follow-up analyses, the results for the standardized error rate were modulated by the total AQ score, but not the total SPQ score. In detail, when AQ score was added as continuous predictor in the $2 \times 2$ ANOVA for standardized error rate, there was a significant main effect of IAT type [$F(1, 29) = 4.57$, $p = 0.04$, $\eta_p^2 = 0.14$] and Stimulation [$F(1, 29) = 5.39$, $p = 0.03$, $\eta_p^2 = 0.16$], suggesting overall higher implicit spirituality than religiosity, and higher R&S after Stimulation compared to Baseline. Furthermore, there was a significant interaction of IAT type x Stimulation [$F(1, 29) = 5.73$, $p = 0.02$, $\eta_p^2 = 0.17$]. Post-hoc paired

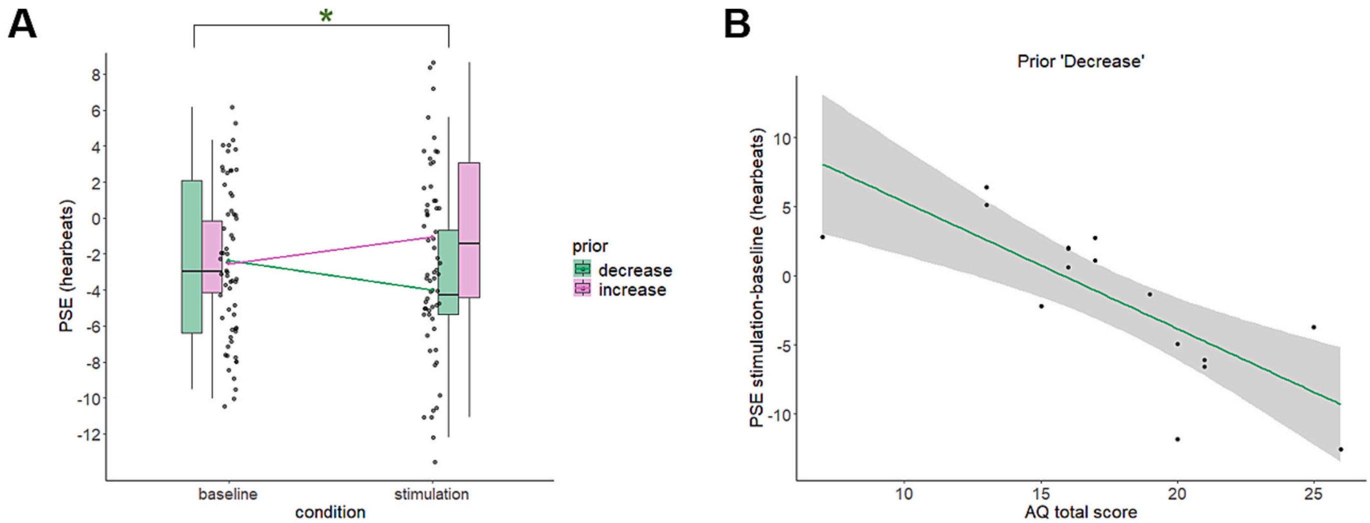


**Fig. 4.** **A.** The PSE values per stimulation condition in the "decrease" and "increase" prior groups; in the boxplot, hinges of the box represent the first and the third quartile, with the line in the middle of the box representing the median and the bottom and top whiskers representing the smallest and the largest value no further than 1.5*IQR from the lower and the upper hinges, respectively. The dots represent individual participants' values. The colored lines show the trend per task block; **B.** Correlation between the shift in the PSE (stimulation-baseline) and the AQ scores in the "decrease" prior group. * = significant difference.

comparisons indicated that the interaction was driven by a significantly higher standardized error rate in the S-IAT after Stimulation compared to the Baseline ($p_{corr} = 0.03$); see Fig. 5. The AQ score did not interact significantly with any of the factors (see Supplementary table 8), therefore, its effects were not investigated further. For the D score and the standardized RTs, there were no significant effects of personality traits (AQ and SPQ) considered as a continuous predictor.

Considering that the changes in the R&S IAT were investigated in relation to the prior manipulation in the HDT, where the effects of the prior induction were limited to the "decrease" prior group and were moderated by the prevalence of the autistic personality traits, we conducted an exploratory moderation analysis to determine whether the prevalence of the autistic traits influenced also the effects of the HDT on the R&S IAT. In detail, to examine whether autistic traits moderated the relationship between changes in the PSE in the HDT and changes in R&S, we conducted a moderation analysis using the PROCESS module in JASP

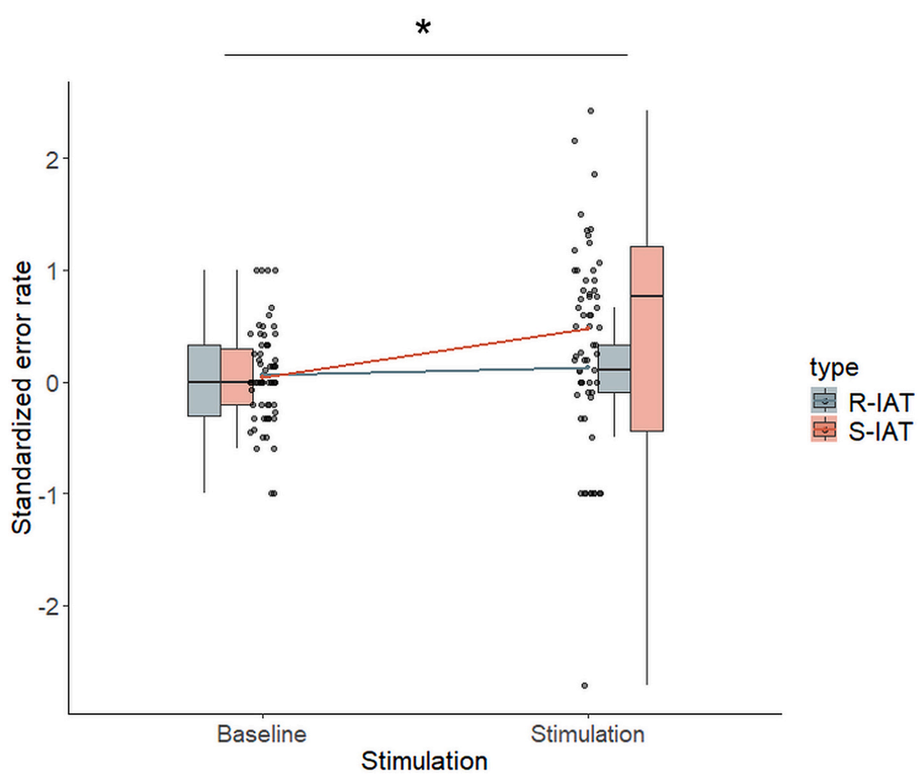


**Fig. 5.** The standardized error rate (accuracy) per IAT type and stimulation condition. In the boxplot, hinges of the box represent the first and the third quartile, with the line in the middle of the box representing the median and the bottom and top whiskers representing the smallest and the largest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

(Hayes, 2018), specifying Model 1. The analysis was conducted separately for the two prior groups of the HDT, since the hypothesized, and partially observed, effects have different direction and magnitude, and separately for the S- and R-IAT. In each model, the dependent variable was the change in the standardized error rate (stimulation-baseline in S-IAT and R-IAT), the independent variable was the change in the PSE (PSE stimulation-baseline), and the prevalence of autistic traits (total AQ score) was included as a continuous moderator. All continuous variables were mean-centered prior to analysis. Confidence intervals were estimated using bias-corrected bootstrapping (5000 bootstrap samples).

In the *"decrease"* prior group, the moderation analysis conducted for the *S-IAT* revealed a significant interaction between the PSE shift and the autistic traits ($\beta = 0.021$, $SE = 0.008$, $p = 0.011$). Conditional effects indicated that the PSE shift in the direction of the prior predicted an increase in implicit spirituality only at low levels of autistic traits ($\beta = -0.14$, $SE = 0.07$, $p = 0.045$), but not at medium ($\beta = -0.08$, $SE = 0.06$, $p = 0.17$) or high levels ($\beta = 0.007$, $SE = 0.05$, $p = 0.89$). These results indicate that the relationship between the PSE shift in the HDT and changes in implicit spirituality is conditional on the prevalence of autistic traits, such that the effect is present at lower levels of autistic traits and diminishes as the trait levels increase. An identical moderation analysis conducted for the *R-IAT* showed a non-significant trend of the interaction between the PSE shift and the autistic traits ($\beta = -0.01$, $SE = 0.006$, $p = 0.096$) and no other significant effects (all $p > 0.05$). In the *"increase"* prior group, the moderation analyses for either of the IATs did not show any significant effects or interactions (all $p > 0.05$).

In summary, implicit spirituality and religiosity increased after the stimulation condition of the cardiac interoception task. This result showed an increase of R&S after the prior induction, but not a dissociation between R&S. When the analysis factored in the prevalence of autistic personality traits, this effect became differentiated, that is there was a significant increase in spirituality, but not religiosity, following the prior induction. An exploratory moderation analysis suggested that, in the "decrease" prior group of the HDT, individual differences in the prevalence of autistic traits shaped the extent to which changes in the HDT in the stimulation condition were associated with the increase in the implicit spirituality but not religiosity.

## 3. Experiment 2 – prediction error manipulation

### 3.1. Methods

#### 3.1.1. Participants

Twenty-seven healthy adult volunteers without history of neurologic and psychiatric diseases gave written informed consent to participate in the study, with the same recruitment procedure used in Experiment 1. All participants were students at the University of Udine (Italy); none of them participated in Experiment 1. 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 (Faul et al., 2007) confirmed that this sample size, with alpha level = 0.05 and power = 0.80 in a 2 × 2 repeated-measures ANOVA, was sufficient to detect a medium-to-large effect size ($f = 0.30$).

#### 3.1.2. Pre-registration of experiments

The method and analysis plan were pre-registered on the Open Science Framework (OSF) prior to data collection (https://osf.io/ng75f/overview). 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.

#### 3.1.3. Setup and procedure

The study had similar design and procedures to Experiment 1, consisting of two sessions of 2.5–3 h each that were administered at least 2 days apart (*Mean* ± *SD* = 6.5 ± 7.1 days). 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 order of the two feedback sessions was counterbalanced across participants. 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 2 × 2 within-subject design with Feedback type (true, false) and Block of HDT (block 1, block 2) as within-subject factors.

The HDT task was the same 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 as follows: 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.

#### 3.1.4. 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). To test the hypotheses about the effects of error feedback reliability on the HDT (hypotheses 2a and 3), each of the psychophysics parameters in the HDT was entered in a 2 × 2 repeated-measures ANOVAs with Feedback type (true, false) and Block (block 1, block 2) as within-subject variables.

To test the hypothesis about the effects of the prior manipulation in the HDT on the R&S (hypothesis 2b), D scores, standardized error rate and standardized RTs in the religious and spiritual IATs were analyzed with 2 × 2 repeated-measures ANOVAs with IAT type (religious, spiritual) and Feedback (true, false) as within-subject variables.

To test the hypothesis about modulation of the effects by personality traits (hypothesis 4b), for each of the parameters, post-hoc 2 × 2 ANOVAs were performed with the addition of the total scores of AQ and SPQ, respectively, as continuous predictors. Whenever significant interactions of AQ or SPQ with other factors were present, follow-up correlation analyses were performed to explore the role of the personality traits in those interactions.

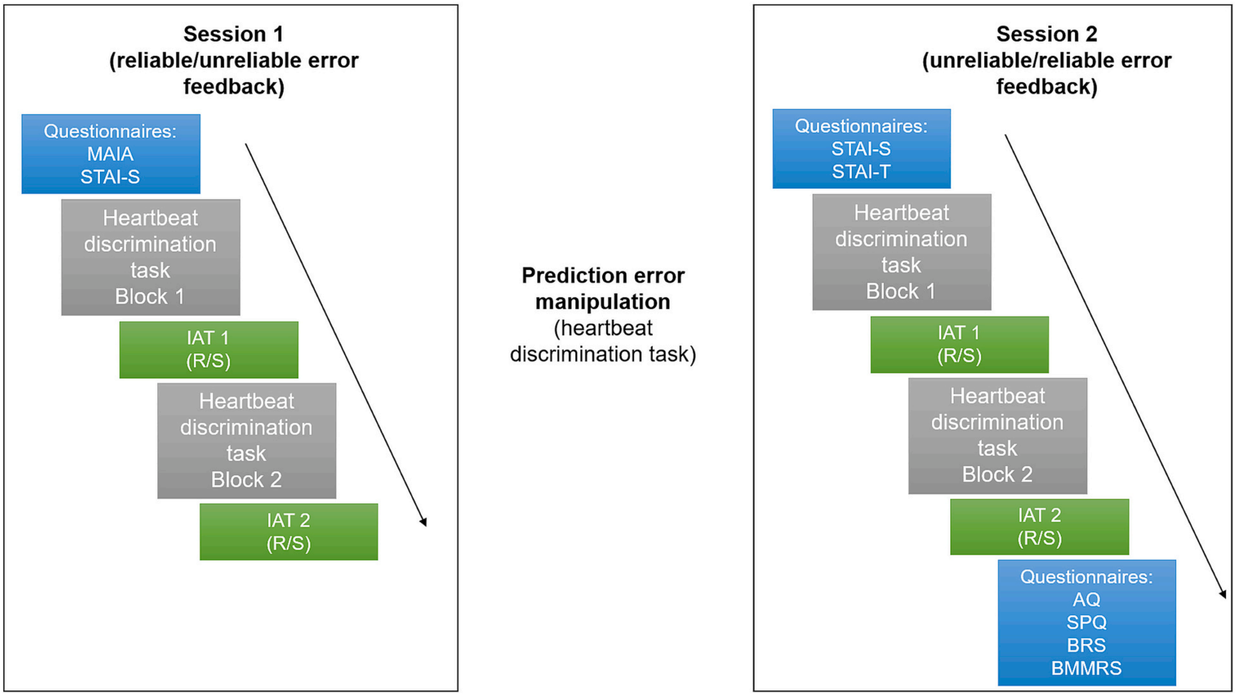


**Fig. 6.** Experiment 2 – experimental design, procedures and timeline.

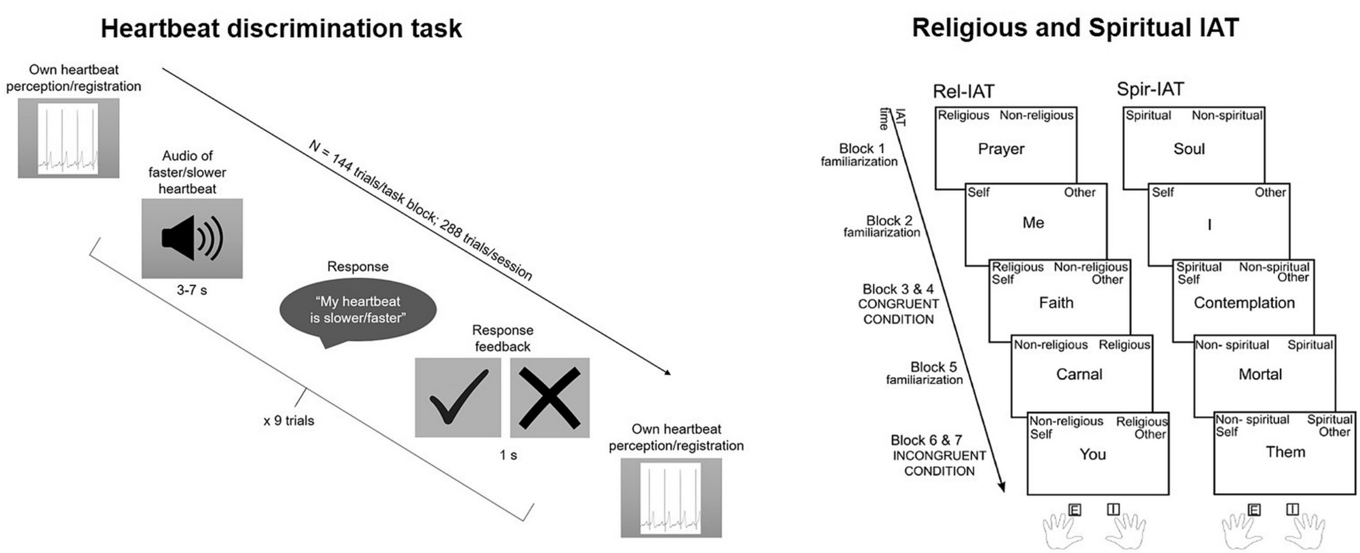


**Fig. 7.** Experiment 2 – timeline of the heartbeat discrimination task and the religious and spiritual IATs.

### 3.1.5. *Data and code availability*

All task 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=98dc29387d6b465399fdfe456e2ce2a0).

## 3.2. *Results*

All descriptive statistics and full output of all statistical analyses are presented in the Supplementary table 10. The sample characterization at questionnaires and the exploratory correlation analysis are presented in the Supplementary materials.

### 3.2.1. *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* 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 (as suggested by their feedback during the debriefing after the study), it successfully induced differences in the subjective perception of the seemingly identical task.

As regards the *psychophysics* results of the HDT, the psychometric function for each condition is plotted in Fig. 8A. A 2 × 2 repeated-measures ANOVAs performed for the PSE showed no significant effects or interactions (see Fig. 8B and Supplementary table 11 for full results).

A 2 × 2 repeated-measures ANOVA performed on the JND showed a

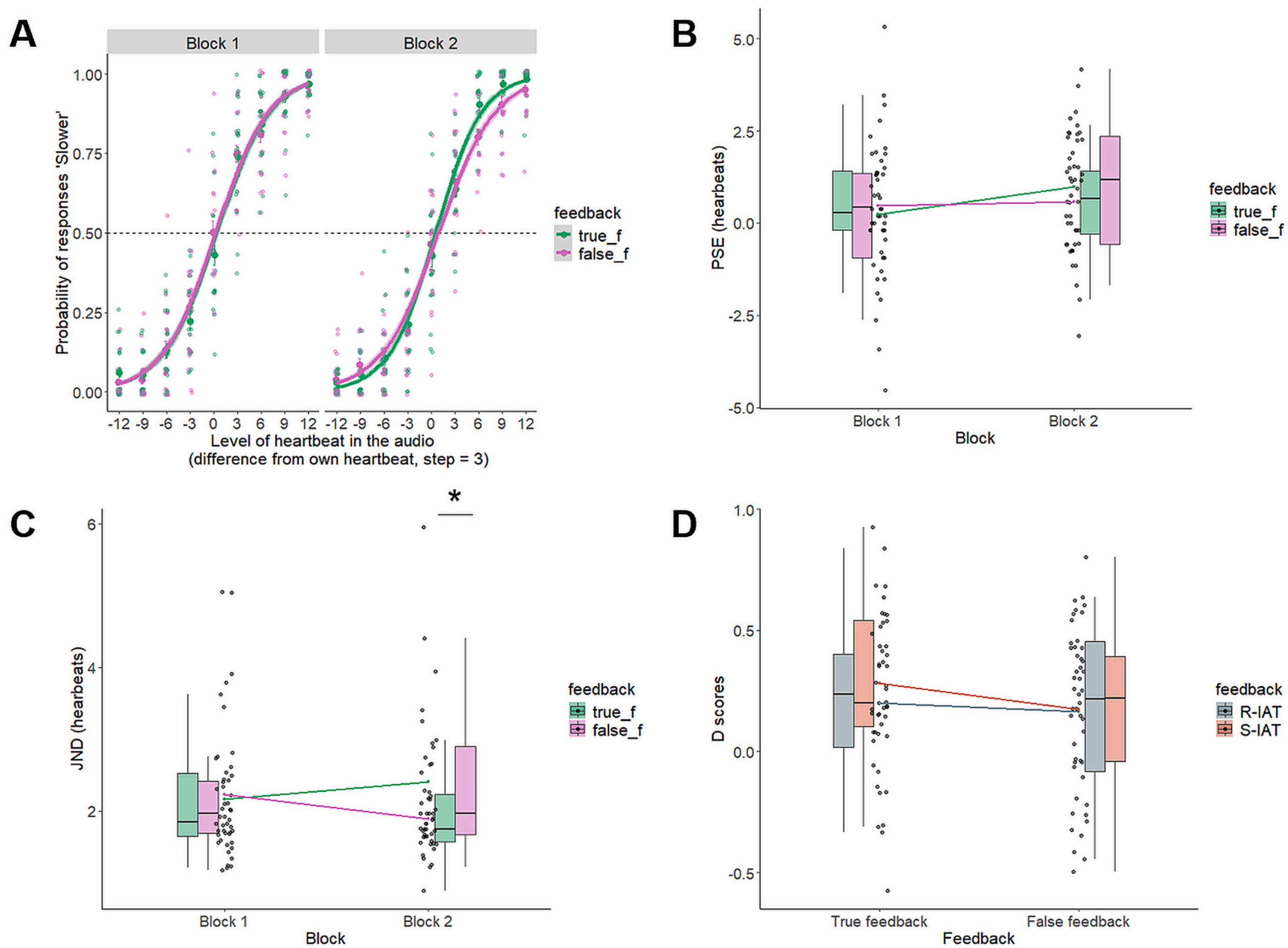


**Fig. 8.** **A**. Psychometric function in the true- and false feedback conditions of the heartbeat discrimination task plotted by task block. The sample mean is represented by the solid line, and the shaded area around it represents the standard error; the bigger dots represent the mean at each level and the whiskers represent the standard error; the smaller dots represent individual participants' values; **B.** The PSE values per feedback type and task block; **C.** The JND values per feedback type and task block; **D.** D scores per IAT type and feedback condition. For panels B—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 dots represent individual participants' values. The colored lines show the trend per feedback type. * = significant difference; "true_f" = true feedback condition, "false_f" = false feedback condition, "R-IAT" = Religious IAT; "S-IAT" = Spiritual IAT.

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. 8C). 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.

Follow-up analyses that considered AQ or SPQ scores as continuous predictors did not yield any significant effects of personality traits.

To summarize, false error feedback did not significantly affect the PSE but resulted in reduced sensitivity (larger JND) compared to the true error feedback. This pattern was modulated by learning effects, since the difference between the feedback types was observed only in the second block of the task, but was not modulated by autistic or schizotypal personality traits.

### 3.2.2. *Religious and spiritual implicit associations tests*

No significant effects or interactions were observed for the D scores (Fig. 8D), standardized error rate and RTs; see Supplementary table 12 for full results.

Considering AQ and SPQ as continuous predictors did not affect the analyses of any of the parameters.

Summarizing, implicit religiosity and spirituality were not affected by the error feedback manipulation in the interoception task, nor was this pattern of results modulated by the prevalence of autistic and schizotypal personality traits.

## 4. Discussion

In the present study, we manipulated priors 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, partially in keeping with the hypotheses, it was possible to induce priors about perceiving one's heartbeat as slower, but not as faster, using verbal suggestions combined with sham brain stimulation, and this effect was stronger in participants with higher prevalence of autistic personality traits. Furthermore, the prior manipulation resulted in increased R&S compared to the baseline condition. This effect was further differentiated, showing significantly increased spirituality, but not religiosity when the prevalence of autistic personality traits was considered (Experiment 1). Instead, decreasing reliability of error feedback in the same HDT led to decreased sensitivity in the heartbeat discrimination but did not induce changes in R&S

(Experiment 2).

### 4.1. Predictive coding manipulation of the heartbeat discrimination task

Regarding the HDT, in Experiment 1, the main hypothesis about the effects of the prior induction on the PSE (hypothesis 1a) was not confirmed, since, despite a visible trend, there was no significant shift in the heartbeat discrimination (the PSE) in the direction of the induced prior. This might be related to the fact that one prior (decrease) was more efficient that the other (increase). Indeed, this became evident when the prevalence of the autistic personality traits was considered in the analysis: the PSE shifted significantly in the direction of the induced prior only in the "decrease" prior group, and this effect was stronger in participants with higher prevalence of autistic personality traits.

Such difference in the efficacy of the two priors (decrease and increase) might be explained by the differences in the conscious perception, or conscious expectations, about slower and faster heartbeat. Indeed, increased heartbeat frequency might be easier to notice consciously because one is normally familiar with the sensations associated with high heart rate in situations of stress, anxiety or vigorous physical activity, that is when heartbeats can be perceived clearer. For this reason, the "increase" prior might not have been credible when participants' expectations about feeling an increased heart rate were not met.

Concerning the role of the autistic personality traits in the susceptibility to the prior manipulation (hypothesis 4a), the results demonstrated that the heartbeat discrimination shifted according to the prior manipulation ("decrease" group) only in the participants with higher prevalence of autistic traits. This might be explained by the baseline differences between the low- and high-AQ groups in the weighting of sensory information vs priors. Indeed, in the baseline condition, participants with lower prevalence of autistic traits had a stronger bias to underestimate the frequency of their own heart rate. It is therefore possible that the presence of a stronger inherent bias, namely stronger pre-existing individual priors at baseline, made the participants with lower prevalence of autistic traits less susceptible to the experimentally induced bias in the stimulation condition. Conversely, participants with higher prevalence of autistic traits, who initially performed the HDT with less reliance on pre-existing expectations about their heart rate, were influenced more by the experimental prior induction. Thus, the experimental prior induction might have been effective only in those individuals who generally factored in less pre-existing priors in interoceptive processing (participants with higher autistic traits). This is in line with the existing studies about the predictive strategies of individuals with high prevalence of autistic traits (Tarasi et al., 2023; Tarasi, di Pellegrino, & Romei, 2022). In addition, all participants, regardless of the prevalence of the autistic traits, tended to become more correct in the second block of the task, or rather, presented the stronger underestimation bias in the first block. The general tendency to perceive one's own heartbeat as slower than it really is has been previously demonstrated, and the mean underestimation has been shown to be around −7 BPM (Legrand et al., 2022). Interestingly, our results suggest the presence of learning effects throughout the HDT because this bias decreased in the second block.

In summary, in Experiment 1 it was possible to induce priors about the decrease, but not the increase, in heartbeat frequency only in individuals with higher prevalence of autistic personality traits, who could be more susceptible to the prior manipulation due to relying less on their own pre-existing interoceptive expectations. Possibly, testing the entire sample only with the decrease prior condition would have yielded significant effects overall.

In Experiment 2, introducing reliable vs unreliable error feedback allowed manipulating the weight of the prediction error, independently from the prevalence of autistic traits. In line with the hypothesis 2a, 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., (Ernst & Steinhauser, 2015, 2017)]. In terms of the predictive coding account, unreliable error feedback would provide false information for the consequent updating of the prediction model, which would lead to increasingly false judgments about the sensory information that would follow. These unreliable judgments about the sensory information, in turn, would increase the reliance on the error feedback in an attempt to correct the errors and make the prediction model to 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 (Bianco et al., 2022). Overall, in the present HDT, the error feedback manipulation acted as hypothesized. Contrary to the hypothesis 4b, however, neither autistic, nor schizotypal personality traits mediated this result. One possible explanation is that the presence of error feedback increased the reliance on the provided sensory evidence and therefore decreased the weight of inherent priors. As a result, the existing expectations about one's own cardiac interoception might have become less relevant in this task, thus reducing the possible effects of the individual differences in the personality traits.

Taken together, the results of the two experiments confirmed, at least in part, that interoceptive processing, in this case, cardiac interoception, might be framed in predictive coding account and predictive processing models (Barrett & Simmons, 2015; Seth, 2013). By selectively modulating the two components of the predictive coding model – the priors and the prediction error – we showed how the differential weighting of these components affects cardiac interoception.

### 4.2. 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 framework of R&S (van Elk & Aleman, 2017), we hypothesized that R&S would increase after a relative boost of priors/predictions (hypothesis 1b), and decrease when more weight would be given to the prediction error monitoring (hypothesis 2b). 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, and would be modulated by the prevalence of autistic and schizotypal personality traits (hypothesis 4).

The results are partially in line with the hypotheses: boosting priors about cardiac interoception increased the implicit R&S, while boosting the reliance on error feedback did not change the R&S levels. Moreover, the effects of prior induction were modulated by the prevalence of the autistic personality traits: when taken into account as a continuous predictor, the effects of prior induction were observed only for the spirituality, but not for the religiosity. A further analysis was conducted to investigate the causal relation between the prior-belief induction effects in the HDT and the subsequent changes in the levels of R&S, considering the role of the prevalence of autistic traits. It showed that, only in the "decrease" prior group of the HDT (that is the group that had significant effects of the prior induction), individual differences in the prevalence of autistic traits shaped the extent to which changes in the HDT in the stimulation condition were associated with the increase in the implicit spirituality but not religiosity. Together, these results suggest that the increase of both R&S observed in the entire sample in the stimulation condition might be driven by the sub-group of participants in whom the stimulation produced significant effects in the HDT, that is the "decrease" prior group. Only within that group, the causal relation between the stimulation-related changes in the interoceptive processing and the effects on R&S was significant and limited to the spirituality but not religiosity. This relation was moderated by the prevalence of autistic traits in a way that it was significant only among participants with lower prevalence of autistic traits.

An increase of implicit spirituality following the successful induction of priors in the HDT, that is the increased weighting of priors in the interoceptive processing, points to the role of predictive processing in R&S and to the stronger relation of interoception with spirituality than with religiosity, as previously suggested by van Elk and Aleman (2017). In particular, it suggests that higher R&S might be rooted in overreliance on the existing priors and predictive models, and reduced updating (correction) of these beliefs based on error feedback. Even though the results of Experiment 2 did not directly demonstrate the role of error feedback, or at least of its reliability, in R&S changes, the relation between the increased reliance on priors and the decreased error monitoring is inherent: the predictive model is maintained, even if it is erroneous, when the error feedback is not taken into account, which means that the model is not updated. Indeed, this mechanism might sustain religious and superstitious beliefs (Risen, 2016), and the present findings provide the direct support of this account.

Crucially, we observed the changes in spirituality even though the predictive processing model was manipulated in relation to interoception, rather than during the measurement of R&S as such. Possibly, increasing the weighting of the beliefs about one's body perception (interoception) and thus decreasing the weighting of the actual perception of the bodily states, increased the blurring of the boundaries of the self, which is one of the core components of spirituality (Hood & Chen, 2005). This, in turn, resulted in the increased levels of the implicit self-representations of the R&S concepts. This finding supports the idea that R&S are rooted in the perception of bodily signals and experiences (van Elk & Aleman, 2017), to the extent that altering the processing of these signals is able to change R&S (Crescentini et al., 2015; Finisguerra et al., 2019; Urgesi et al., 2010).

The dissociation between R&S in terms of their changes following the modulation of interoceptive processing is in line with the theoretical accounts of R&S that define religiosity as the cognitive and the ritualistic dimensions of the religious commitment, and spirituality as its experience-related dimension (Glock, 1962). Based on this, it is reasonable to assume that the spiritual dimension should be rooted more in the bodily experiences compared to the religious experiences. Indeed, it has been recently demonstrated that stimulating the vagus nerve decreased spirituality but not religiosity, possibly through boosting interoception but not exteroception (Finisguerra et al., 2019). Moreover, the study by Van Cappellen and LePage Drummond (2024) that investigated the link between interoceptive sensibility and various facets of R&S showed that interoceptive sensibility had the strongest association with spiritual experiences, rather than with religious practices. In line with this, the present findings suggest the differential weighting of interoceptive information in R&S, especially highlighting the role of priors about one's interoceptive processing in spiritual but not religious experiences.

Finally, the effect that the autistic traits prevalence had on the relation between the stimulation-related changes in the HDT and the increase of spirituality in the IAT is in line with the notion that higher levels of autistic traits is related to lower levels of spirituality, and vice-versa (Crespi et al., 2019). It is possible that the participants with lower prevalence of autistic traits showed a larger increase in spirituality because they were initially more prone to being spiritual than the participants with higher level of autistic traits. Overall, these results suggest that the effects of prior manipulation are dependent on the baseline state of the balance between the weighting of prior and prediction error in the processing of internal bodily signals.

### 4.3. Validity of the heartbeat discrimination task

Using a valid and sensitive measure of interoceptive accuracy has been a major challenge in psychological research (Brener & Ring, 2016; Murphy et al., 2019), and several types of measures have been proposed (Körmendi & Ferentzi, 2024). The variant of the HDT employed in the present study was developed in order to allow inducing directional effects of prior 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 (Khalsa & Lapidus, 2016; Whitehead et al., 1977). This approach is similar to the heart rate discrimination task introduced by Legrand et al. (2022), and it provides several important methodological advantages over the classical HDT. Namely it allows quantifying the bias in the heartbeat perception and its precision, while being based on a dynamic set of stimuli that are created online based on the actual participants' heart rate.

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 difficult [majority of participants have d' < 0.75 (Desmedt et al., 2023)], while in the present study, the performance was well above chance level. Furthermore, when considering the correlations between the psychophysics and the metacognitive results in both experiments (see Supplementary materials), they were coherent: in both experiments, lower sensitivity (higher JND) was associated with higher subjective difficulty; in Experiment 2, higher sensitivity (lower JND) was related to better perceived performance. In addition, only in Experiment 1, the tendency to perceive the own heart rate as faster (i.e., more positive PSE) 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, as also supported by the correlations between the psychophysics results and the questionnaire scores concerning interoceptive awareness and anxiety levels. To summarize, the newly developed variant of the HDT could be considered appropriate in terms of task difficulty, psychometric properties and relationship with metacognitive interoceptive judgments and interoceptive awareness.

### 4.4. Study limitations

It is important to acknowledge the limited sample size in the presented experiments, especially in the analyses performed within each prior type group. Another limitation concerns the use of explicit self-report measures (questionnaires) to obtain the measures of personality traits. Compared to measures like psychiatric assessments, this might limit the conclusions about the role of autistic and schizotypal personality traits in the predictive processing of interoceptive information and R&S, and together with the limited sample size, limit the generalizability of the present findings. Furthermore, it is necessary to acknowledge that our experimental design implied that one of the IATs was presented between the two blocks of the HDT. Theoretically, one cannot exclude that being exposed to religious or spiritual concepts might have increased the reliance on priors in the consecutive block of the HDT. However, it is unlikely because: 1) in Experiment 1, the effects of prior induction were not stronger in block 2 (that is after being exposed to the first IAT) compared to block 1; 2) in Experiment 2, where no priors were induced but the error feedback was presented, participants' performance followed the feedback, and these effects were stronger in block 2 (after completing the first IAT) than in block 1. This suggests that, even if participants relied on their own pre-existing priors, their responses were driven by the error feedback and this effect got stronger in the second block. Finally, the shift in the responses in the HDT following the prior induction cannot be unambiguously attributed to the shift in the heart rate perception and exclude other confounding factors, such as a general bias in the response behavior. Nevertheless, it is less likely that the results in the HDT in Experiment 1 are related to a general response bias rather than to the experimentally induced priors because, if the former was the case, the general response bias should have been present in both groups of participants (increase and decrease) because they experienced identical sham TMS protocol combined with instructions that differed only in direction of the prior ("increase" or "decrease"). Instead, the prior induction was successful only in the decrease prior group, indicating that the observed effects may be, at least partially, related to cardiac interoception per se.

### 4.5. 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 priors when the expectations were induced about the decrease of the heartbeat frequency, or with the manipulation of error feedback reliability. Spirituality but not religiosity increased following the prior induction in the HDT only in the group susceptible to the prior manipulation in the HDT ("decrease" prior), and this effect was moderated by the prevalence of autistic personality traits. Instead, neither spirituality, nor religiosity changed following the boosted reliance on prediction error monitoring. Together, these results provide empirical support to the theoretical framework of R&S that is based on the predictive coding account (van Elk & Aleman, 2017), suggesting that R&S rely more on predictions and less on the sensory information and prediction error monitoring. Furthermore, they support the notion that, compared to religiosity, spirituality relies more on interoceptive information processing.

Future studies might focus on investigating the neural/neurophysiological indices of the observed behavioral changes in the cardiac interoception and 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: priors may be reflected in the neuronal activity in alpha and beta frequencies, while prediction error is related to the activity in the gamma frequency (Arnal & Giraud, 2012; Betti et al., 2021; Chao et al., 2018). 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 (Tarasi, di Pellegrino, & Romei, 2022; Tarasi, Trajkovic, et al., 2022). From this perspective, investigating the patterns of brain oscillations that might be at the basis of the behavioral results of the present study might provide further insights into the predictive coding mechanisms of R&S and interoception.

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## CRediT authorship contribution statement

**Maria Pyasik:** Writing – original draft, Visualization, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Elena Marini:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Giuseppe Ippolito:** Writing – review & editing, Software, Methodology, Conceptualization. **Gabriele Fusco:** Writing – review & editing, Methodology, Conceptualization. **Luca Tarasi:** Writing – review & editing, Conceptualization. **Alessandra Finisguerra:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Vincenzo Romei:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Cosimo Urgesi:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

## Declaration of competing interest

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

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.actpsy.2026.107185.

## Data availability

All raw and processed data are publicly available in the OSF repository (https://osf.io/4jvsp/?view_only=98dc29387d6b465399fdfe456e2ce2a0).

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