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Brice Beffara, Amélie Bret, Nicolas Vermeulen, Martial Mermillod

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Resting high frequency heart rate variability selectively predicts cooperative behavior

Highlights

Vagal activity is proposed to be associated with prosociality.

No data confirms this association at a behavioral level in healthy human adults.

Vagal activity was estimated by high frequency heart rate variability (HF-HRV).

Prosociality was measured as cooperation in a hawk–dove game.

HF-HRV predicted cooperation only when the hawk–hawk payoff was low.

Abstract

This study explores whether the vagal connection between the heart and the brain is involved in prosocial behaviors. The Polyvagal Theory postulates that vagal activity underlies prosocial tendencies. Even if several results suggest that vagal activity is associated with prosocial behaviors, none of them used behavioral measures of prosociality to establish this relationship. We recorded the resting state vagal activity (reflected by High Frequency Heart Rate Variability, HF-HRV) of 48 (42 suitable for analysis) healthy human adults and measured their level of cooperation during a hawk–dove game. We also manipulated the consequence of mutual defection in the hawk–dove game (severe vs. moderate). Results show that HF-HRV is positively and linearly related to cooperation level, but only when the consequence of mutual defection is severe (compared to moderate). This supports that i) prosocial behaviors are likely to be underpinned by vagal functioning ii) physiological disposition to cooperate interacts with environmental context. We discuss these results within the theoretical framework of the Polyvagal Theory.

Keywords

Heart rate variability, Autonomic flexibility, Prosociality, Cooperation, Payoff

1. Introduction

Social behaviors are widespread in the animal world. All behaviors, including social behaviors, depend on specific neurobiological processes and brain–body interactions [101]. Social behaviors concern interactions with other organisms, and

can take several forms, either antisocial (e.g. aggression) or prosocial (e.g. cooperation). As highlighted by Taborsky and Oliveira [104], one property of social stimulations is to add a large amount of variability in the environment. As an organism interacts with other organisms of similar properties, feedbacks generate quasi-infinite loops increasing uncertainty with quasi-infinite degrees of freedom. Social interactions therefore increase the changing rate of the environment. When environmental changes happen faster than the phenotypic properties acquired through evolution, behavioral and physiological flexibility significantly increase Darwinian fitness and the probability of survival [80], [104]. Default behaviors underpinned by (relatively) stable physiological mechanisms may not be sufficient to cope with those faster changes. Typically, one important evolutionary heritage of animals – including humans – is a stress mode, efficient to detect threat and to cope with it [12], [17], [109], [116]. This ability to cope rapidly with danger is very relevant in dangerous environments. However, the cost of the defense is high and benefits are poor in safer environments because there is no threat to deal with [72]. In the same time, a lot of species have the ability to adopt adapted behaviors to the changing environment by inhibiting this default mode. Important differences exist between species and between individuals within species. The polyvagal theory [82] precisely explains how these differences are expected to explain and predict prosociality.

The polyvagal theory [82] thus proposes a theoretical framework describing how the evolution of the nervous system – and especially the autonomic nervous system – led to the diversity of interaction styles observed in vertebrates. Originally, the polyvagal theory emerged to provide an anatomo-functional perspective on emotional processing in mammals. The theory emphasizes that the heart–brain connection, through the vagal system, is subdivided in two branches in mammals. In the model, this particular subdivision is thought to play a substantial part in the generation of primary emotions. The current version of the theory integrates the anatomo-functional evolution of the autonomic nervous system in a phylogenetic perspective of the emotional life in mammals [84]. The heart–brain connection has evolved into an anatomical and functional separation between the two vagal streams. With the sympathetic nervous system, those two branches constitute three possible levels of reaction toward environmental changes. The unmyelinated vagal stream is considered to be the more archaic of the three systems. The behavioral correlate of this unmyelinated vagal activity is immobilization (freezing) and is associated with major physiological changes such as bradycardia. The sympathetic-adrenal nervous system underlies fight-flight activation and is secondary in the time scale of phylogenetic evolution. Finally, the polyvagal theory proposes that mammals benefit from the third component: the myelinated vagus branch. This is supposed to allow self-soothing and non-aggressive communication with other animals. Vagal communication between the heart and the brain is closely associated with the neural regulation of the striated muscles of the face and head involved in emotion processing (as well as speech production). In the framework of the polyvagal theory, emotion perception, emotion production and self-soothing are the functional mediation between the unmyelinated vagal activity and prosocial behaviors. The emotion perception, production and self-soothing skills related to vagal activity have been largely investigated in the past ten years [31], [88], [113]. Importantly, the polyvagal theory is also a physiological theory of social behaviors. The aim of the current study is precisely to test the association between vagal functioning and social behaviors since this dimension has not been explored yet. The theory emphasizes the capital role of physiological conditions on reactivity to environmental stimulation [84] and

then describes the need for internal flexibility in order to socially interact. The model identifies the myelinated heart–brain connection as the “social engagement system” and postulates that it underlies prosocial behaviors [83], [84], [85].

Invasive and non-invasive methods have been developed in order to quantify the vagal activity corresponding to the myelinated heart–brain connection. Among them, the spectral analysis of heart rate variability is a reliable non-invasive method to obtain a marker of the autonomic nervous system activity [38], [106]. More specifically, the high frequency component of heart rate variability (HF-HRV) is a good marker of the vagal parasympathetic activity [1], [8], [9], [10], [22], [50], [51], [52], providing a rigorous assessment of the myelinated heart–brain connection activity.

Numerous studies have highlighted significant and reliable relationships between HF-HRV and socio-emotional skills in humans. HF-HRV has been shown to be associated with emotion regulation and well-being [32], good mental state perception and emotion perception abilities [88], self-regulation and self-reported social engagement [31], behavioral measures of social sensitivity [70] and self-reported or perceived prosociality [59]. These studies provide strong evidence that vagal activity (tone or flexibility) is associated with emotional skills (regulation and perception of emotions) involved in social behaviors. They also bring out that individual differences in heart–brain interactions predict social engagement motives, social engagement behaviors and prosocial motives. However, it is of high importance to test this association with prosocial behaviors since prosocial attitudes/motives and behaviors are not necessarily congruent [5], [14], [74]. So far, previous evidence in this direction therefore suggests that vagal activity is associated with subjective perception of social skills in oneself or in others and with emotional skills expected to underlie social relationships. However, it is not possible to conclude that vagal functioning actually predicts actual prosocial behaviors. The only work in this direction was carried out by Miller et al. [69] who highlighted the association between altruism at a behavioral level and vagal functioning in young children. However, to the best of our knowledge, previous studies did not investigate the relationship between vagal activity and a behavioral measure of prosociality in healthy human adults yet.

Several behaviors can be categorized as prosocial. Cooperation is one of them and has been widely studied in numerous populations, perspectives, and paradigms [115]. Cooperation can be defined as an action leading to a mutual reward or benefit between the co-actors [7], [95]. In laboratory experiments, social dilemmas are among the most used experimental tasks available to investigate cooperation processes in healthy human adults. Typically, social dilemmas often take the appearance of a 2 by 2 matrix representing all the possibilities of the interaction between 2 persons: the payoffs. Indeed, in this configuration, each participant/player has two options. The number of different possible consequences (depending on the option chosen by both of the players), is therefore $2 * 2 = 4$. The two options can be slightly different across the different types of dilemmas. However they almost always represent a “competitive” versus a “cooperative” choice (e.g. “taking the money” vs. “letting the money” or “denouncing” vs. “protecting” a partner). Depending on the decision of each player, the consequence can be favorable or unfavorable, identically for both of the players or differently across them. The consequences (i.e. the payoffs) can be manipulated and different styles of dilemmas can be created on the basis of these consequences.

The most famous of these social dilemma is the prisoner dilemma. However different dilemmas, such as the hawk–dove game (also known as the game of

chicken/chicken game or snowdrift game) have been developed in order to simulate other types of interactions [91]. The difference between the prisoner's dilemma and the hawk–dove game is the most costly outcome of the dilemma. In the hawk–dove game, the most costly outcome is a joint defection from the two players (i.e. both players chose the “competitive” option). In the prisoner's dilemma it is a unilateral cooperation, i.e. when the other player chooses the competitive option [93]. This particularity make the hawk–dove game be a good model for representing animal conflict situations [33], [98]. Indeed, the “hawk” (cooperative) and the “dove” (competitive/aggressive) strategies are widespread in animals, both between and within species. Korte et al. [61] point out the balance observed in nature between these two strategies, as two different ways to cope with stress. They show that dividing animals into “hawks” vs. “doves” allows to account for gene*environment interactions in the management of resources, social interactions, and adaptation to the environment. They reviewed previous studies to propose that cooperation is associated with behavioral flexibility and parasympathetic dominance while aggression/competition is linked with rigidity and sympathetic dominance. The polyvagal theory proposes HF-HRV as a marker of physiological flexibility. Physiological flexibility is the amount of variations observable in the activity of an organ or a group of organs, during a given period of time. Here HF-HRV is an index of changes occurring in heart rate within a short period of time. This reflects the activity of the myelinated vagus nerve which connects the heart and the brain and which is able to produce short-term variations in heart rate because i) the vagus nerve reaches the sinus node via the release of acetylcholine. High quantity of acetylcholinesterase in the sinus node results in short effects of vagal inputs, the acetylcholine being quickly hydrolyzed (a kind of influence impossible via the sympathetic-adrenal nervous system [106], [109]) and ii) myelin allows increased axonal conduction velocity necessary for short-term modulation of the heart's activity (fast stimulation onset and offset, a kind of influence more limited for unmyelinated vagal fibers [30], [48], [49]). Myelinated vagal connection between the heart and the brain is therefore a factor of flexibility allowed by rapid information transmission between the central and the autonomic nervous system about internal and external modifications. The consequence is therefore a fine adaptation of the metabolism depending on environmental demand. As social interactions increase environmental variations, the polyvagal theory suggests that the advantage of physiological flexibility could underlie social engagement by allowing the fast adaptation to environmental demand. Inhibiting the threat response to uncertainty [109] allows to process information deeper and adopt non-aggressive behaviors [61]. These cognitive and behavioral properties arise from the degree of physiological flexibility described above. The polyvagal theory [82] allows to predict that the degree of flexibility coming from the myelinated vagal heart–brain interaction (not taken into account in the work of Korte et al. [61]) should lead to the non-aggressive behavior typical of the dove strategy. As proposed by Keltner et al. [55], we take physiological flexibility as a default propensity to prosociality. As a consequence, the association between physiological flexibility and prosociality should be clearer when the environment does not exert an important pressure to cooperate, that is to say, when the impact of individual factors is higher. The manipulation of double-defection (hawk–hawk strategy) can modulate the pressure to cooperate. When the risk of hawk vs. hawk is severe, we expect that all individuals should cooperate more by the pressure of the payoff [91]. However, when the risk is more moderate, we make the assumption that higher HF-HRV individuals should be more prosocial than lower ones. Indeed they should rely on their default tendency to

cooperate even if the external pressure is low. When the uncertainty produced by the payoff matrix is low (more external pressure increasing the probability of a dove strategy), we expect that individual differences in HF-HRV should have minor impact on behaviors and vice versa. Physiological flexibility is therefore expected to allow a cooperative decision when confronted to uncertainty while a default threat mode should foster competitive behaviors [61]. All in all, resting-state HF-HRV should be positively associated with the cooperation level in the hawk–dove game. Besides, we also predict that the association should be stronger in the condition where external pressure to cooperate is low.

2. Methods

In [Section 2](#) and [Section 2.7](#), we report how we determined our sample size, all data exclusions, all manipulations, and all measures in the study [96].

2.1. Sample

Initial sample was composed of 48 young healthy human adults. Participants were recruited via advertisements (mailing list and poster). All participants were first year (non-repeaters) psychology students of University Grenoble-Alpes and did not study social dilemmas/economic games in psychology courses yet. This experiment was the first or one of their first testing and the first concerning social dilemmas/economic games. Participants were French or bilingual in French. They provided written informed consent before the participation. The study was part of a global project reviewed and approved by the University human ethics committee from Grenoble, France (Grenoble ethics committee notice number 2014-05-13-49 and 2014-05-13-48). To be eligible, participants had to be aged between 18 and 60 years, with a normal or normal-to-corrected vision, explicitly reported an absence of psychiatric, neurologic, hormonal, or cardio-vascular disease, and with no medical treatment (with the exception of contraception). Smoking, energizing drinks (e.g. coffee, tea) and psychotropic substances (e.g. alcohol, cannabis) were prohibited to each participant the day of the experiment. They had also to avoid eating or drinking (water was allowed) the 3 h preceding the experiment in order to limit the influence of digestion on autonomic functioning (Short-term HRV measurement can be biased by the digestion of food since viscera are innervated by the autonomic nervous system [38], [41], [87]). The participants received experimental credits in return of their participation.

2.2. Sample size

We planned between 45 and 50 participants to take part in the study. Anticipating possible exclusions due to technical problems, we determined our sample size expecting between 40 and 45 participants suitable for final analysis. This sample size was set on the basis of previous studies carried-out in the framework of the polyvagal theory [82] and the neurovisceral integration model [107]. To our knowledge, none of the previous studies tested the association between HF-HRV and a behavioral measure of prosociality in healthy human adults. We then based our estimation on recent works [54], [77], [78] highlighting a link between HF-HRV and behavioral measures of attention, inhibition or emotional self-regulation. We waited for a similar association between HF-HRV and prosocial behaviors [55], [84], [108]. In this framework, a sample size of 40–45 [54], [77], [78] is adequate to observe an

association between HRV and the behavioral responses of interest when expecting an interaction with an experimental manipulation, with an effect size of $R^2 \sim .15$ (ranging from .10 and .20 depending on the studies).

2.3. Procedure

The experiment took place in a quiet and dimmed room. All participants were tested between 0900 h and 1200 h. The total experiment lasted less than one hour and a half. After a global description of the experiment, participants were asked to go empty their bladder before starting the experiment. After that, they were taught how to install the Bioharness™ heart rate monitor. They were left in autonomy in an isolated room for the installation of the heart rate monitor. Then, they seated in a chair, leant against the backrest, legs uncrossed. The experimenter checked the signal and the experiment started. During a first step, the participant seated with no particular task to perform for 10 min. The instructions were to relax and that cardiac activity will be recorded. The first 5 min allowed the participant to shift in a quiet state and the ECG data for HRV baseline computation was recorded for the following 5 min. ECG data was recorded during spontaneous breathing [27], [57], [62], [65], [70], [81]. After this first phase, the hawk–dove game session started (see description below). The task was re-explained to the participant with a short video before starting. When this step ended, the participant completed the control surveys on the laptop. The experimenter stayed out the room during the experiment but was available for eventual questions between the different steps of the experiment.

2.3.1. Hawk–dove game

We used a customized version of previous hawk–dove tasks reliable for payoff manipulation and physiological investigation [29], [42], [112]. Participants completed 12 trials of the social dilemma. The resources involved in the dilemma were experimental credits for psychology exams. Each trial was different from others by the amount in play and the design of the matrix (Table 1). The payoff for mutual Dove (DD) could be $\lambda = 0.48, 0.40, 0.32, 0.24, 0.16, 0.08$. In case of Hawk (H) strategy from one player and Dove (D) strategy from the other player (HD), the amount earned for H was 118€, namely, respectively, 0.66, 0.55, 0.44, 0.33, 0.22, 0.11, and the amount earned for D was 58€, namely, respectively, 0.30, 0.25, 0.20, 0.15, 0.10, 0.05. We manipulated the consequence (payoff) of mutual H (HH_p) in the dilemma. The amount earned for mutual H was either equal to 38€ (“moderate” (HH_{mod}) consequence of HH interaction), namely, respectively, 0.18, 0.15, 0.12, 0.09, 0.06, 0.03, or 18€ (“severe” (HH_{sev}) consequence of HH interaction), namely, respectively, 0.06, 0.05, 0.04, 0.03, 0.02, 0.01. Therefore, there was indeed $2(HH_p) * 6(\text{amount values}) = 12$ different matrices. The values were established in order to i) respect a credible maximum winnable amount of credits across all the trials ($\max = 2(0.66 + 0.55 + 0.44 + 0.33 + 0.22 + 0.11) = 4.62$) because students could get a maximum of 5 experimental credits for the semester, and ii) respect a constant distance between outcomes: $HD - DD = DD - DH = DH - \text{mod} + \text{sev}2$.

Table 1. Hawk–Dove payoff matrix a) moderate b) severe consequence of HH interaction.

Empty Cell	a)	Dove	Hawk	b)	Dove	Hawk
Dove		λ, λ	58€118€		λ, λ	58€118€
Hawk		118€58€	38€38€		118€58€	18€18€

Each matrix represented the amount of experimental credits won by each player, corresponding to each choice combination (HD, DD, DH, HH, see [Table 1](#)). The participants made their choices only on the basis of the payoffs, meaning that it was never explicitly stated that a choice was competitive or cooperative. D and H labels were replaced by neutral labels with colors. D and H in the first row of the matrix (participant's side) were both replaced by “Your choice” and D and H in the first line (virtual confederate's side) were both replaced by “The choice of the other student” in order to indicate each player's side. Background colors (blue or green) were alternatively used in either D cells or H cells of the matrix in order to differentiate the two options in an implicit way. Participants had to answer whether they wanted to choose the blue or the green option, knowing that the other participant also had the same choice to do. Background colors were counterbalanced (including half trials with blue for H/green for D and half trials with green for H/blue for D) across payoff values in order to control for the effect of the color. Each matrix was presented for 30 s during which participants had to examine the matrix and make their decision. Following these 30 s they had 3 s to press the key (left or right arrow on the keyboard) to give their answer. Left and right arrow could correspond to the blue or green choice. This association between side and color changed across trial, again in a counterbalanced design.

The 12 different trials were always played with/against a new (virtual) participant in order to avoid strategic processes likely to occur within the same dyad. Indeed the aim was to measure the default tendency to cooperate [55]. Therefore, that is why each matrix was unique and why the (real) participant never knew the issue of an interaction (she/he was told that only the sum of the outcomes will be known at the end of the experiment). In reality, each participant received the same amount of experimental credits at the end of the experiment (when all the real participants completed the experiment, in order to avoid the diffusion of the fake task), corresponding to the time spent for completing the experiment.

2.3.2. Cover-story

Participants were recruited for a protocol concerning physiology and social reasoning in dyads. Cooperation and competition were never mentioned. The other student supposed to be the other participant was in fact a virtual confederate, different for each trial. Few months before the experiment, we recorded 30 s videos during which actors (graduate students, 6 males, and 6 females) mentally solved multiplications displayed on the screen of a computer. Multiplications were spatially organized in a matrix similar to the hawk-dove matrix. Actors seated (centered) in front of the screen at a distance of 70 cm (during, the real experiment, participants seated at about this distance of the computer). The background was white such as the wall of the experimental room where the real participants completed the experiment. Actors were told to act i) naturally but ii) neutrally during the task such as their visual behavior could be i) close to the behavior of real participants in the experiment but ii) without influencing the behavior of a real player. With the written consent of each actor, the 30 s video was displayed to participants (in the top left cell of the matrix) during each hawk–dove matrix in order to simulate a webcam video of another participant.

2.3.3. Control trials

In order to control that the effects of our factors on participant's responses was not due to difficulties in understanding the instructional set, we also included control trials in the experiment. Control trials were organized following the same spatial disposition as hawk–dove matrices. Each matrix was filled with 13 numbers, either even or odd. The numbers were randomly generated (3 digits, between 100 and 999) before the experiment and all participants viewed the same numbers. The task of the participant was to determine whether there was more even or odd numbers in each matrix. Participants had to answer with the left or right arrow in order to choose the “even” or the “odd” response. As the control matrix had the same appearance compared to the experimental matrix, colors were also displayed, and the association between response side (left or right), response (even or odd) and color (blue or green) was counterbalanced across trials. This control task was composed of 6 trials, randomly displayed across the experimental trials.

2.4. Physiological measurement

The electrocardiogram (ECG) data was recorded with a Zephyr Bioharness™ 3.0 [119]. The Bioharness™ is a class II medical device presenting a very good precision of measurement for ECG recording in low physical activity conditions [44], [45], [46]. It has been used for ECG measurements in both healthy and clinical populations, presenting a very high-to-perfect correlation with classical hospital or laboratory devices [16], [118]. The Bioharness™ provides both comfort for the participant and allow reliable HRV extraction for the researcher [67]. The chest strap's sensor measures electrical activity corresponding to the classical V4 lead measurement (5th intercostal space at the midclavicular line) through conductive Lycra fabric. A single-ended ECG circuit detects QRS complexes and incorporates electrostatic discharge protection, both active and passive filtering and an analog-to-digital converter. Interbeat intervals are derived by Proprietary digital filtering and signal processed with a microcontroller circuit. The ECG sensor sampling frequency is 250 Hz and the resolution 0.13405 mV, ranging from 0 to 0.05 V [111]. After a slight moistening of the 2 ECG sensors, the chest-strap was positioned directly on the skin, at the level of the inframammary fold, under the lower border of the pectoralis major muscle. The recording module communicated with an Android® OS smartphone by Bluetooth®. The application used to acquire the signal emitted by the Bioharness™ was developed, tested, and validated by C novas et al. [24]. The Android® OS device used to record the signal was an LG-P990 smartphone (Android® version 4.1.2.).

2.5. Control for confounding factors

To control for confounding variables likely to be linked to HRV, participants completed questionnaires detailing life habits, demographic data and emotional traits [88]. Physical activity was assessed with the International Physical Activity Questionnaire (IPAQ, [25]), composed of 9 items that calculate an index reflecting the energy cost of physical activities (Metabolic Equivalent Task score, MET). The IPAQ has been validated in French [15], [97] and widely used in French surveys [92]. Participants also completed the Depression Anxiety and Stress scales (DASS-21; [66]). The DASS-21 is a 21-item questionnaire, validated in French [90], and composed of three subscales evaluating depression, anxiety and stress traits. We also recorded the size, weight, age and sex of the participants and their daily cigarette

consumption. Participants answered final surveys on a DELL latitude E6500 laptop. Surveys were built and displayed with E-prime software (E-prime 2.0.10.242 pro).

2.6. Physiological signal processing

For the ECG recording of each other participants, R-R interval data was extracted from the Android® device and imported into Kubios [11], [105] as a text file. Signal was visually inspected for artifact [86], [88], [114]. A piecewise cubic spline interpolation was applied to correct artifacts (ectopic beats, [56]) for participants presenting a corrupted RR interval series (bigger/smaller than ~ 0.45 to 0.15 s – depending on average HR – compared to the local average RR interval series). RR series were interpolated by piecewise cubic spline to obtain equal sampling intervals and regular spectrum estimations. A sampling rate of 4 Hz was used. We then extracted the frequency component of HRV from RR interval data. The LF (0.04–0.15 Hz) and HF (0.15–0.4 Hz) component were extracted using an autoregressive model method. The autoregressive model order was set at 16 [13].

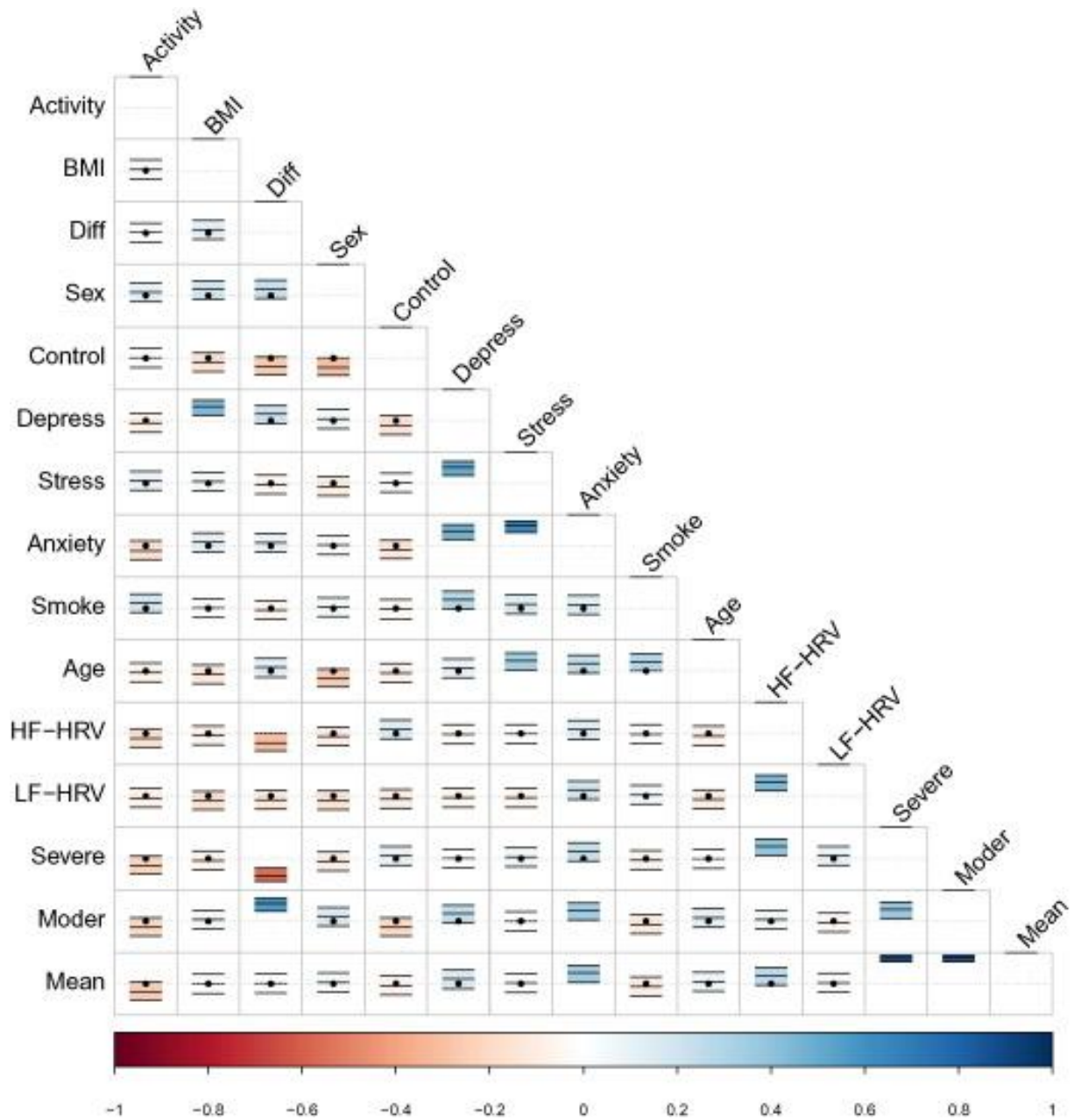
2.7. Data analysis

Originally, a total of 48 participants were included in the study. Four participants were excluded from the sample before data analysis: one because of a noisy signal impossible to correct, one due to a technical recording problem, one other because he did not perform the hawk–dove task, and the last one because he showed suspicion toward the cover story. Statistical analyses were conducted using RStudio®, version 0.99.489 for Linux [89] and are reported with the knitr [117], papaja [4] and rmarkdown [2] packages. Extreme data [73] inconsistent with resting-state recording conditions (owing to possible technical measurement problems, for example) were detected by examining the distribution of raw HF-HRV levels. A raw HF-HRV value was then considered to be a resting-state outlier if it was greater/less than the upper/lower quartile \pm three times the interquartile range [59], [81]. Based on this criterion, 2 participants were excluded from the sample (raw HF-HRV powers of 3417.24 and 7370.77 ms^2 while the mean of the group was 710.14 ms^2 with the lower quartile = 332.02 ms^2 and the upper quartile = 947.59 ms^2). Finally, the measure of resting-state HF-HRV baseline was calculated as the natural logarithm of the raw HF-HRV power in order to correct the right-skewed distribution [59], [81] and centered to the mean in order to facilitate the interpretation of parameters. 42 participants (mean age = 18.67, sd = 1.07, min–max = 18–23, 37 females) were included in final data analysis. A total of 490 data points (42 participants * 12 trials – 14 missing values) were available for statistical analysis on hawk–dove game data. 236 data points were available for analysis on the control task responses (42 participants * 6 trials – 16 missing values). Data were analyzed using HF-HRV (continuous) and HH payoff (2 modalities, recoded $HH_{sev} = -0.5$ and $HH_{mod} = +0.5$, within subject) as independent variables and cooperation as a binary dependent variable (1 = cooperation (dove) 0 = competition (hawk)) in a mixed-effects logistic regression. Effect sizes are interpreted through relative risks [34] computed as $\text{relativerisk} = \text{oddsratio}(1 - p_0 + p_0 * \text{oddsratio})$, where p_0 is the baseline risk, in our case, the mean cooperation level. For analysis on the control task, HF-HRV (continuous) and proportion of even over odd numbers (3 modalities, within subject) as independent variables and response accuracy as a binary dependent variable (1 = correct and 0 = false). We analyzed our data by the fit generalized linear mixed-effects models function (glmer), computed using the package “lme4” [6].

Model selection was completed using AICc (corrected Akaike information criterion) and Evidence Ratios - ER_i - [20], [21], [39], [103]. AICc provides a relative measure of goodness-of-fit but also of parsimony by sanctioning models for their numbers of parameters. AICc is more severe on this last point than AIC ($AICc = AIC + 2 \frac{K}{n} + 1 \frac{K(K+1)}{n(n-K)}$ where K is the number of parameters and n the sample size.). We computed the difference between best (lower) and other AICs with $\Delta_{AICc} = AICc_i - AICc_{min}$. The weight of a model is then expressed as $w_i = \frac{e^{-2\Delta_{AICc_i}}}{\sum_j e^{-2\Delta_{AICc_j}}}$. From there, we can compute the Evidence Ratio: $ER_i = \frac{w_i}{w_{best}}$. Even if quantitative information about evidence is more precise, we also based our decision on Kass and Raftery [53] and Snipes and Taylor [100], i.e. minimal ($ER_i < 3.2$), substantial ($3.2 < ER_i < 10$), strong ($10 < ER_i < 100$) and decisive ($100 < ER_i$) evidence. If the model with the lower AICc included more parameters than others, we considered it as relevant if the evidence was at least substantial. If the model with the lower AICc included less parameters than others, we chose it even if evidence was minimal. After that, we checked if 0 was outside the 95% CIs of the parameters of interests.

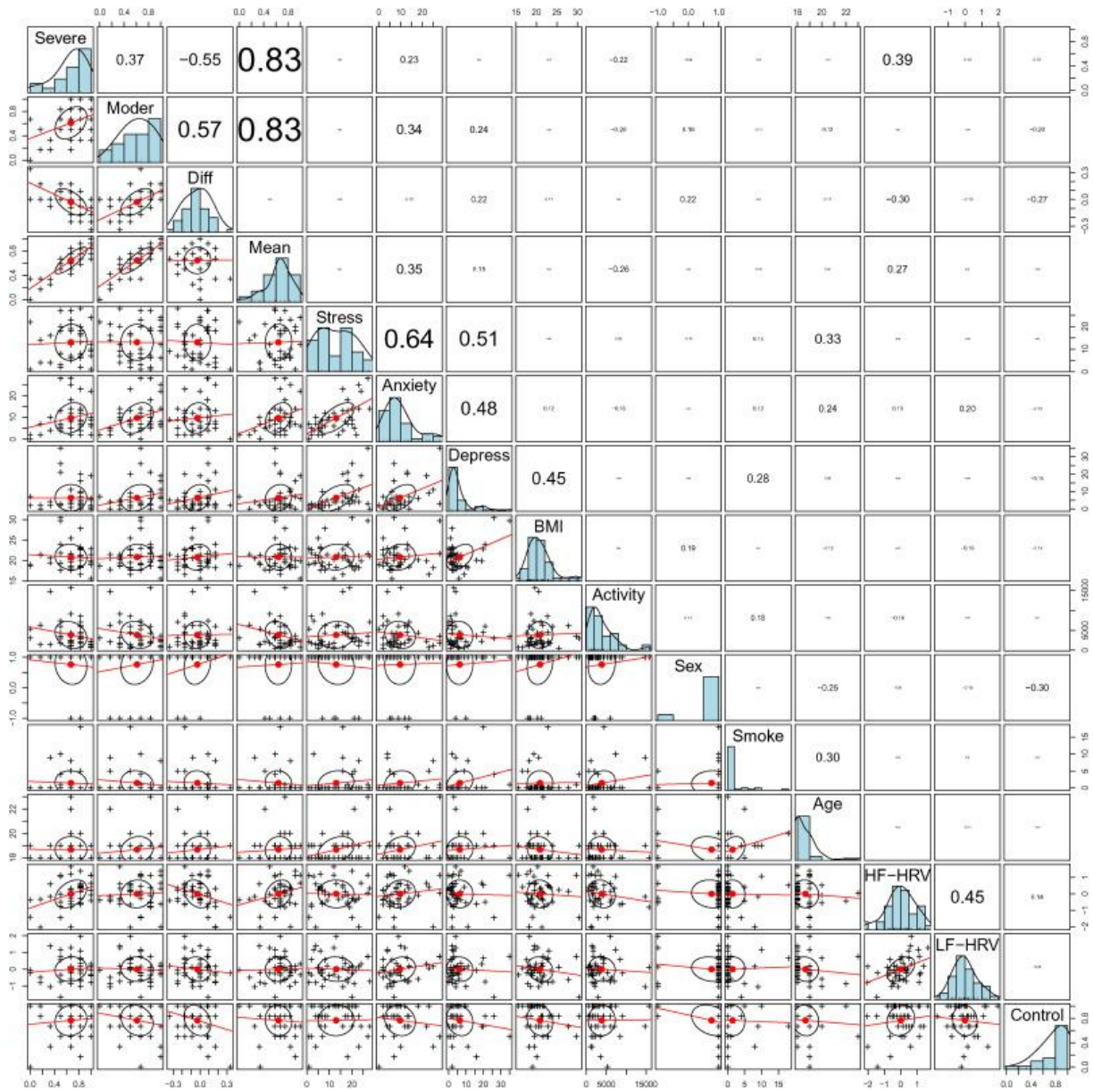
3. Results

We first computed Pearson correlations (Fig. 1, Fig. 2¹) in order to determine whether or not we should correct HRV for confounding factors (traits) measured at the end of the experiment. Fig. 1 shows that all the confidence intervals for parameters of association between these variables and HRV included 0. We therefore considered that it was not necessary to correct HRV for them. Side associations could be noticed and we report them only of information purpose as multiple comparisons can easily lead to false positives (type I errors). Participants with higher BMIs had higher scores of depression. Higher scores of depression were associated with higher scores of stress and anxiety which were also positively linked between them. Older individuals showed higher stress scores. We could also observe that HF-HRV was positively associated with LF-HRV and also with cooperation in the HH_{sev} condition (18 \diamond). However HF-HRV was negatively associated with the difference of cooperation between HH_{sev} and HH_{mod} (38 \diamond). Conversely, higher anxiety scores predicted higher cooperation levels in the HH_{mod} condition. To finish, people more cooperative in one were also more cooperative in the other condition.



1. [Download : Download high-res image \(441KB\)](#)
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Fig. 1. Correlation confidence intervals between recorded variables. Confidence regions represent 95% CIs and are marked with a black dot when including 0.



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Fig. 2. Scatter plots, distributions, and Pearson correlation coefficients between recorded variables. R values' font sizes are proportional to the strength of the correlation.

We used logistic mixed effect models in order to get a more accurate estimation of the association between HF-HRV and cooperation.

We first selected the relevant random factors to include in our models. Whether for the hawk–dove game or the control task, only participants were appropriate as random factors. Indeed models including only “participants” showed the lowest (best) AICc with the lowest number of parameters (Table 2, Table 3).

Table 2. Comparison of random effects in models for cooperation, ordered by AICc relative to the model with the lowest (best) AICc.

Empty Cell	<i>K</i>	<i>AICc</i>	Δ_{AICc}	<i>Weight</i>
<i>ppt</i>	2	604.2	0	0.742

Empty Cell	<i>K</i>	<i>AICc</i>	Δ_{AICc}	<i>Weight</i>
<i>ppt + val</i>	3	606.4	2.208	0.246
<i>ppt + val + HH_{slope}</i>	6	612.3	8.147	0.013
<i>val</i>	2	632.8	28.69	0

Note. *K* is the number of parameters in the model. *ppt* = participants, *val* = amount values, *HH* = *HH_{payoff}*.

Nb. Models *ppt + val + HRV_{slope}* and *ppt + val + HRV_{slope} + HH_{slope}* failed to converge.

Table 3. Comparison of random effects in models for control task, ordered by *AICc* relative to the model with the lowest (best) *AICc*.

Empty Cell	<i>K</i>	<i>AICc</i>	Δ_{AICc}	<i>Weight</i>
<i>ppt</i>	2	206.5	0	0.904
<i>ppt + HRV_{slope}</i>	5	211.9	5.375	0.062
<i>ppt + prop_{slope}</i>	5	213.1	6.584	0.034
<i>ppt + HRV_{slope} + prop_{slope}</i>	8	219.9	13.35	0.001

Note. *K* is the number of parameters in the model. *ppt* = participants, *prop* = proportion of even over odd numbers.

We first compared the parsimony of models containing main effects (HF-HRV and *HH_p*) and interaction effect (bilinear, Table 4). Model comparison showed weak (minimal) evidence in favor of main effect's models but substantial evidence ($0.504/0.152 = 3.32$) toward the interaction model compared to the intercept model. We decomposed the interaction in order to get the simple slopes of HF-HRV on cooperation on each condition of *HH_p* and then estimate the effect size of HF-HRV on cooperation on each *HH_p* condition. We could notice a reversed pattern compared to our hypothesis, i.e. a positive (and 0 outside 95% CI) parameter in the “severe” condition but the 95% CI of the parameter in the “moderate” condition included 0 (Table 5). The results then suggest a positive link between HF-HRV and cooperation but only in the “severe” condition (Fig. 3). The relative risk was equal to 1.16. This means that, for each unity of HF-HRV, cooperation probability is increasing of about 16% in this group. The model therefore predicts a probability of cooperation ~ 0.89 for the highest HF-HRV participant while a probability ~ 0.48 for the lowest. It is difficult to compare effect sizes from a mixed-effects logistic regression with effect sizes from previous results obtained by classical linear regression [40]. However, we can roughly indicate that an approximated R^2 computed from averaged data (not binary responses) would be $0.39^2 \sim 0.16$ (Fig. 2), which is usually considered as a medium effect size [43] and corresponds to the range of effect sizes obtained in previous findings associating HF-HRV and emotional/attentional functioning [54], [77], [78].

Table 4. Comparison of models for cooperation, ordered by *AICc* relative to the model with the lowest (best) *AICc*.

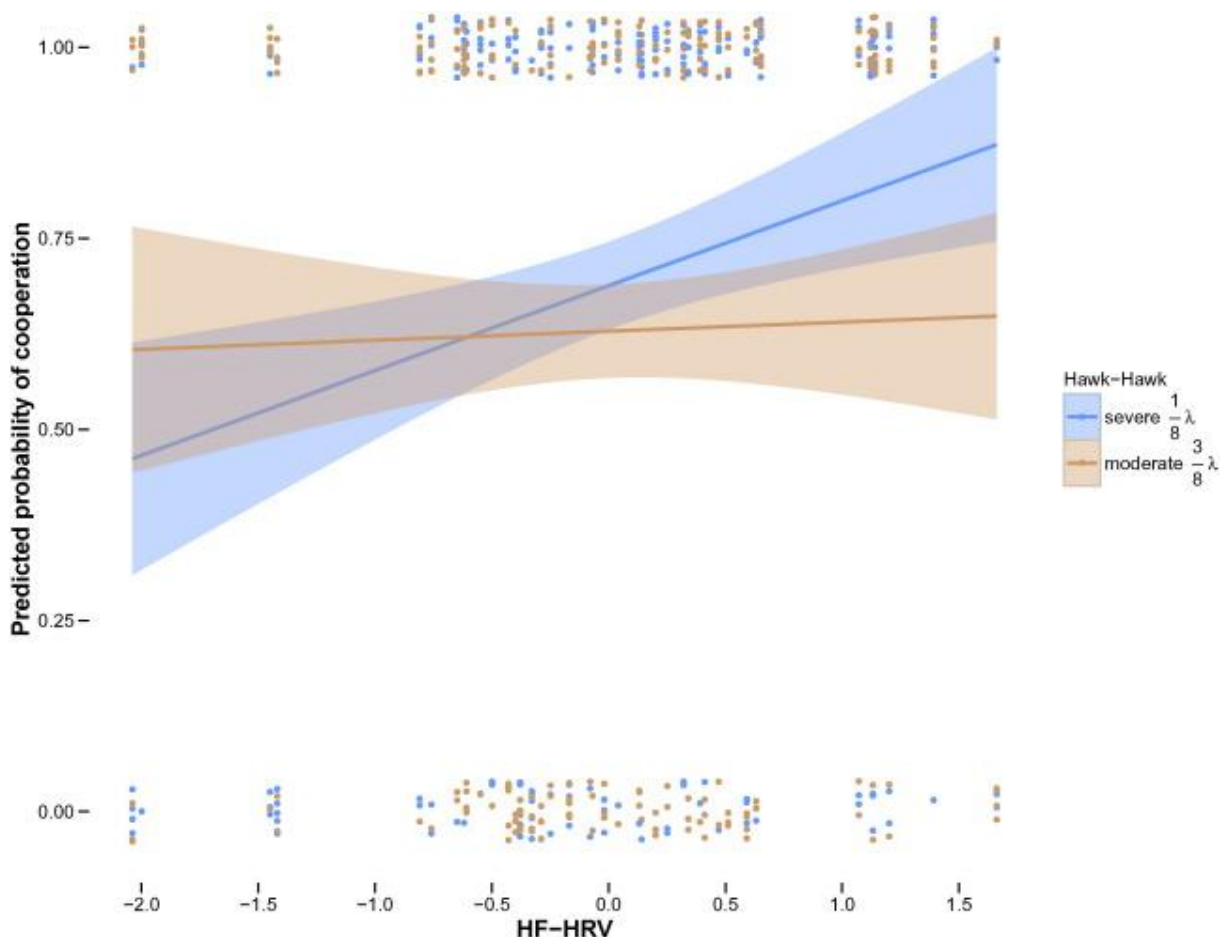
Empty Cell	<i>K</i>	<i>AICc</i>	Δ_{AICc}	<i>Weight</i>
<i>Int + HRV + HH_p + HRV * HH_p</i>	5	601.8	0	0.504
<i>Int + HH_p</i>	3	603.9	2.13	0.174
<i>Int + HRV</i>	3	603.9	2.173	0.17
<i>Int</i>	2	604.2	2.398	0.152

Note. K is the number of parameters in the model. Int = Intercept. All models include participants as a random factor.

Table 5. Coefficient estimates (Est), standard errors (SE) and odds ratios (OR) with 95% CI (Lwr, Upr) for Est and OR.

Empty Cell	<i>Est</i>	<i>SE</i>	<i>Lwr Est</i>	<i>Upr Est</i>	<i>OR</i>	<i>Lwr OR</i>	<i>Upr OR</i>
<i>HRV</i>	0.337	0.207	- 0.075	0.767	1.401	0.928	2.154
<i>HH_p</i>	- 0.347	0.208	- 0.761	0.062	0.707	0.467	1.064
<i>HRV*HH_p</i>	- 0.529	0.251	- 1.033	- 0.039	0.589	0.356	0.961
<i>HRV_{severe}</i>	0.601	0.247	0.118	1.112	1.825	1.125	3.039
<i>HRV_{moderate}</i>	0.072	0.236	- 0.4	0.552	1.075	0.67	1.736
<i>HRV_{severe}²</i>	- 0.321	0.205	- 0.738	0.09	0.725	0.478	1.094
<i>HRV_{moderate}²</i>	0.332	0.213	- 0.079	0.776	1.394	0.924	2.173

Note. This table reports coefficient from the best model (including all parameters). As all variables were centered to the mean for analysis, these coefficients approximate coefficients from simpler models.



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Fig. 3. Predicted probability of cooperation as a function of HF-HRV and HH payoff. Linear fit for HF-HRV. Confidence regions represent 95% CIs.

We also wanted to explore whether the quadratic association observed by Kogan et al. [58], [59] was reproduced in our data. We then included the quadratic HF-HRV parameter in our model (Table 6). The interaction between this parameter and HH_p seemed to add information in data description. However, 95% CI of simple slope parameters included 0, which limits the conclusions we can draw about this quadratic interaction. What is more, the interaction mainly suggests that low and high HF-HRV participants are more cooperative than medium HF-HRV participants in the “moderate” condition, which is a reversed U-shaped compared to Kogan et al. [58], [59]. For these reasons, even if the overall model seems better with a quadratic interaction, we choose to be cautious and to rely only on the bilinear interaction.

Table 6. Comparison of models for cooperation, including quadratic terms, ordered by AICc relative to the model with the lowest (best) AICc.

Empty Cell	<i>K</i>	<i>AICc</i>	Δ_{AICc}	<i>Weight</i>
<i>Int + HRV + HRV² + HH_p + HRV * HH_p + HRV² * HH_p</i>	7	599.8	0	0.656
<i>Int + HRV + HH_p + HRV * HH_p</i>	5	601.8	1.991	0.243
<i>Int</i>	2	604.2	4.389	0.073
<i>Int + HRV + HRV²</i>	4	606.1	6.316	0.028

Note. K is the number of parameters in the model. Int = Intercept. All models include participants as a random factor.

As shown in Table 7, there was minimal evidence for an association between HF-HRV and accuracy in the control task, independently of the experimental condition. This suggests that the association observed between HF-HRV and cooperation is unlikely to be due to difficulties in performing the task or problems in understanding the instructions.

Table 7. Comparison of models for control task, ordered by AICc relative to the model with the lowest (best) AICc.

Empty Cell	<i>K</i>	<i>AICc</i>	Δ_{AICc}	<i>Weight</i>
<i>Int + HRV</i>	3	206.4	0	0.42
<i>Int</i>	2	206.5	0.1	0.399
<i>Int + prop</i>	3	208.7	2.298	0.133
<i>Int + HRV + prop + HRV * HH_p</i>	5	211	4.574	0.043
<i>Int + HRV + HRV² + prop + HRV * prop + HRV² * prop</i>	7	215.4	8.943	0.005

Note. K is the number of parameters in the model. ppt = participants, prop = proportion of even over odd numbers. All models include participants as a random factor.

4. Discussion

The principal aim of this study was to test one of the statements of the polyvagal theory [82], [83], [84], [85] according to which the myelinated vagal heart–brain connection is a physiological correlate of pro-social behaviors. For that purpose, we computed the HF-HRV baseline level of participants as a non-invasive marker of this heart–brain connection [1], [50], [51], [52]. At a behavioral level, we operationalized pro-sociality as the level of cooperation (dove strategy) in a hawk–dove game [33], [98]. We manipulated the severity of the Hawk–Hawk interaction with 2

different payoffs (either severe (18♦) or moderated (38♦) HH). We hypothesized that HF-HRV would be associated with cooperation in both situations, but expected a weak association between HF-HRV and cooperation (dove strategy) in the “severe” condition and a stronger association in the “moderated” condition. Indeed, we predicted that HF-HRV would be associated with a default pro-social tendency [55], that is to say a tendency to cooperate (“dove” strategy) even if the external constraint to choose “dove” (HH_p) was low. Instead, we found the opposite pattern with an association between HF-HRV and cooperation only in the HH_{sev} condition and very weak evidence of a link between the two variables in the HH_{mod} condition. According to us, two main explanations can emerge from this result. The first explanation is that higher resting-state HF-HRV participants are more likely to perform utilitarian choices. This would mean that these individuals choose the option generating the highest payoff in a probabilistic point of view [28], [37]. On the other hand, another explanation would be that HF-HRV is associated with cooperation only when the danger for the dyad is high (HH_{sev}). In other words, higher resting-state HF-HRV participants would be more sensible to a risk occurring for both participants, corresponding to an increased sensitivity for the group's health. In this way they might want to protect both themselves and the other participant from negative outcome, which would completely be a pro-social choice, contrary to the utilitarian hypothesis. However, when confronted to the case of moderated HH, they could consider that the group is not importantly threatened by HH, and therefore does not necessarily focus on a “more prosocial” option compared to low resting-state HF-HRV participants.

Obviously, these two propositions are totally post-hoc and seriously need further testing in order to determine which one is the more plausible. Interestingly however, these two mechanisms are not necessarily mutually exclusive. In the current configuration, prosociality is not opposed to self-interest. When protecting the dyad from the hawk vs. hawk risk, individuals protect themselves as they are included in the dyad. Therefore, pure altruism is not necessary to adopt the “dove” strategy, prosociality can be both other and self-oriented at the same time. It is also important to notice that the mechanisms involved in processing social dilemmas interact between themselves and do not operate in a all-or-none principle. This is what Declerck et al. [26] propose with three neural networks underlying cooperation, namely, cognitive control, the processing of reward and social cognition. At a prefrontal level, comparing this functional subdivision with the work of Amodio and Frith [3], the integration of external incentives would be associated with the dorsal-posterior subdivision of the prefrontal cortex, the processing of outcomes by the ventral-orbital subdivision of the prefrontal cortex, and the processing of social signals by the anterior part of the prefrontal cortex. What we observe in our study is that HF-HRV predict cooperation but only when self-interests and the interests of the other player are importantly jeopardized by external constraints. Dealing with this situation necessitates to i) identify and be receptive to the variations of external constraints and ii) understand the consequences of such constraints. At the intersection between the work of Declerck et al. [26] and Amodio and Frith [3], the main prefrontal cerebral regions expected to underlie these functions are situated in the dorsal (sensitivity to external incentives) and the ventral regions (anticipation of possible outcomes). Across all task (i.e. emotional and non emotional), the prefrontal neural correlates of HF-HRV are found in the dorsal and ventral regions, following the nomenclature proposed by Amodio and Frith [3], Lane et al. [63], and Thayer et al. [109]. These prefrontal correlates of HF-HRV correspond well with the integration of external constraints and evaluation of outcomes necessary during social dilemmas

as described by Declerck et al. [26]. As a consequence, we propose that the increased prosociality associated with higher resting HF-HRV levels observed in our study can be – at least partially – explained by better integration and management of the negative outcome induced by the severe hawk-hawk payoff. It is to notice that this process is probably different from pure utilitarian decisions which aim to increase positive consequences for oneself at the expense of the other player. Indeed recent data show that utilitarian (and not deontological) judgment is associated with lower HRV levels in morals dilemmas [76]. Moreover, anterior regions of the prefrontal cortex correlate with HRV specifically during emotional situations [109], which suggests that the “social cognition” network [3], [26] can be particularly recruited by high HRV individuals in emotional contexts, which does not support the “pure-utilitarian hypothesis”. Further studies are needed to evaluate the central nervous system (prefrontal) recruitment associated with HF-HRV levels during social dilemmas.

Prefrontal networks are involved in cardiac regulation but heart–brain interactions bring direct and indirect bidirectional connections with other cortical (in particular the cingulate cortex and the insula) and subcortical areas (notably the hypothalamus and the amygdala) into play [71], [108]. Cerebral activations in this cortico-subcortical network account for the differences observed in HF-HRV which suggests that the incorporation of one's autonomic/visceral variations (cingulate cortex, insula and amygdala) and the regulation of physiological states (ventrolateral prefrontal cortex) are closely related to cardiovascular integration and control [47], [64]. This suggests that interoception (detection what happens in one's body), cognitive control and physiological regulation of the perceived changes in the body states are functionally associated with HF-HRV. Several works have highlighted that higher vagally mediated heart rate variability is correlated with better connection and integration of prefrontal and subcortical functions which fosters better cognitive skills, adaptability and self-regulation [47], [108], [109], [110].

As a matter of fact, neurocardiac regulation via the myelinated vagus nerve (as indexed by HF-HRV) is associated with calming and self-soothing [68], [84], [102]. HF-HRV is also positively correlated with emotion regulation [31], [99], cognitive control and working memory abilities [23], [35], and more efficient inhibition, attentional engagement and disengagement toward emotionally negative stimuli [75]. HF-HRV and associated cognitive functions therefore share common central nervous system correlates. These cognitive and regulation skills associated with HF-HRV may explain the adoption of a cooperative strategy depending on the context and the risky consequences associated.

In line with the polyvagal hypothesis, HF-HRV was then positively associated with the level of cooperation in the hawk–dove game, but only in one experimental condition. The hawk–dove task measured, inter alia, the behavioral tendency to cooperate in a one shot design and HF-HRV is theoretically considered as a physiological correlate of the default tendency to pro-sociality [55]. The present work tends to confirm this assumption that vagal heart–brain connection is a physiological vector of pro-sociality, at least in healthy humans adults.

However, and more importantly, our results also bring evidence toward the fact that the physiological default tendency to cooperate (HF-HRV) interacts with environmental factors (here, the severity of HH). This is in line with the theory proposed by Porges [82] where rapid communication between the heart and the brain via the myelinated vagus is expected to allow adaptation to environmental variations. One can then deduce that the default neurocardiac state of an organism can lead to different outcomes depending on the demand of the situation.

In this work we measured the HF-HRV but we did not experimentally provoke the HF-HRV level. As a consequence, several hypotheses can be made concerning the direction of the link between the vagus nerve activity and pro-social behaviors. Some authors propose that the influence is bilateral, meaning that higher vagal tone could be responsible of improved social functioning and that increased social functioning could also enhance vagal tone [60]. However, this conclusion is also made on the basis of measured vagal tone, which limits the conclusions in terms of causality in the vagal-to-social direction.

Several theoretical frameworks allow to interpret the current results and especially to explain why vagal tone is associated with cooperation. Some authors [55] suggest that the vagus nerve activation is likely to foster an attentional focus on other individuals. We indeed propose that attention might be a mediator of the association between HF-HRV and cooperation, but not necessarily only attention oriented toward others. Undoubtedly, information processing determines behavior. Information processing constitutes a set of physiological mechanisms which necessarily answer to internal and external needs. This was in fact the core message of the polyvagal theory at its beginning [82]. We therefore endorse, exactly as in the polyvagal theory, that a calm and soothed organism has a better ability to orient its attention toward relevant stimuli without automatically falling into a default mode response to threat [109]. This is confirmed by a set of recent studies showing that healthy adults with higher resting HF-HRV levels show better bottom-up and top-down attentional functioning compared to healthy adults with lower baselines [75]. More precisely, lower HF-HRV predicts fast and maintained vigilance toward stimuli related to threat, suggesting difficulties in inhibiting the default response mode to threat and uncertainty. These attentional difficulties are opposed with the sensation of safety and associated with increased stress. Perception of safety or positive social interactions normally contribute to maintain or even enhance a healthy physiological state while decreasing the level of long-term stress [18], [19]. Conversely, negative social interactions seem to affect the stress level in the other direction [94]. The mechanisms in play between the environment and the organism therefore seem totally bidirectional [60]. Interestingly, the association between HF-HRV and information processing has also been extensively investigated over the last twenty years. Notably, the neurovisceral integration model [107], [108] describes how heart–brain interactions are likely to underlie the default reaction of organisms to threatening events. The idea is that HF-HRV is a marker of physiological flexibility which allows a good adaptation of the organism to environmental variations [36]. Flexible attention orientation to stimuli would then generate the difference in cooperation between high and low HF-HRV individuals. Indeed, theoretical models [55], [84], [110] predict that low HF-HRV organisms show a rigid attentional bias to threatening events, principally functioning on a fight-flight default response. On the other hand, more flexible individuals show the ability to focus on a broader set of cues, including social cues which in return increase flexibility by decreasing stress levels [18], [19], [60].

There are still strong needs to replicate these results and to get more precise estimates of the effect size of heart-brain interactions on pro-social behaviors. Further studies should investigate the evolution of HF-HRV during the social dilemma in order to determine whether the flexible adaptation of vagal activity during the cognitive-affective demand of the task also predicts cooperation [70], [79]. The next experimental step is also to determine if attentional skills mediate the link between physiology and social behaviors. Importantly, as suggested before [70], it is also time to experimentally increase HF-HRV in order to measure the causal effect of physiological flexibility on pro-social behaviors.

5. Conclusions

We aimed to test the polyvagal theory [84] according to which heart–brain interactions play a part in prosocial behaviors. We observed that efficient heart–brain interactions (as indexed by HF-HRV) were indeed associated with the probability to choose a prosocial option but only when the risk of double defection was high. We interpret this physiology–environment interaction as a default tendency for high HF-HRV individuals to act for the safety of the dyad. However, other hypothesis can be drawn, and further studies are required to answer this question. Nevertheless, this association between HF-HRV and a behavioral measure of pro-sociality tends to confirm the statements of the polyvagal theory [84], at least for healthy human adults.

Disclosures

The authors report no relationships that could be construed as a conflict of interest.

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