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Research Article

The intricate brain–heart connection: The relationship between heart rate variability and cognitive functioning

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ABSTRACT

In the last years, there has been a growing interest in the brain–heart connection. A core aspect of this connection appears to be the autonomic nervous system, particularly through the vagus nerve. Accordingly, vagally mediated heart rate variability (vmHRV) is currently considered as an index of top-down control processes involved in cognition and emotion regulation. Recent evidence indicates that higher vmHRV is associated with enhanced cognitive performance across multiple domains, such as executive functions, memory, attention, and language skills.

From this premises, this study examined the relationship between cardiac vagal tone, as indicated by heart rate variability (vmHRV), and cognitive functions. A sample of 143 healthy young adults completed a comprehensive neuropsychological battery. The results revealed a strong correlation between resting vmHRV and cognitive functions, particularly in executive processes. Participants with higher resting vagal tone showed superior cognitive performance in tasks requiring cognitive control, motor and cognitive inhibition, cognitive flexibility, and working memory in comparison to those with lower resting vagal tone. Furthermore, vagal-mediated heart rate variability was also found to be associated with memory, attention, and executive performance. The current research provides new insights into the interactions between cognitive and autonomic systems, further supporting evidence for body-brain interactions.

Introduction

The study of heart-brain communication has recently received increased attention due to evidence supporting its bidirectional nature. The traditionally understanding of the heart-brain axis posits that the brain transmits signals to the heart to regulate cardiac functions. However, recent evidence suggests that the heart can also communicate with the brain, offering new insights into the bidirectional nature of this interaction. This perspective supports the bio-psychosocial perspective, which proposes that physiological, psychological, and cognitive health are interrelated and influence physical, mental, and social well-being (Balconi et al., 2019; Forte et al., 2019). Numerous studies have focused on the autonomic nervous system as a potential physiological correlate of cognitive functioning (Magnon et al., 2022; Forte et al., 2019; Porges, 2007; Thayer and Lane, 2009). The autonomic and central nervous systems are bidirectionally connected via the vagus nerve in a dynamic relationship that is fundamental to maintaining homeostasis, i.e., a key concept in physiology (Laborde et al., 2019). Accordingly, autonomic nervous system activity serves as an index of an organism's self-regulatory capacities, promoting flexibility and adaptability in a changing environment [for additional theoretical consideration, see the neurovisceral integration model; Thayer & Lane, 2000]. Many studies have employed autonomic signals to explain how environmental factors may indirectly affect cognitive functions through peripheral stimulation, thereby establishing a bidirectional relationship between external and internal variables. The measurement of heart rate variability (HRV) is a valuable approach for understanding the changes in autonomic functions in response to physiological and psychological influences. In recent years, HRV has become a widely used noninvasive index of cardiac control (Quintana and Heathers, 2014; Shaffer et al., 2014; Shaffer and Ginsberg, 2017). HRV refers to the naturally occurring fluctuations in the time intervals between successive heartbeats (Laborde et al., 2019). Typically, HRV measurements include those in the time and frequency domains. In the time domain, the root mean square of successive differences (RMSSD) is associated with vagal activity (McCraty and Shaffer, 2015). In the frequency domain, the high-frequency band (HF, 0.15–0.4 Hz) is a marker of parasympathetic activity, which is associated with vagal activity (Shaffer and Ginsberg, 2017), while the

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low-frequency band (LF, 0.04–0.15 Hz) is traditionally considered a marker of sympathetic activity, which it is also influenced by parasympathetic activity (Hayano and Yuda, 2019). Vagally mediated HRV is considered the most relevant index of self-regulatory ability (Thayer et al., 2012). Changes in its reactivity have been observed following physical and mental loading (Laborde et al., 2019). Moreover, a resting-state synchronization hypothesis has been tested since autonomic reactivity to cognitive load typically involves peripheral responses as a consequence of central responses. Vagally mediated resting-state HRV is associated with activity in several neural networks, including brain areas involved in attentional, executive, and memory processes (e.g., the prefrontal cortex; Thayer and Lane, 2009). This suggests that it may exert an ascending influence on the brain and, thus, on cognitive processes. Higher vagally mediated resting-state HRV has been associated with better performance in tasks assessing emotion recognition (Quintana et al., 2012), heartbeat detection (Lischke et al., 2021), cognitive flexibility (Colzato et al., 2018), cognitive inhibition (Ottaviani et al., 2018), working memory (Laborde et al., 2015), memory retrieval (Gillie et al., 2014), and memory discrimination (Feeling et al., 2021).

Recent systematic reviews and *meta*-analyses (Forte et al., 2019; Magnon et al., 2022) have confirmed the association between HRV and cognitive functioning. These studies have highlighted that vagally mediated resting-state HRV is specifically associated with executive functioning and appears to be an autonomic marker of executive functions performance. However, the results of studies investigating the role of HRV in other cognitive functions, such as memory and attention, have been inconsistent (Forte et al., 2019). Consequently, the strength of the relationship between HRV and cognitive functioning remains to be fully determined. This latter association has yet to be validated for multiple reasons. One reason is that experimental paradigms have often focused on specific cognitive functions (i.e., executive functions), which has resulted in a substantial gap in the investigation of a comprehensive framework. To the best of our knowledge, no study has simultaneously investigated a wide range of cognitive functions. Accordingly, the aim of the present study was to establish a connection between vagally mediated HRV (vmHRV) and cognitive functions using a differentiated neuropsychological battery covering a wide range of cognitive domains. In light of the findings of previous studies (For a review see Forte et al., 2019; for a *meta*-analysis see Magnon et al., 2022), we hypothesized that different cognitive patterns would be observed for different cognitive abilities. A previous *meta*-analysis (Magnon et al., 2022) demonstrated that vagally mediated HRV predicts cognitive inhibition and cognitive flexibility with greater accuracy than working memory. We hypothesized that vmHRV is particularly associated with performance on goal-directed tasks involving adaptive psychological regulation and flexible cognitive processes, such as cognitive inhibition and cognitive flexibility. Given that tasks inducing mental stress (i.e., working memory tasks) have been found to be associated with decreased vagal-mediated HRV (Park and Thayer, 2014), we also expected a relationship with working memory, which requires greater cognitive engagement and results in a predominance of the sympathetic nervous system (Duschek et al., 2009). In the memory domain, our expectations align with previous findings (Muthukrishnan et al., 2017; Shah et al., 2011) that revealed a relationship between memory load and HRV. We expected to observe differences in immediate verbal memory between the high and low vmHRV groups. Moreover, According to prior research (Divjak et al., 2024; Frewen et al., 2013) that demonstrated vmHRV can assess implicit language knowledge, we hypothesized that higher vmHRV would be associated with improved lexical access. Finally, to better define the cognitive phenotype of the heart-brain association, we also analyzed global cognitive function and multiple confounding variables historically associated with cognitive performance and/or autonomic response, such as sex (Sztajzel et al., 2008), body mass index (BMI; Karason et al., 1999), anxiety (Thayer et al., 1996; Forte et al., 2021b), stress (Dishman et al., 2000), smoking behavior (Hayano et al., 1990), and heart rate (Gąsior et al., 2016).

Materials and methods

Participants

According to the suggestions of Laborde et al. (2019), the sample size was determined using G*Power 3 software (multiple analysis of variance; $\alpha = 0.05$, $(1 - \beta) = 0.95$, $d = 0.25$). Accordingly, a sample size of at least 120 participants was estimated. However, due to the potential risk of cardiac rhythm disruption, we estimated a sample size of 150 participants to be adequate. The participants were recruited through advertisements placed on the university campus and online. All participants enrolled in the study voluntarily and signed informed consent forms. Participants who had a history of psychiatric diagnoses, medical conditions, drug abuse, or medications that could affect HRV data were excluded ($n = 7$). The final sample consisted of 143 university students (mean age = 23.73 ± 2.69 years, range 18–30 years; 63 % females). Given that vmHRV has consistently been associated with positive outcomes (Thayer and Lane, 2009), stability over time (Bertsch et al., 2012), and heritability (Neijts et al., 2014), we considered HRV as an independent variable. For this reason, participants were divided into two groups (low and high vmHRV) using a median split of HF, as described by Laborde et al. (2019). Consequently, participants with high vagal tone ($n = 71$; mean age: 23.32 ± 2.99; 59 % female; mean ln-HF: 6.64) and those with low vagal tone ($n = 72$; mean age: 23.73 ± 2.69; 63 % female; mean ln-HF: 4.95) were included in the study.

Instruments and measures

Sociodemographic interview

A face-to-face semistructured anamnestic sociodemographic interview was also conducted to obtain information on age, education, and daily habits, such as alcohol consumption (the number of drinks per week), smoking (number of cigarettes per day), and coffee intake (number of cups per day).

Blood pressure and heart rate

Systolic and diastolic blood pressure and heart rate were recorded through an electronic device (Omron M3; HEM-7200-E, Omron Healthcare, Kyoto, Japan).

Height and weight

An Omron professional digital balance, calibrated in kg, was used to measure the weight. The height of each participant was measured by using a wall-mounted anthropometer. These measurements were used to calculate the BMI by dividing the weight (in kilograms) by the height (in meters squared).

Heart rate variability

The electrocardiogram (ECG) was recorded using a Firstbeat Bodyguard 2 heart rate monitoring system (Firstbeat Analytics, Jyväskylä, Finland). The signal was detected using two Ag/AgCl electrodes (Ambu BlueSensor L, Ballerup, Denmark), one applied under the right collarbone and the other under the left rib cage. HRV was assessed by calculating high-frequency HRV (HF-HRV; 0.15–0.40 Hz), which reflects changes in vagal control of the heart (Wehrwein et al., 2016), and low-frequency HRV (LF-HRV, 0.04–0.15 Hz), which represents a mix of vagal and sympathetic activity (Laborde et al., 2017) and is modulated by baroreflexes (Shaffer and Ginsberg, 2017). The signals were analyzed using Kubios software (Kubios Oy, Kupio, Finland). Each participant's resting HRV was recorded according to standard protocols (Malik, 1998; Laborde et al., 2017). During the resting phase, the HRV was recorded for five minutes while the participants were seated with their knees at a 90° angle and both feet flat on the ground. Time-domain measures, indexed by the root of the mean squared successive differences in beat-to-beat intervals (RMSSD), and frequency-domain measures, reflected by high-frequency (HF) changes in the heartbeat, were evaluated. Given that HF components (0.15–0.40 Hz) of heart rate changes have been proposed to serve as proxies for parasympathetic control and cardiac vagal tone (Berntson et al., 1997; Laborde et al., 2019), we chose to utilize HFs to classify participants according to their level of parasympathetic dominance.

Global cognitive functioning

Abstract reasoning performance was assessed using Raven's Standard Progressive Matrices (Raven & Court, 1938). The Mini-Mental State Examination (MMSE; Italian validation: Measso et al., 1993) was employed to measure overall cognitive functioning.

Cognitive task

Apparatus. Computerized versions of the cognitive tasks were displayed on a 17-inch monitor with a screen resolution of 1024 × 768 pixels using E-Prime software. Responses were gathered using both the keyboard (Stroop; WCST; n-Back) and mouse (Go-NoGo; ToL). Participants were positioned at a fixed distance of approximately 56 cm from the monitor.

A broad range of cognitive functions was evaluated to gain a better understanding of the relationship between ANS activity and cognitive functioning.

Stroop task

The Stroop task is widely used to evaluate executive functions, such as cognitive inhibition and interference control. The task involved the administration of target stimuli consisting of colored words (Font: Courier New; Font size: 60; colors: yellow, red, blue, and green) semantically related to the colors YELLOW, RED, BLUE, and GREEN. Each word could be presented with an ink color related to its semantic meaning (congruent condition; e.g., RED written in red ink) or another color (incongruent condition; e.g., RED written in blue ink). The participant was required to respond as quickly and accurately as possible by pressing the key corresponding to the ink color (key "A"= red; key "S"= green; key "K"= blue; key "L"= yellow). The experiment began with a practice block of 15 trials that provided feedback on correct execution. Afterward, a block of 120 randomly presented trials (60 congruent and 60 incongruent trials) was presented. Before each trial, an initial fixation cross was displayed for 400 ms. The target stimulus remained on the screen for 3000 ms or until the participant's response. Reaction times (RTs) of correct responses were collected, and the Stroop effect (mean RTs incongruent trials – mean RTs congruent trials) was computed.

Go/No-Go task

The Go/No-Go Task assesses motor inhibition, which may be defined as the ability to control a pre-potent motor response. The stimuli consisted of two geometric shapes, each measuring 960x720 pixels, positioned in the center of the screen against a black background. The Go stimulus was a green circle, while the No-Go stimulus was a green triangle. The participants were instructed to keep their gaze fixed on the center of the screen throughout the duration of the experiment. The initial screen, which featured a fixation cross, was displayed for a duration of 500 ms. Then, both the target stimuli (Go) and the nontarget stimuli (No-go) were presented in a random order, with three, four, or five Go trials being presented for each No-Go trial. Each stimulus remained in the center of the screen for 750 ms or until the participant's response. The task required participants to promptly press the left mouse key as quickly as possible when the green circle appeared in the center of the screen. When the green triangle appeared, participants were required to wait for the stimulus to disappear. The task consisted of 100 trials divided into two blocks of 50 trials each. At the start of the experiment, a practice block was presented with 12 trials and feedback on accuracy. The number of false alarms, which are considered to be the motor component of inhibition, was calculated by summing the inappropriate responses to "no-go" stimuli.

N-back task

The n-back task is a widely used method for assessing working memory. The stimuli consisted of alphabetical letters presented in the center of the screen (Font: Palatino Linotype; Font size: 30) with a white background. The task involved two consecutive sessions: one-back and two-back. In each session, a sequence of stimuli (duration: 2500 ms) was presented, followed by a blank screen (ISI: 500 ms). In the one-back session, the participant evaluated each stimulus as either identical to the previous stimulus (Target) or differing from it (Nontarget). In the two-back session, the participant indicated whether each stimulus matched or differed from the stimulus presented in the two previous trials. The participants used the "X" key for target stimuli and the "M" key for nontarget stimuli to record responses. The task included 40 trials for the one-back block and 40 for the two-back block. In each block, 30 % of the trials were targeted. The accuracy percentage for both the one-back and two-back procedures was considered a measure of working memory.

Computerized Wisconsin card sorting test (WCST)

A computerized version of the WCST was employed to assess cognitive flexibility. The test requires the participant to match a set of cards according to specific characteristics of the four stimulus cards. Two sets of 64 cards are presented. The cards have four possible suits (i.e., stars, crosses, circles, and triangles). Each suite has four possible colors (i.e., red, yellow, green, or blue). Each card can have a different number of suits, from one to four.

The cards are sorted by reference to four stimulus cards with one red triangle, two green stars, three yellow crosses, and four blue circles. The participant must select a single card from the deck and place it in correspondence with one of the four initial stimulus cards. The experimenter provides feedback on the correctness of each answer to guide the participant in inferring the adopted criterion (i.e., color, shape, number, respectively) for sorting the cards. The participant disregards any other criteria based on this feedback until making ten consecutive correct choices. Then, the criterion for the correct answer changes, and the procedure is repeated until both decks of cards are completed. Different indices can be derived from this test. This study utilized the global score, which is calculated by subtracting the completed categories multiplied by 10 from the number of cards administered ([card administered − (completed categories*10)]. This score is inversely proportional to performance, with a lower score indicating better performance. Additionally, perseveration errors were recorded as an index of difficulty in shifting the set during the task completion procedure.

Iowa gambling task (IGT)

The Iowa Gambling Task (IGT) was used to evaluate decision-making. A digital version with complete superimposition on the original version was utilized in this study. Four decks of cards (i.e., A, B, C, and D) were presented as stimuli on a green background. To reduce distraction and prevent subjects from using an unnecessary strategy guided by certain types of cards, the back and front of the decks were identical, with a red cover and a joker of spades, respectively. Each card on the deck could lead to a win or a loss. However, the frequency and amount of wins and losses differed between the decks. Decks A and B were considered disadvantageous. They involved a larger short-term win ($ 100) but a long-term loss. Decks A and B differed in the frequency and magnitude of the loss. The loss was more frequent on deck A but less plentiful than on deck B. With every ten cards drawn for each deck, there was a loss of $ 1250 against a win of $ 1000. Overall, both decks A and B lead to a loss of $250 for every ten cards drawn. Decks C and D were more advantageous because they resulted in a smaller short-term payout amount ($ 50 each). Like those of decks A and B, the frequency and magnitude of the loss also differed. Deck C had more frequent losses but was a lesser entity than deck D. Every 10 cards drawn on these decks resulted in a win of $500 with a loss of $250. Therefore, they resulted in a win of $250 for every 10 cards selected. On the screen, participants can see the amount of money they have won (written in green) and lost (written in red). The amount of money held was updated with each selection. The task required participants to select one card from one deck at a time. Each participant started with a $2,000 credit, which could increase or decrease throughout the game. Participants were informed that some decks were more advantageous than others. Participants selected their preferred deck by pressing one of four corresponding keyboard keys until they completed one hundred selections. The participants were unaware of this rule. Participants also did not know when a loss would appear. The present study utilizes the same loss conditions as those of Bechara et al. (2005).

Tower of London (TOL)

Planning abilities were assessed using an electronic adaptation of the Tower of London task (Shallice, 1982). The task was administered via Pebl 2.1 software (Mueller and Piper, 2014 Computer software retrieved from https://pebls.sf.net.) on a personal computer equipped with a 15-inch monitor. The responses were enabled through mouse control. The task involved arranging three colored discs (blue, green, and red) in a predetermined order on a structure with three vertical sticks shown on the top screen. The frame remains uniform, but white, movable discs are present at the bottom of the screen. Across 12 trials, the participant must order the discs by manipulating the disks one at the time to recreate the predetermined configuration. The whole sequence must be carried out mentally before executing the sequence. For each trial, only a predetermined number of movements can be made, and the number of available movements is shown on a vertical bar on the side of the screen. The total TOL score was calculated by the Pebl program, considering the number of trials correctly completed in the minimum possible moves. A lower total score indicated poorer planning performance.

Verbal fluency

Verbal fluency was evaluated in the semantic (SVF) and phonological (PVF) categories. The SVF was assessed by speaking for 1 min using different semantic class words (animals, fruits, and automotive brands). This category is highly sensitive for evaluating the access and semantic organization of the mental lexicon. Participants were given the following instructions: “Tell me as many animals/fruits/automotive brands as you can remember”, and the researcher recorded the time and the words. The PVF was evaluated by the utterance of words beginning with the letters “L”, ”F“, and “P” separately in 1 min. Participants were given the following instruction: ”Tell me as many words as you know that begin with the letter L/F/P, excluding proper nouns and names of cities“. Both tests were timed with a common clock, and the emission was recorded through an audio file using a recorder, allowing for later transcription and analysis by the researchers.

Rey Auditory-Verbal Learning test (RAVLT)

The RAVLT was used to assess both short-term (memory recognition) and long-term (delayed memory) verbal memory. The procedure involved reading a list of 15 words (list A) out loud to the subject five times consecutively. Each attempt was followed by a spontaneous retrieval test. After a 15-minute interval, the examiner must recall the list of words from list A without a new reading. The memory recognition test scores were calculated by adding the correct answers. The same procedure was used for the delayed memory test

General procedure

The study was conducted in accordance with the Declaration of Helsinki and was approved by the Local Ethics Committee (Department of Dynamic and Clinical Psychology— “Sapienza” University of Rome; number: 0001166). Prior to the experimental procedure, participants received instructions they had to follow before beginning the study, which included abstaining from smoking, consuming coffee 2 h before the test, and consuming alcohol 24 h prior. The experiment was carried out at the Laboratory of Health Psychology: Cognitive and Psychophysiological Assessment of the Department of Dynamic, Clinical and Health Psychology of the University of Rome Sapienza. After providing informed consent, a face-to-face semistructured sociodemographic anamnestic interview was conducted. Then, weight and height were measured. Then, the MMSE and standard progressive matrices were administered, and resting HRV was recorded for 5 min in accordance with established guidelines (Laborde et al., 2017; Malik, 1998). Subsequently, cognitive tests were administered. All participants were individually assessed, and the order of tasks was randomly assigned through block randomization, with all tasks divided into five blocks. The procedure lasted approximately 90 min and took place in a quiet, dark, silent, and temperature-controlled room.

Data analysis

The results are reported as the mean ± SD. Univariate analyses of variance (ANOVAs) were performed to examine the differences between groups. Group (High-HRV, Low-HRV) was used as the independent variable; demographic information (age, education), lifestyle aspects (smoking, coffee, alcohol, BMI), physiological variables (systolic and diastolic blood pressure, HRV), and cognitive measures (Raven’s standard progressive matrices, MMSE) were used as dependent variables. A chi-square analysis was also conducted to compare the differences in high and low HRV between sexes and smoking habits. The main hypotheses were tested through different ANOVAs in which the independent variable was the Group (High-HRV or Low-HRV). The following dependent variables were considered: (a) the number of global uncorrected responses and the number of perseverative errors in the WSCT, (b) the number of losses in the Iowa Gambling Task, (c) the number of correct responses for semantic fluency and phonological fluency, (d) the number of correct responses of immediate and differed retrieval in the Rey Auditory-Verbal Learning Test, (e) the total score in the Tower of London, (f) the number of false alarms in the GoNoGo task, (g) the number of correct responses in the One-Back and Two-Back tasks, and (h) the Stroop effect for the Stroop task. In addition, a mixed design analysis, Group x Congruency (Congruent, Incongruent), was conducted for the Stroop task, considering the mean number of correct responses. Planned comparisons were used to analyze significant interactions. For all the statistical analyses, the significance level was set at $p < 0.05$. However, given that several univariate ANOVAs were performed, the Bonferroni correction was applied to correct for multiple comparisons; accordingly, $p < 0.02$ was selected as the threshold level for significance. Statistical analyses were performed using Statistica software (ver.10.0, Dell, Round Rock, USA) and JASP.

Results

Demographic variables

The chi-square test did not reveal significant differences between the high-HRV and low-HRV groups for sex or smoking status ($X2 < 2$; all $p > 0.17$; see Table 1). The ANOVAs between the two groups (High-HRV, Low-HRV) did not reveal significant differences in age, years of education, BMI, waist-to-height ratio, systolic and diastolic blood pressure, mean arterial pressure, the number of cigarettes smoked per day, the number of cups of coffee consumed daily, or alcohol consumption per week (all $F < 2.01$; all $p > 0.1$; see Table 1). However, the two groups differed significantly in heart rate ($F_{1,141} = 7.13$; $p = 0.009$; $\eta2 = 0.05$). Consistently, the low-HRV subgroup had a greater heart rate than the high-HRV subgroup. See Table 1.

Table 1
Means (M) and standard deviations (SD) of descriptive variables considering HRV groups.

	High HRV (N = 71)	Low HRV (N = 72)	F/χ^2	p
Sex			<1	0.56
Male	29	26		
Female	42	46		
Age	23.32 (2.99)	23.73(2.69)	<1	0.39
Years of Education	16.39(2.08)	16.29(1.82)	<1	0.75
BMI	22.28 (3.11)	23.11 (3.82)	2.01	0.15
Waist-to-Height Ratio	0.45 (0.05)	0.46 (0.05)	<1	0.69
SBP	116.08 (10.52)	117.80 (11.81)	<1	0.36
DBP	71.02 (7.22)	72.62(8.65)	1.39	0.24
HR	73.91 (10.00)	79.51 (14.00)	7.13	0.009
MAP	86.01 (7.30)	87.66 (8.80)	1.45	0.23
Smoke			1.88	0.17
Yes	24	32		
No	47	40		
N° Cigarettes	2.62 (4.54)	3.83 (5.68)	1.99	0.16
N° Coffee	1.87 (1.61)	1.88 (1.53)	<1	0.95
Alcohol per week	3.09 (4.24)	3.88 (4.88)	1.06	0.30
Ln-HF	6.64 (0.35)	5.95 (0.49)	89.49	0<.001

Ln-HF: natural logarithm of High Frequency; SPB: Systolic Blood Pressure; DBP; Diastolic Blood Pressure; MAP: Mean Arterial Pressure; HR: Heart Rate; BMI: Body Mass Index.

Cognitive tasks

Between-group ANOVAs (High-HRV; Low-HRV) revealed significant differences in Immediate Recall on the Rey Auditory Verbal Learning Test ($F_{1,141} = 15.6$; $p < 0.001$; η2 = 0.10); Digit Span Backward test ($F_{1,141} = 11.54$; $p < 0.001$; η2 = 0.07); Phonological test ($F_{1,141} = 11.97$; $p < 0.001$; η2 = 0.08); Semantic Fluency test ($F_{1,141} = 0.58$; $p = 0.01$; η2 = 0.04); Total Score on the Iowa Gambling Task ($F_{1,141} = 3.69$; $p = 0.02$; η2 = 0.03); Stroop Effect test ($F_{1,141} = 4.56$; $p = 0.03$; η2 = 0.03); Two-back task ($F_{1,141} = 6.86$; $p = 0.01$; η2 = 0.02); Tower of London score ($F_{1,141} = 10.21$; $p = 0.002$; η2 = 0.07); and Global score In the tested cognitive tasks, the high-HRV group performed better than the low-HRV group. No other differences were found. See Table 2.

Mixed ANOVA of reaction times in the Stroop task highlighted a significant main effect of congruency ($F_{1,141} = 278.57$; $p < 0.001$; η2 = 0.66), and Group ($F_{1,141} = 9.49$; $p = 0.002$; η2 = 0.06) demonstrated shorter reaction times in congruent trials than in incongruent trials (mean difference: −70) and in the high-HRV group than in the low-HRV group (mean difference: −47). Moreover, the Group × Congruency interaction ($F_{1,141} = 4.60$; $p = 0.03$; η2 = 0.03) was associated with shorter reaction times in the high-HRV group than in the low-HRV group in both congruent trials (mean difference: −38; $p = 0.01$) and incongruent trials (mean difference: −56; $p < 0.001$).

Discussion

The present study aimed to enhance the understanding of the relationship between resting-state vagally mediated heart rate variability (vmHRV) and cognitive performance across a comprehensive range of domains. To achieve this, we evaluated and compared cognitive performance in young adults with higher vmHRV, as indexed in the frequency domain, to those with lower vmHRV. Our findings reveal multiple associations between vmHRV and cognitive performance, providing further support for the neurovisceral integration model proposed by Thayer and Lane (2009). Thayer et al. (2012) suggest that the vagus nerve serves as the psychophysiological pathway connecting the prefrontal cortex and the anterior cingulate cortex, which are crucial for regulating inhibitory and self-regulatory abilities, as well as overall cognitive functioning (Thayer et al., 2012).

Specifically, the results indicate that high resting autonomic parasympathetic activation is associated with adaptive executive functions, particularly cognitive inhibition and cognitive flexibility. These cognitive domains are more strongly associated with heart rate variability (HRV). These findings are supported by several authors who have proposed that vagally mediated HRV (vmHRV) is especially linked to performance on goal-directed tasks requiring adaptive psychological regulation and flexible cognitive processes, such as cognitive inhibition and cognitive flexibility (Segerstrom and Nes, 2007; Park and Thayer, 2014). These processes demand substantial self-regulatory effort, which is associated with parasympathetic activity. They are also relevant to tasks that induce mental stress due to cognitive load, such as tasks assessing working memory (Forte et al., 2019; Magnon et al., 2022). These results align with the neurovisceral integration model (NIM), which posits that the regulation of these specific cognitive functions is mediated by vmHRV. According to Thayer and Lane (2009), regulatory and inhibitory processes are essential prerequisites for executive functioning. Moreover, executive control plays a critical role in attention, memory, and guided decision-making. High HRV is generally associated with improved self-regulation (Thayer and Lane, 2009).

The physiological, behavioral, emotional, and cognitive processes involved in self-regulation may share a common physiological signal, namely vagal tone, which is dependent on the medial prefrontal structures (Thayer & Lane, 2009). Consequently, elevated heart rate variability (HRV) serves as an endophenotype for both frontal lobe functioning and physical health (Kemp & Quintana, 2013). A reduction in vagal tone may indicate inadequate prefrontal inhibitory control (Friedman, 2007; Thayer & Lane, 2000). Our findings provide support for this hypothesis and corroborate previous evidence (for a review, see Forte et al., 2019), highlighting that individuals with high resting vagal heart rate variability (vmHRV) exhibit enhanced inhibitory control compared to those with low resting vmHRV.

High resting vmHRV was also associated with better performance on

Table 2
Means (M) and standard deviations (SD) of cognitive performance considering groups with high an low HRV.

	High HRV (N = 71)	Low HRV (N = 72)	F/χ^2	p
MMSE	29.70 (0.51)	29.70 (0.51)	<1	0.36
SPM total	48.55 (6.11)	46.15 (8.66)	2.82	0.08
SPM (A-D)	41.42 (4.43)	39.63 (6.02)	3.16	0.06
RAVLT Immediate Recall	58.97 (7.59)	54.21 (6.54)	15.56	0<.001
RAVLT Delayed Recall	13.16 (1.71)	12.70 (2.00)	2.04	0.15
Digit Span Forward	6.56 (1.09)	6.29 (1.06)	2.26	0.13
Digit Span Backward	5.56 (0.99)	4.94 (1.17)	11.54	0<.001
Phonological Fluency	51.37 (9.09)	44.41 (13.60)	11.97	0<.001
Semantic Fluency	53.10 (9.6)	48.73 (10.82)	5.58	0.01
IGT Score	9.04 (25.61)	0.69 (23.05)	3.69	0.03
Stroop Task (RT)				
Congruency	679.72 (81.95)	717.69 (97.16)	6.30	0.01
Incongruency	740.87 (88.74)	796.88 (106.91)	11.54	0<.001
Stroop Effect	61.24 (42.84)	79.02 (56.42)	4.56	0.03
Go-NoGo False Allarm	0.12 (0.11)	0.12 (0.10)	<1	0.96
N-BACK				
One-Back	0.94 (0.06)	0.93 (0.11)	<1	0.42
Two-Back	0.88 (0.12)	0.81 (0.16)	6.86	0.01
TOL-Score	25.94 (6.50)	22.24 (6.91)	10.21	0.002
WCST				
Global score	23.79(22.84)	34.31 (30.84))	4.88	0.02
Perseverative Errors	7.23 (6.09)	9.46 (7.24)	3.61	0.06
Non Perseverative Errors	8.07 (8.70)	11.70 (12.43)	3.70	0.06

RAVLT: Rey Auditory-Verbal Learning Test; IGT: Iowa Gambling Task; SPM: Standard Progressive Matrices; TOL: Tower of London; WCST: Wisconsin Card Sorting Task; MMSE: Mini Mental State Examination; RT: Reaction Times.

tasks assessing working memory (e.g., digit span backward and two-back tasks), cognitive flexibility (e.g., WCST), planning (e.g., TOL), and decision-making (e.g., IGT score). These findings suggest a shared neurobiological basis. Several studies have demonstrated a correlation between vagal regulation of cardiac control and prefrontal cortex activation (Lane et al., 2009; Forte et al., 2021a; Forte et al., 2021b; Forte et al., 2021c). Thayer et al. (2012) conducted a *meta*-analysis and found significant correlations between HRV and neuronal activity in the ventromedial prefrontal cortex (PFC), a brain region primarily associated with executive functions (Alvarez and Emory, 2006; Ridderinkhof et al., 2004). Consequently, reduced activity in the PFC negatively impacts cognitive abilities related to this brain region (Thayer and Lane, 2009). As HRV appears to reflect PFC activity, higher vmHRV is associated with improved performance across all executive domains (Thayer and Lane, 2009). This finding suggests that the resting state is equally related to all executive abilities. The results of this study confirm the hypothesis that resting-state vmHRV is potentially linked to the efficient functioning of prefrontal-subcortical inhibitory circuits that drive flexible and adaptive responses to environmental demands (Thayer & Lane, 2000; Thayer and Lane, 2009; Forte et al., 2022). Another interest finding pertains to the Stroop Task, the results of which revealed significant differences. According to previous studies (Forte et al., 2023), HRV appears to be associated with higher cognitive conflict resolution abilities in individuals exhibiting higher HRV. This result suggests that they have enhanced abilities in managing environmental requests and modulating behavioral and physiological responses accordingly.

With regard to other cognitive domains, we observed associations with immediate verbal memory and language performance. These findings can be interpreted in light of previous evidence. Concerning memory, some studies have focused on sleep, suggesting that parasympathetic activity during REM sleep strongly predicts improvement in implicit priming in a creativity task (Whitehurst et al., 2016). However, studies investigating the effect of HRV on memory during wakefulness have yielded mixed results. For instance, one study demonstrated that individuals with poor vagal autonomic functioning (low resting HRV) showed a greater tendency to form false memories (Feeling et al., 2021). Furthermore, cardiac vagal tone has been demonstrated to be positively correlated with enhanced memory for emotionally charged stimuli (Mattarozzi et al., 2019; Wendt et al., 2019), although no correlation was observed with memory for neutral stimuli. In contrast, several studies have shown that HRV during wakefulness does not predict episodic memory performance (Zeki Al Hazzouri et al., 2018). However, our sample did not yield any results for long-term memory, a function that was not investigated in most cases. The significant relationship between autonomic response and immediate memory may be explained by the influence of memory load on the autonomic nervous system. Indeed, Backs and Seljos (1994) showed that individuals with poor memory have a greater decrease in heart period variability (i.e., lower rMSSD). Accordingly, in the case of higher resting vmHRV, even when the parasympathetic response decreases, the high starting level allows high performance to be maintained.

Regarding language, the existing literature provides limited evidence. However, our findings are consistent with those of previous studies indicating that a decrease in HRV, as measured by the NN50, is associated with the number of grammatical violations. HRV decreases in direct proportion to the increased number of errors (Divjak et al., 2024). This could be considered a cardiovascular response to language, supporting the assumption that language users have absorbed the typical patterns of their mother tongue and, therefore, autonomically respond to their violation. Accordingly, vmHRV can be used to assess linguistic knowledge and lexical access skills.

The present study addresses the limitations highlighted in recent systematic reviews and *meta*-analyses (Forte et al., 2019; Magnon et al., 2022) regarding the underexposure of certain cognitive domains or the lack of a comprehensive analysis. However, despite the promising findings, this study has several limitations. The relatively small sample size prevents the generalization of the results. Further studies should include a larger sample size to clarify the discrepancy between these results and those of previous studies and to yield more generalizable results (Britton et al., 2008). Moreover, the relatively young age of the participants makes it challenging to generalize the results to other age groups, such as the elderly. Given the prevalence of cognitive impairment in older adults (Corbo and Casagrande, 2022; Guarino et al., 2020; Forte and Casagrande, 2020; Forte et al., 2020), extending the study to this population could be interesting, especially for understanding the trend of functional association across the lifespan. Furthermore, it is of great importance to assess the relationship between HRV and the interplay between executive functions and other attentional systems, such as selective attention and alertness. The attention network test (e.g., Federico et al., 2013; Spagna et al., 2014) could be employed to evaluate this connection while also enabling the examination of the association between HRV and hemispheric functioning (Casagrande et al., 2021; Spagna et al., 2016). Moreover, regarding your concerns about our choice to dichotomize the HRV variable, we understand that dichotomization may sometimes oversimplify the data. However, our decision was informed by an interest to underline a threshold effects on cognitive performance, in line with previous research (Forte et al., 2019).

Finally, we assumed that HF-HRV is an index of the parasympathetic response, while previous studies have suggested that this parameter could be influenced by other factors, such as the respiration rate (Laborde et al., 2017). Therefore, further studies are needed to investigate potential distinctions between time- and frequency-domain measures.

Conclusions

The present study examines the potential association between vagally-mediated heart rate variability and cognitive functioning, offering a comprehensive analysis of various cognitive domains. For the first time, we provide a broad examination to determine if the relationship observed in previous studies is general or specific. Our findings indicate that: a) High vmHRV positively influences cognitive functions overall; b) Higher vmHRV is strongly associated with executive functioning, but also shows significant associations with language and memory. These results support the neurovisceral integration model. Nevertheless, further research is needed to delve into the underlying pathways and address the methodological limitations identified in this study, in order to enhance the consistency and generalizability of these findings.

CRediT authorship contribution statement

Giuseppe Forte: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Maria Casagrande:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Conceptualization.

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References

Alvarez, J.A., Emory, E., 2006. Executive function and the frontal lobes: a meta-analytic review. Neuropsychol. Rev. 16 (1), 17–42.

Backs, R.W., Seljos, K.A., 1994. Metabolic and cardiorespiratory measures of mental effort: the effects of level of difficulty in a working memory task. Int. J. Psychophysiol. 16 (1), 57–68.

Balconi, M., Venturella, I., Fronda, G., de Filippis, D., Salati, E., Vanutelli, M.E., 2019. To rate or not to rate? Autonomic response and psychological well-being of employees during performance review. The Health Care Manager 38 (2), 179–186.

Bechara, A., Damasio, H., Tranel, D., Damasio, A.R., 2005. The Iowa Gambling Task and the somatic marker hypothesis: some questions and answers. Trends Cognit. Sci. 9 (4), 159–162.

Berntson, G.G., Thomas Bigger Jr., J., Eckberg, D.L., Grossman, P., Kaufmann, P.G., Malik, M., Van Der Molen, M.W., 1997. Heart rate variability: origins, methods, and interpretive caveats. Psychophysiology 34 (6), 623–648.

Bertsch, K., Hagemann, D., Naumann, E., Schaechinger, H., Schulz, A., 2012. Stability of heart rate variability indices reflecting parasympathetic activity. Psychophysiology 49 (5), 672–682.

Britton, A., Singh-Manoux, A., Hnatkova, K., Malik, M., Marmot, M.G., Shipley, M., 2008. The association between heart rate variability and cognitive impairment in middle-aged men and women. The Whitehall II Cohort Study. Neuroepidemiology 31 (2), 115–121. https://doi.org/10.1159/000148257.

Casagrande, M., Agostini, F., Favieri, F., Forte, G., Giovannoli, J., Guarino, A., Martella, D., 2021. Age-related changes in hemispherical specialization for attentional networks. Brain Sci. 11 (9), 1115.

Colzato, L.S., Jongkees, B.J., de Wit, M., van der Molen, Steenbergen, L., 2018. Variable heart rate and a flexible mind: Higher resting-state heart rate variability predicts better task-switching. Cognit. Affect. Behav. Neurosci. 18, 730–738.

Corbo, I., Casagrande, M., 2022. Higher-level executive functions in healthy elderly and mild cognitive impairment: a systematic review. J. Clin. Med. 11 (5), 1204.

Dishman, R.K., Nakamura, Y., Garcia, M.E., Thompson, R.W., Dunn, A.L., Blair, S.N., 2000. Heart rate variability, trait anxiety, and perceived stress among physically fit men and women. Int. J. Psychophysiol. 37 (2), 121–133.

Divjak, D., Sun, H., Milin, P., 2024. Physiological responses and cognitive behaviours: Measures of heart rate variability index language knowledge. J. Neurolinguist. 69, 101177.

Duschek, S., Muckenthaler, M., Werner, N., Del Paso, 2009. Relationships between features of autonomic cardiovascular control and cognitive performance. Biol. Psychol. 81 (2), 110–117.

Federico, F., Marotta, A., Adriani, T., Maccari, L., Casagrande, M., 2013. Attention network test—The impact of social information on executive control, alerting and orienting. Acta Psychol. 143 (1), 65–70.

Feeling, N., Williams, D.P., Speller, L.F., Loftus, E.F., Koenig, J., Thayer, J.F., 2021. Resting state heart rate variability and false memories. Int. J. Psychophysiol. 159, 17–22.

Forte, G., Casagrande, M., 2020. Effects of blood pressure on cognitive performance in aging: a systematic review. Brain Sci. 10 (12), 919.

Forte, G., De Pascalis, V., Favieri, F., Casagrande, M., 2020. Effects of blood pressure on cognitive performance: a systematic review. J. Clin. Med. 9 (1), 34.

Forte, G., Favieri, F., Casagrande, M., 2019. Heart rate variability and cognitive function: a systematic review. Front. Neurosci. 13, 710.

Forte, G., Morelli, M., Casagrande, M., 2021a. Heart rate variability and decision-making: autonomic responses in making decisions. Brain Sci. 11 (2), 243.

Forte, G., Favieri, F., Oliha, E.O., Marotta, A., Casagrande, M., 2021b. Anxiety and Attentional Processes: The Role of Resting Heart Rate Variability. Brain Sci. 11 (4), 480.

Forte, G., Morelli, M., Grässler, B., Casagrande, M., 2021c. Decision making and Heart Rate variability: a systematic review. Appl. Cognit. Psychol. https://doi.org/10.1002/acp.3901. Accepted Author Manuscript.

Forte, G., Troisi, G., Pazzaglia, M., Pascalis, V.D., Casagrande, M., 2022. Heart rate variability and pain: a systematic review. Brain Sci. 12 (2), 153.

Forte, G., Troisi, G., Favieri, F., De Pascalis, V., Langher, V., Casagrande, M., 2023. Inhibition and heart rate variability in experimentally Induced Pain. J. Pain Res. 3239–3249.

Frewen, J., Finucane, C., Savva, G.M., Boyle, G., Coen, R.F., Kenny, R.A., 2013. Cognitive function is associated with impaired heart rate variability in aging adults: the Irish longitudinal study on aging wave one results. Clin. Autonomic Res. 23 (6), 313–323. https://doi.org/10.1007/s10286-013-0214-x.

Friedman, B.H., 2007. An autonomic flexibility–neurovisceral integration model of anxiety and cardiac vagal tone. Biol. Psychol. 74 (2), 185–199.

Gąsior, J.S., Sacha, J., Jeleń, P.J., Zieliński, J., Przybylski, J., 2016. Heart rate and respiratory rate influence on heart rate variability repeatability: effects of the correction for the prevailing heart rate. Front. Physiol. 7, 356.

Gillie, B.L., Vasey, M.W., Thayer, J.F., 2014. Heart rate variability predicts control over memory retrieval. Psychol. Sci. 25 (2), 458–465. https://doi.org/10.1177/0956797613508789.

Guarino, A., Forte, G., Giovannoli, J., Casagrande, M., 2020. Executive functions in the elderly with mild cognitive impairment: a systematic review on motor and cognitive inhibition, conflict control and cognitive flexibility. Aging Ment. Health 24 (7), 1028–1045.

Hayano, J., Sakakibara, Y., Yamada, M., Ohte, N., Fujinami, T., Yokoyama, K., Takata, K., 1990. Decreased magnitude of heart rate spectral components in coronary artery disease. Its relation to angiographic severity. Circulation 81 (4), 1217–1224.

Hayano, J., Yuda, E., 2019. Pitfalls of assessment of autonomic function by heart rate variability. J. Physiol. Anthropol. 38, 1–8.

Karason, K., Mølgaard, H., Wikstrand, J., Sjöström, L., 1999. Heart rate variability in obesity and the effect of weight loss. Am. J. Cardiol. 83 (8), 1242–1247.

Kemp, A.H., Quintana, D.S., 2013. The relationship between mental and physical health: insights from the study of heart rate variability. Int. J. Psychophysiol. 89 (3), 288–296.

Laborde, S., Lautenbach, F., Allen, M.S., 2015. The contribution of coping-related variables and heart rate variability to visual search performance under pressure. Physiol. Behav. 139, 532–540.

Laborde, S., Mosley, E., Thayer, J.F., 2017. Heart rate variability and cardiac vagal tone in psychophysiological research–recommendations for experiment planning, data analysis, and data reporting. Front. Psychol. 8, 213.

Laborde, S., Strack, N., Mosley, E., 2019. The influence of power posing on cardiac vagal activity. Acta Psychol. 199, 102899.

Lane, R.D., McRae, K., Reiman, E.M., Chen, K., Ahern, G.L., Thayer, J.F., 2009. Neural correlates of heart rate variability during emotion. Neuroimage 44 (1), 213–222.

Lischke, A., Pahnke, R., Mau-Moeller, A., Weippert, M., 2021. Heart rate variability modulates interoceptive accuracy. Front. Neurosci. 14, 612445.

Magnon, V., Vallet, G.T., Benson, A., Mermillod, M., Chausse, P., Lacroix, A., Dutheil, F., 2022. Does heart rate variability predict better executive functioning? A systematic review and meta-analysis. Cortex.

Malik, M., 1998. Heart rate variability. Curr. Opin. Cardiol. 13 (1), 36–44.

Mattarozzi, K., Colonnello, V., Thayer, J.F., Ottaviani, C., 2019. Trusting your heart: Long-term memory for bad and good people is influenced by resting vagal tone. Conscious. Cognit. 75, 102810.

McCraty, R., Shaffer, F., 2015. Heart rate variability: new perspectives on physiological mechanisms, assessment of self-regulatory capacity, and health risk. Global Adv. Health Med. 4 (1), 46–61.

Measso, G., Cavarzeran, F., Zappalà, G., Lebowitz, B.D., Crook, T.H., Pirozzolo, F.J., Grigoletto, F., 1993. The mini-mental state examination: Normative study of an Italian random sample. Dev. Neuropsychol. 9 (2), 77–85.

Mueller, S.T., Piper, B.J., 2014. The psychology experiment building language (PEBL) and PEBL test battery. J. Neurosci. Methods 222, 250–259.

Muthukrishnan, S.P., Gurja, J.P., Sharma, R., 2017. Does heart rate variability predict human cognitive performance at higher memory loads. Indian J. Physiol. Pharmacol. 61 (1), 14–22.

Neijts, M., Van Lien, R., Kupper, N., Boomsma, D., Willemsen, G., De Geus, E.J., 2014. Heritability of cardiac vagal control in 24-h heart rate variability recordings: Influence of ceiling effects at low heart rates. Psychophysiology 51 (10), 1023–1036.

Ottaviani, C., Zingaretti, P., Petta, A.M., Antonucci, G., Thayer, J.F., Spitoni, G.F., 2018. Resting heart rate variability predicts inhibitory control above and beyond impulsivity. J. Psychophysiol.

Park, G., Thayer, J.F., 2014. From the heart to the mind: cardiac vagal tone modulates top-down and bottom-up visual perception and attention to emotional stimuli. Front. Psychol. 5, 278.

Porges, S.W., 2007. The polyvagal perspective. Biol. Psychol. 74 (2), 116–143.

Quintana, D.S., Guastella, A.J., Outhred, T., Hickie, I.B., Kemp, A.H., 2012. Heart rate variability is associated with emotion recognition: Direct evidence for a relationship between the autonomic nervous system and social cognition. Int. J. Psychophysiol. 86 (2), 168–172.

Quintana, D.S., Heathers, J.A., 2014. Considerations in the assessment of heart rate variability in biobehavioral research. Front. Psychol. 5, 805.

Raven, J.C., Court, J.H., 1938. Raven's Progressive Matrices. Western Psychological Services, Los Angeles, CA.

Ridderinkhof, K.R., Ullsperger, M., Crone, E.A., Nieuwenhuis, S., 2004. The role of the medial frontal cortex in cognitive control. Science 306 (5695), 443–447.

Segerstrom, S.C., Nes, L.S., 2007. Heart rate variability reflects self-regulatory strength, effort, and fatigue. Psychol. Sci. 18 (3), 275–281.

Shaffer, F., Ginsberg, J.P., 2017. An overview of heart rate variability metrics and norms. Front. Public Health 5, 258.

Shaffer, F., McCraty, R., Zerr, C.L., 2014. A healthy heart is not a metronome: an integrative review of the heart's anatomy and heart rate variability. Front. Psychol. 5, 1040.

Shah, A.J., Su, S., Veledar, E., Bremner, J.D., Goldstein, F.C., Lampert, R., Vaccarino, V., 2011. Is heart rate variability related to memory performance in middle-aged men? Psychosomatic Med. 73 (6), 475–482.

Shallice, T., 1982. Specific impairments of planning. Philosophical Transactions of the Royal Society of London. B, Biological Sciences 298 (1089), 199–209.

Spagna, A., Martella, D., Sebastiani, M., Maccari, L., Marotta, A., Casagrande, M., 2014. Efficiency and interactions of alerting, orienting and executive networks: The impact of imperative stimulus type. Acta Psychol. 148, 209–215.

Spagna, A., Martella, D., Fuentes, L.J., Marotta, A., Casagrande, M., 2016. Hemispheric modulations of the attentional networks. Brain Cogn. 108, 73–80.

Sztajzel, J., Jung, M., Bayes de Luna, A., 2008. Reproducibility and gender-related differences of heart rate variability during all-day activity in young men and women. Ann. Noninvasive Electrocardiol. 13 (3), 270–277.

Thayer, J.F., Lane, R.D., 2000. A model of neurovisceral integration in emotion regulation and dysregulation. J. Affect. Disord. 61 (3), 201–216.

Thayer, J.F., Lane, R.D., 2009. Claude Bernard and the heart–brain connection: Further elaboration of a model of neurovisceral integration. Neurosci. Biobehav. Rev. 33 (2), 81–88.

Thayer, J.F., Friedman, B.H., Borkovec, T.D., 1996. Autonomic characteristics of generalized anxiety disorder and worry. Biol. Psychiatry 39 (4), 255–266.

Thayer, J.F., Åhs, F., Fredrikson, M., Sollers III, J.J., Wager, T.D., 2012. A meta-analysis of heart rate variability and neuroimaging studies: implications for heart rate variability as a marker of stress and health. Neurosci. Biobehav. Rev. 36 (2), 747–756.

Wehrwein, E.A., Orer, H.S., Barman, S.M., 2016. Overview of the anatomy, physiology, and pharmacology of the autonomic nervous system.

Wendt, J., König, J., Hufenbach, M.C., Koenig, J., Thayer, J.F., Hamm, A.O., 2019. Vagally mediated heart rate variability and safety learning: Effects of instructions and number of extinction trials. Psychophysiology 56 (10), e13404.

Whitehurst, L.N., Cellini, N., McDevitt, E.A., Duggan, K.A., Mednick, S.C., 2016. Autonomic activity during sleep predicts memory consolidation in humans. Proceedings of the National Academy of Sciences 113 (26), 7272–7277.

Zeki Al Hazzouri, A., Elfassy, T., Carnethon, M.R., Lloyd-Jones, D.M., Yaffe, K., 2018. Heart rate variability and cognitive function in middle-age adults: the coronary artery risk development in young adults. Am. J. Hypertens. 31 (1), 27–34.