Biological Psychology 81 (2009) 110–117

Contents lists available at ScienceDirect

Biological Psychology

journal homepage: www.elsevier.com/locate/biopsycho

Relationships between features of autonomic cardiovascular control and cognitive performance

Stefan Duschek[a,*], Magdalena Muckenthaler[a], Natalie Werner[a], Gustavo A. Reyes del Paso[b]

[a] Ludwig-Maximilians-Universität München, Department Psychologie, Leopoldstr. 13, 80802 Munich, Germany
[b] Universidad de Jaén, Departamento de Psicología, Facultad de Humanidades y CC.EE., 23071 Jaén, Spain

ARTICLE INFO

Article history:
Received 28 July 2008
Accepted 11 March 2009
Available online 24 March 2009

Keywords:
Heart rate variability
RSA
Baroreflex
Cognition
Cognitive performance
Attention

ABSTRACT

The study investigated relationships between autonomic cardiovascular control and attentional performance. In 60 healthy subjects R-wave to pulse interval (RPI), respiratory sinus arrhythmia (RSA), heart rate variability in the mid-frequency (MF) band and sensitivity of the cardiac baroreflex (BRS) were assessed at rest and during a visual attention test. All parameters decreased markedly during test execution. Lower values of resting BRS predicted increased performance. On-task RPI, RSA, MF power and BRS were inversely related to attentional functioning, with RSA accounting for the largest portion of test score variance. The inverse association between resting BRS and performance is discussed as reflecting the bottom-up modulation of cerebral function by baroreceptor activity. The results concerning the on-task measures suggest that a pattern of cardiovascular adjustment including enhanced sympathetic and reduced vagal cardiovascular influences, as well as baroreflex inhibition may induce an adaptive state associated with improved cognitive-attentional functioning.

1. Introduction

Interactions between states of the autonomic nervous system and cognitive performance have a long tradition as a topic of psychological research. Classic concepts from motivational psychology suggested an inverted u-shaped association between unspecific activation and mental functioning (Hebb, 1955; Yerkes and Dodson, 1908). According to this, best functional conditions are expected at midrange arousal, and both overarousal and underarousal are accompanied by declines in performance. Cardiovascular psychophysiology has also contributed to this line of research, the respective models relating changes in cardiovascular activity to facilitation or inhibition of information processing (Lacey and Lacey, 1970) or energetic mobilization of the organism when faced with a situation requiring behavioral adjustment (Obrist, 1981). However, although this certainly constitutes a beneficial approach, empirical work in this field remains relatively sparse (cf. Hansen et al., 2003).

Both the sympathetic and parasympathetic systems contribute to cardiovascular regulation (Levy and Pappano, 2007). Sympathetic influences are transmitted through efferent fibres to the sinus node, the myocardium and the vascular musculature, their activation leading to increases in heart rate, cardiac contractility and vascular tone. Parasympathetic influences are widely, but not completely, restricted to the modulation of heart rate through inhibiting sinus node activity. In addition, the cardiac baroreflex is involved. In this negative feedback loop changes in the activity of the arterial baroreceptors due to fluctuations in blood pressure are responded to with compensatory changes in heart rate and contractility. A complex network of brain stem units subserve cardiovascular autonomic control including, e.g. the nucleus of the solitary tract (NTS), the dorsal motor nucleus (DMN), the nucleus ambiguus (NA) and the rostral ventrolateral medulla (RVLM) (van Roon et al., 2004). Bilateral direct and indirect connections exist between this network and cortical areas, which form an important link between cardiovascular regulation and cognition (Dembowsky and Seller, 1995; Rau and Elbert, 2001).

The present study aimed at investigating relationships between features of sympathetic, parasympathetic and baroreflex cardiovascular control and attentional performance. Hypotheses concerning the role of the sympathetic system may be derived from findings supporting the traditional view of an inverted u-shaped association between unspecific arousal and mental capacity. For instance, sympathetic activation induced by moderate physical exercise led to increased performance on attention tasks, whereas a reduction in performance was observed during higher workload (e.g. Chmura et al., 1994; Yagi et al., 1999). The degree of exercise-induced catecholamine release was also reported to be associated with attentional functioning, the relationship between plasma catecholamine level and performance being inversely u-shaped (Chmura et al., 1994; Peyrin et al., 1987). Memory processes are

* Corresponding author. Tel.: +49 89 21805297; fax: +49 89 21805233.
E-mail address: duschek@psy.uni-muenchen.de (S. Duschek).

0301-0511/$ – see front matter © 2009 Elsevier B.V. All rights reserved.
doi:10.1016/j.biopsycho.2009.03.003

also sensitive to modulations in sympathetic arousal, adrenergic stimulation and blockade produced memory improvement and impairment, respectively (Cahill et al., 1994; Cahill and Alkire, 2003; Maheu et al., 2004). Sympathetic cardiovascular tone may be estimated based on the measurement of R-wave to pulse interval (RPI) (Contrada et al., 1995; Hugdahl, 2001). RPI is given by the time interval between the occurrence of the R-wave and arrival of the pulse at a peripheral location (Marie et al., 1984; Obrist, 1981). Despite not being a pure sympathetic parameter, RPI decreases subject to increasing beta-adrenergic influences on myocardial contractility (Contrada et al., 1995). To the best of our knowledge, RPI has not as yet been related to cognitive performance.

More theoretical and empirical contributions are available concerning the interaction between parasympathetic cardiovascular control and attentional performance. Parasympathetic influences on heart rate can be reliably quantified by respiratory sinus arrhythmia (RSA), the variation in heart rate that occurs during a breathing cycle. The RSA is mediated through inhibitory vagal fibres to the sinus node (Berntson et al., 1997; Task Force, 1996) and may be derived from the high frequency (HF) band of the heart rate variability spectrum that is habitually associated with respiration. Porges (1992) proposed a theoretical framework on the link between cardiac vagal tone and interindividual differences in attention. Building on earlier models (Lacey, 1967; Obrist et al., 1970), he postulated that higher resting levels of cardiac vagal tone are associated with improved attentional capacity. This is consistent, for instance, with Richards' (1987) observation of reduced distractibility in infants with high baseline RSA. Suess et al. (1994) presented school children with a continuous performance task and found perceptual sensibility to be positively related to resting RSA. In young adults, levels of cardiac vagal tone indexed by heart rate variability were associated with better reaction time performance (Porges, 1972, 1973). A group of sailors with higher heart rate variability displayed better performance on working memory and continuous performance tests than those with lower heart rate variability (Hansen et al., 2003).

Functional features of the cardiac baroreflex, particularly its sensitivity expressed as change in heart cycle duration per unit of blood pressure change, have also been related to cognitive performance. Baroreflex sensitivity (BRS) can be determined in the time domain using sequence analysis of spontaneously occurring covariation between systolic blood pressure and heart cycle duration (Duschek and Reyes del Paso, 2007; Parati et al., 2000). Yasumasu et al. (2006) reported an inverse association between BRS assessed during the execution of serial subtractions and task performance. Reyes del Paso et al. (in press) also found better arithmetic performance (addition of three-digit numbers) in individuals with lower on-task BRS. Yasumasu et al. (2006) interpreted their finding in the context of the intake rejection hypothesis (Lacey and Lacey, 1970), according to which increased heart rate due to baroreflex inhibition facilitates internal cognitive elaboration such as required by an arithmetic task. Alternatively, they considered that the inverse association may reflect interindividual differences in mental effort invested in the task. BRS was shown to decrease with increasing mental load (Reyes del Paso et al., 1996; Robbe et al., 1987). Assuming a positive relationship between mental effort and task performance, it may be expected that lower on-task BRS is accompanied by better performance. However, it should not be overlooked that the findings of Yasumasu et al. (2006) and Reyes del Paso et al. (in press), though certainly promising, are restricted to arithmetic processing and thus cannot be generalized to other domains of cognitive functioning.

Spectral power in the mid-frequency (MF) band of the heart rate variability spectrum is another parameter of cardiac autonomic regulation, which may more accurately represent mental load than BRS. Oscillations in this so-called 0.10 Hz component reflect both sympathetic and parasympathetic effects on sinus node activity (van Roon et al., 2004). A number of studies indicated that their magnitude is inversely related to the individual degree of effort during execution of a cognitive task (Boucsein and Backs, 2000; van Roon et al., 2004). On account of this, it seemed useful also to include MF power in the present analysis.

As a secondary aim, the study investigated interindividual differences in task induced cardiovascular modulations. Porges (1992) postulated an association between resting cardiac vagal tone and the extent of cardiovascular reactivity. This is consistent with studies that have revealed more pronounced heart rate responses to various stimuli in children and adults with higher baseline heart rate variability (DeGangi et al., 1991; Porges, 1972; Porter et al., 1988). Cardiovascular reactivity to cognitive demands may also relate to task performance. Duschek (2005) found a positive correlation between systolic and diastolic blood pressure increases during the execution of five attention tasks and performance on each of them. In infants, greater decreases of RSA during mental testing were related to higher functional levels (DeGangi et al., 1991). Interindividual differences in cardiovascular modulation possibly reflect different degrees of autonomic adjustment as well as motivation on a task, both of which may contribute to performance. However, inconsistent findings, i.e. missing or even inverse associations between cardiovascular reactivity and mental performance, were also reported (Backs and Seljos, 1994; Wright et al., 2005). Thus, the current state of research does not allow definite conclusions.

In the present study, attentional capacity was assessed using a classic letter cancellation test ("Attentional Performance Test", Test d2, Brickenkamp, 1994). Tasks of this type address the cognitive components of selective and sustained attention that are undoubtedly of vast importance in everyday life (Johnson and Proctor, 2004; Posner and Rafal, 1987). In the test subjects have to select and mark as many target stimuli as possible in a given amount of time, hence it also has certain load on speed of information processing. Autonomic parameters were recorded under resting conditions and during execution of the task. One may assume that features of autonomic control assessed during cognitive processing show the closest link to performance. On the other hand, on-task measures are influenced by factors such as mental effort, emotional stress or subjectively experienced task difficulty. In contrast, baseline measures are free of these confounding variables.

The following predictions were made: (1) Taking an inverted u-shaped association between unspecific sympathetic arousal and mental performance into account, and assuming an experimental situation in which sympathetic overactivity is unlikely to occur, an inverse relationship between RPI and attentional performance may be expected. (2) On account of Porges' (1992) model, we predicted a positive correlation between resting RSA and performance. (3) Our findings on baroreflex function (Reyes del Paso et al., in press; Yasumasu et al., 2006) suggest that individuals with increased BRS should exhibit poorer performance. (4) Given the inverse association between oscillations in the MF band and mental effort load, and supposing better performance in the case of higher effort, MF power assessed during task execution should correlate negatively with performance. (5) Considering Porges' (1992) hypothesis, we expected higher cardiovascular reactivity in individuals with higher resting RSA. (6) Even though the available database is somewhat controversial, the likely association between mental effort and autonomic reactivity suggests stronger reactivity to be related to increased performance.

2. Methods

2.1. Participants

Sixty university students (28 men, 32 women) with a mean age of 24.5 years (SD = 3.7) participated. Exclusion criteria comprised severe physical diseases, psychiatric disorders, as well as the use of psychoactive drugs or medication affecting the cardiovascular system. All subjects were right handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). Mean systolic and diastolic blood pressure taken prior to experimental procedure were 115.1 mmHg (SD = 11.7) and 74.6 mmHg (SD = 8.0), respectively. Mean heart rate was 74.1 beats per minute (SD = 12.8).

2.2. Cognitive test

The Test d2 (Brickenkamp, 1994) is a paper–pencil test in which a target stimulus has to be identified among a variety of distractor items. The target stimulus is defined as the letter d with two apostrophe marks, each of which may be located above or below the letter. The letter p with different numbers of apostrophe marks as well as the letter d with one, three or four apostrophe marks serve as distractors. The stimuli are arranged in 14 rows, each containing 47 letters. Subjects have 20 s in which to work on each row. After 20 s have elapsed, she/he is instructed to immediately move on to the next row (test duration 4 min, 40 s). The subjects are asked to work as quickly and exactly as possible.

Three parameters were used to quantify speed and accuracy of performance: (1) the total number of processed stimuli including both correct responses (i.e. marked targets and skipped distractors) as well as mistakes (i.e. skipped targets and marked distractors), (2) the percentage of mistakes among the processed stimuli and (3) "attentional capacity" defined as the number of marked targets minus the number of marked distractors. The latter index has been reported to be particular reliable and tamper-resistant (Brickenkamp, 1994).

2.3. Procedure

At the beginning of the experimental session, blood pressure was taken sphygmomanometrically using an automatic inflation monitor (Omron M9 Premium, Omron, USA). ECG and blood pressure were continuously recorded at rest (baseline) and during execution of the Test d2. During the 5 min baseline participants were asked to sit still, not to speak and to relax with their eyes open.

ECG was recorded at a sample rate of 500 Hz applying a Biopac 150 system (Biopac Systems Inc., USA). Two active electrodes (Ag/AgCl) were placed at the right mid-clavicle and the lowest left rib. The back of the left hand was grounded. Respiration was monitored with the same system using a piezoelectric thoracic belt (sample rate 500 Hz). Blood pressure was continuously assessed by means of a Finapres 2300 BP device (Ohmeda, USA). The cuff of the Finapres was fixed onto the left index finger of each subject, and that hand was positioned at the level of the heart. The blood pressure data were analogously exported and recorded using the Biopac (sample rate 500 Hz).

3. Data analysis

3.1. Data reduction

The ECG raw signal was processed using the software AcqKnowledge 3.8.1 that allows R-spike detection and quantification of R–R intervals. Beat-by-beat values were edited for artifacts, replacing the respective values by linear interpolation. The same software was applied for peak detection in the respiratory signal and computation of respiratory rate.

The time series of R–R intervals were subjected to Fast-Fourier transformation. For this purpose, software, which follows Task Force (1996) guidelines and was designed by the "Biosignal Analysis and Medical Imaging Group" (Niskanen et al., 2004) was used. Spectral power density was expressed in absolute units (ms^2). RSA was indexed by spectral power density in the frequency range from 0.15 to 0.40 Hz, i.e. the HF band. According to recent suggestions (Denver et al., 2007), respiratory rate was not controlled for in the computation of RSA. The MF band was defined as spectral power density in the frequency range between 0.07 and 0.14 Hz (Aasman et al., 1987; Althaus et al., 1998).

BRS was determined based on the continuously recorded blood pressure data using a program published by Reyes del Paso (1994). The program locates sequences of three to six consecutive heart cycles ("reflex sequences") in which systolic blood pressure increases are accompanied by increases in heart cycle duration, and those in which blood pressure decreases are accompanied by decreases in heart cycle duration. Since a time lag of one heartbeat is known to produce the best estimates of BRS (Steptoe and Vögele, 1990), each systolic value was paired with the duration of the cycle immediately following. 1 mmHg and 2 ms were applied as minimal criteria for changes in blood pressure and heart cycle duration, respectively. For the quantification of BRS, the interval between systolic points ("intersystolic interval") was taken as an index of heart cycle duration. When one of these reflex sequences was detected, the regression line was computed across all heart cycles of the given sequence. BRS was expressed as the change in heart cycle duration (in ms) per mmHg blood pressure change, measured by the slope of the regression line (Parati et al., 2000; Steptoe and Vögele, 1990). The validity of this method has been documented, for instance, by comparisons with spectral analysis and invasive methods (Parlow et al., 1995; Reyes del Paso, 1994).

RPI was computed based on the ECG readings and the blood pressure curves taken from the finger. It was indexed by the time elapsed between the R-spike and the closest following systolic point (Obrist, 1981).

3.2. Statistic analysis

Values of all physiological parameters were averaged across the baseline and the period of task execution, respectively. In order to obtain a more complete picture, in addition to the indices of cardiovascular autonomic control, R–R interval, systolic blood pressure revealed by the Finapres technique, and respiratory rate were included in the analysis. Changes in the indices between both conditions were analyzed by means of one-way ANOVA procedures. Moreover, reactivity scores were computed as the relative (percent) changes between the baseline and the task period. These were related to baseline RSA using Pearson correlations.

Physiological parameters assessed during baseline and task execution, as well as reactivity scores were correlated with the indices of the Test d2. In order to get further insight into the pattern of associations, multiple regression analyses were conducted with the physiological parameters as predictors and performance indices as dependent variables. Three separate regressions analyses (i.e., one for each performance parameter) were computed for the physiological values assessed during baseline, three for the physiological parameters recorded during task execution, and another three for the reactivity scores. A "stepwise" procedure was applied for entry and removal of predictors. In this method the predictor which explains the largest part of variance of the dependent variable is the first to enter the model. Subsequently, this predictor is partialed out and the next predictor is selected from the remaining ones according to the same criteria. This procedure is repeated until no significant predictor is left. Finally, Pearson correlations between baseline RSA and the reactivity scores were computed.

4. Results

Table 1 displays the values of the physiological parameters assessed during baseline and execution of the Test d2. During the task RPI, RSA, MF power, BRS and R–R interval significantly decreased, and systolic blood pressure as well as respiratory rate rose significantly.

Pearson correlations were computed for the relationships between baseline RSA and the reactivity scores, i.e. the relative changes in the physiological parameters. Higher values of baseline RSA were significantly associated with stronger reductions in R–R interval ($r = -.22$, $p = .049$), RSA ($r = .33$, $p < .01$) and MF power ($r = .28$, $p = .016$). The remaining correlations did not reach significance (RPI: $r = .06$, BRS: $r = -.09$, systolic blood pressure: $r = -.12$, all $p > .05$).

On the Test d2 subjects processed on average 526.4 stimuli (SD = 74.3). The mean percentage of mistakes was 20.7% (SD = 10.3), and mean attentional capacity was 197.6 (SD = 36.4). Men and women did not differ significantly in their performance (number of

Table 1
Mean values (SD in brackets) of the physiological parameters, $F[1,59]$- and p-values of the one-way ANOVA.

	Baseline	Task period	F	p
RPI (ms)	290.5 (31.7)	273.7 (38.3)	8.3	<.01
RSA (ms^2)	519.2 (813.8)	103.3 (101.0)	18.5	<.01
MF power (ms^2)	329.7 (363.3)	135.7 (109.2)	17.8	<.01
BRS (ms/mmHg)	15.9 (9.2)	10.9 (6.1)	50.0	<.01
R–R interval (ms)	823.8 (134.9)	710.1 (123.5)	153.4	<.01
Systolic blood pressure (mmHg)	112.5 (20.6)	122.9 (24.1)	18.4	<.01
Respiratory rate (cycles/min)	14.6 (3.8)	21.4 (4.1)	149.8	<.01

processed stimuli, men: M = 525.7, SD = 77.2; women: M = 527.0, SD = 72.8; percentage of mistakes, men: M = 21.9%, SD = 11.0; women: M = 19.8%, SD = 9.1; attentional capacity, men: M = 194.7, SD = 38.7; women: M = 200.1, SD = 34.7; all $p > .05$).

Correlations between the physiological variables (baseline values, on-task values, reactivity scores) and the three indices of performance are given in Table 2. There were significant negative correlations between BRS assessed during baseline and both the number of processed stimuli and attentional capacity. The correlation between BRS and the percentage of mistakes was also significant but positive. The same pattern of significant correlations was found for baseline R–R interval. The correlations between the on-task values, RSA, MF power, BRS and R–R interval on the one hand and the total number of processed stimuli as well as attentional capacity on the other hand were significant and negative. There was a significant negative correlation between on-task RPI and the number of processed stimuli. Furthermore there was a significant positive correlation between on-task RSA, MF power, BRS and R–R interval on the one hand and the percentage of mistakes on the other. With regard to the reactivity scores, we found a significant negative correlation between RPI reactivity and the number of processed stimuli, and a significant positive correlation between RSA reactivity and the percentage of mistakes, indicating a trend towards better performance in individuals with stronger decreases in RPI and RSA.

Table 2
Pearson correlations between the physiological parameters (baseline, task execution and reactivity) and performance on the Test d2.

	Total number of stimuli	Percentage of mistakes	Attentional capacity
Baseline			
RPI	−.01	−.03	−.07
RSA	−.04	.04	−.04
MF power	.02	.01	−.05
BRS	−.29*	.32*	−.35**
R–R interval	−.27*	.25*	−.31**
Systolic blood pressure	.02	−.03	.09
Task execution			
RPI	−.27*	.18	−.19
RSA	−.35**	.37**	−.29*
MF power	−.29*	.34**	−.23*
BRS	−.31**	.28*	−.28*
R–R interval	−.31**	.22*	−.29*
Systolic blood pressure	.03	.00	.02
Reactivity			
RPI	−.25*	.20	−.14
RSA	−.20	.23*	.18
MF power	−.10	.07	−.10
BRS	−.02	−.09	.09
R–R interval	−.11	−.03	.00
Systolic blood pressure	.05	.04	−.09

* $p < .05$.
** $p < .01$.

Table 3 displays the standardized Beta-weights resulting from the stepwise regression analyses. The three analyses based on the physiological parameters assessed during baseline each revealed a single model (total number of stimuli: R = .29, percentage of mistakes: R = .32, attentional capacity: R = .35). In all three cases only BRS significantly predicted performance (see Fig. 1). The analyses for the physiological parameters recorded during task execution also yielded one model each (total number of stimuli: R = .35, percentage of mistakes: R = .37, attentional capacity: R = .29). Here, only RSA significantly predicted the three performances parameters (see Fig. 2). The regression analyses based on the reactivity scores did not reveal any significant models.

5. Discussion

The study revealed an increase in blood pressure during attentional processing, while R–R interval, R-wave to pulse interval, heart rate variability in the respiratory and mid-frequency bands, as well as the sensitivity of the cardiac baroreflex decreased. Higher levels of baseline RSA were associated with more pronounced task induced declines in R–R interval, RSA and MF power. Lower resting BRS predicted higher values in all parameters of attentional capacity. When assessed during task execution, lower values of R–R interval, RPI, RSA, MF power and BRS were related to increased performance. Regression analyses indicated that RSA accounted for the largest portion of test score variance of all on-task measures.

The physiological modulations reflect differential contributions of the sympathetic, parasympathetic and baroreflex systems to cardiovascular adjustment to the demands related to cognitive activity. The magnitude of RPI is predominantly determined by beta-adrenergic effects on myocardial contractility (Furedy et al., 1996; Hugdahl, 2001). Contrada et al. (1995), for instance, showed dose-dependent reductions in RPI following pharmacological sympathetic stimulation, whereas parasympathetic stimulation yielded only slight effects. The reduction in RPI during mental activity may thus be attributed to increased contractility mainly resulting from beta-sympathetic activation. However, to a smaller degree, changes in RPI also occur subject to vascular factors (Contrada et al., 1995; Newlin, 1981). Hence, task-related increases in vascular tone, mediated by the alpha-sympathetic system, have also to be taken into account.

Reductions in heart rate variability during cognitive activity are well-known (Althaus et al., 1998; Duschek et al., 2008a; van Roon

Table 3
Regression analyses for the prediction of performance on the Test d2 from the physiological parameters assessed during baseline and task execution (standardized Beta-weights).

	Total number of stimuli	Percentage of mistakes	Attentional capacity
Baseline			
RPI	.01	−.05	−.05
RSA	.20	−.23	.26
MF power	.04	−.02	.08
BRS	−.29*	.32*	−.35**
R–R interval	−.11	.04	−.13
Systolic blood pressure	−.06	.06	−.01
Task execution			
RPI	−.15	.05	−.06
RSA	−.35**	.37**	−.29*
MF power	−.18	.23	−.13
BRS	−.13	.03	−.14
R–R interval	−.02	.04	−.19
Systolic blood pressure	−.18	.06	−.03

* $p < .05$.
** $p < .01$.

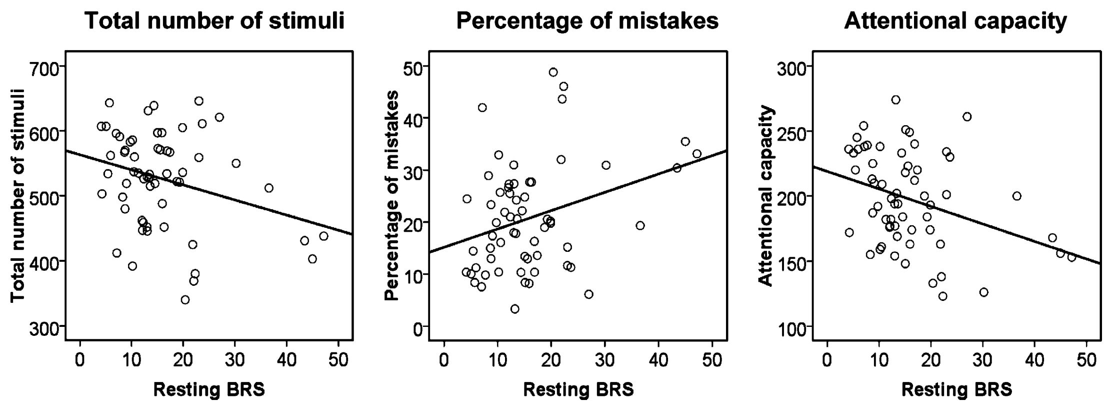

Fig. 1. Scatter plots for the relationships between resting BRS and the indices of the Test d2.

et al., 1995). There is broad consent that oscillations in the respiratory range are exclusively mediated by the parasympathetic system, thus the reduction in RSA evidently reflects vagal withdrawal (Berntson et al., 1997; Denver et al., 2007). In contrast to this, multiple mechanisms contribute to slower oscillations including alpha and beta sympathetic as well as parasympathetic drive (Berntson et al., 1997). The MF band is thought to be sensitive to the amount of mental workload invested in a task (Boucsein and Backs, 2000; Mulder and Mulder, 1981). Aasman et al. (1987), for instance, demonstrated systematic decreases in MF power with increasing load on working memory. Althaus et al. (1998) reported that attentional processing load was more closely related to oscillations in the MF band than to those in the HF band. Similar results were obtained using naturalistic tasks such as flight simulation or car steering (Mulders et al., 1982; Veltman and Gaillard, 1993, 1998). Considering this, the decline in MF power observed in the current study may reflect sympathetic and parasympathetic adjustment to cognitive effort during task execution.

Reductions in BRS during cognition have been previously observed as well (Duschek et al., 2008a,b; Reyes del Paso et al., 1996, 2004; Yasumasu et al., 2006). Baroreflex inhibition contributes to task related declines in parasympathetic outflow. The baroreflex exerts its influence on the heart through the vagus nerve, thereby being a powerful source of parasympathetic cardiac control (Sleight et al., 1995). Reyes del Paso et al. (1996), for instance, found that vagal blockade reduced BRS to values close to zero. After beta-adrenergic blockade, during which heart rate is predominantly under vagal control, BRS accounted for more than 90% of the heart rate variance. Evidently, the baroreflex system constitutes only one among a variety of sources of vagal influences on heart rate. This is underlined by structural interactions between the autonomic control units in the brain stem and their connections with further brain areas. The NTS plays an integrative role within the baroreflex system (van Roon et al., 2004). It includes the first synapse of the baroreceptor afferents and gives rise to projections to the NA and the DMN, which constitute the starting points of vagal efferents through which the cardiac response is executed. However, all these nuclei are closely connected with the hypothalamus and higher brain areas. While cortical influences on the baroreflex are transmitted by descending pathways to the NTS, the control of higher brain units on the NA and DMN enables direct modulation of vagal outflow independent of the reflex (Berntson et al., 1993; van Roon et al., 2004).

The correlations of resting RSA with task induced changes in R–R interval, RSA and MF power are in line with reports of stronger heart rate responses in individuals with more pronounced baseline heart rate variability (Porges, 1972; Porter et al., 1988; DeGangi et al., 1991). Altogether, these findings support the notion of Porges (1992) that stronger autonomic reactivity is to be found in individuals with higher resting cardiac vagal tone. One may assume that higher baseline levels of vagal tone allow stronger stress-induced vagal withdrawal as well as reductions in cardiovascular parameters related to the vagal control system.

Lower resting BRS and R–R interval predicted better attentional functioning. This held true for the speed aspect of performance represented by the number of processed stimuli of the Test d2, as well as its accuracy dimension, i.e. the percentage of mistakes and the index of attentional capacity. Regression analyses did not reveal an independent association between R–R interval and performance, which is consistent with the view that during rest R–R interval strongly depends on baroreflex function (Reyes del Paso et al., 1996). The finding is in line with former observations of an inverse relationship between on-task BRS and arithmetic performance (Yasumasu et al., 2006; Reyes del Paso et al., in press). As an

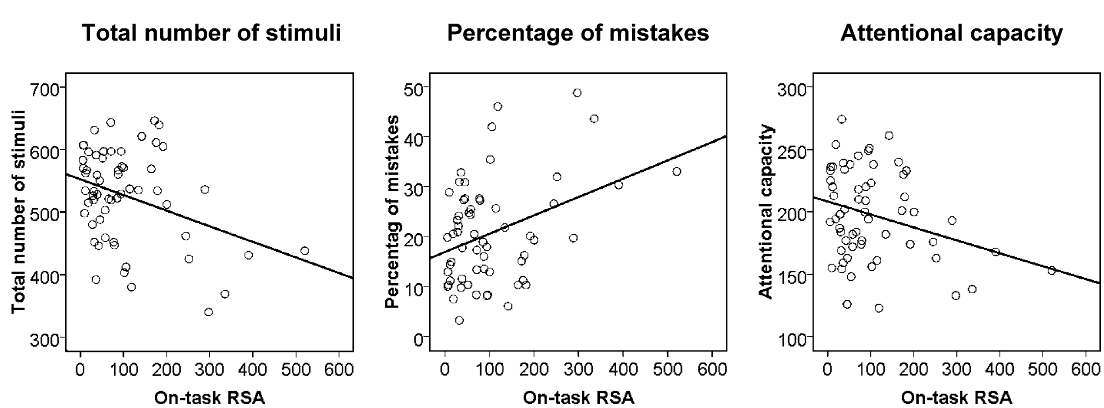

Fig. 2. Scatter plots for the relationships between on-task RSA and the indices of the Test d2.

explanation for their finding Yasumasu et al. (2006) proposed an improvement of conditions for environmental rejection and internal processing in the case of baroreflex inhibition (Lacey and Lacey, 1970). Alternatively, they argued that higher levels of mental effort may lead both to stronger reductions in BRS and better performance. Both considerations cannot explain the present result. The Test d2 requires rapid detection and identification of external stimuli. Thus, in the context of the Laceys' theory it induces a condition of sensory intake rather than environmental rejection. Any influence from mental effort can be ruled out given that baseline BRS was recorded a short time before execution of the Test d2.

The result may be best explained by taking into account the well-known bottom-up effects of cardiovascular afferents on cerebral functioning. In addition to its role in blood pressure regulation, the baroreceptor system is known to modulate central nervous activity, with baroreceptor activation exerting a generalized inhibiting effect on the brain (Rau and Elbert, 2001). This effect includes, for example, the attrition of cortical excitability (Rau et al., 1993), reduction of sensorimotor performance (McIntyre et al., 2007), decrease of muscle tone (Dworkin et al., 1994), and dampening of pain sensitivity (Bruehl and Chung, 2004). With respect to anatomical and physiological features, the baroreceptor system is commonly subdivided into its "cardiac" and "central nervous" branches (Reyes del Paso et al., 2004). The reflexive control of heart activity is mediated by the cardiac branch, with its sensitivity determining the extent of change in heart cycle duration elicited by phasic blood pressure fluctuations. While the cardiac branch is confined to the network of autonomic control in the brain stem, the inhibitory effect of baroreceptor activation on brain activity is mediated by the central nervous branch, which connects brain stem nuclei with cortical units (Dembowsky and Seller, 1995). Knowledge concerning the interplay of the two branches of the baroreceptor system remains sparse. It was suggested, however, that interindividual differences in the sensitivity of the cardiac branch can also affect the degree of inhibition mediated by the central nervous branch (Duschek et al., 2007; Reyes del Paso et al., in press). According to this, higher activity of the cardiac branch implies stronger inhibiting effects. This hypothesis is supported, for instance, by a finding in the field of pain perception. Duschek et al. (2007) reported an inverse association between BRS (recorded both at rest and during painful stimulation) and subjective pain intensity, indicating stronger pain inhibition in the case of higher BRS. One may argue that baroreceptor related inhibition can also affect cognitive functioning, which would explain the inverse association between BRS and attentional performance.

Resting RSA was unrelated to performance, a result which conflicts with Porges' (1992) model predicting an association between higher resting levels of cardiac vagal tone and improved attentional capacity. One should, however, not overlook that the studies supporting this view (e.g. Porges, 1972, 1973; Suess et al., 1994; Hansen et al., 2003) were based on tasks that clearly differ from the Test d2. The applied reaction time, continuous performance and working memory tests certainly all have high loads on sustained attention. However, here stimuli were consecutively presented, mostly with defined intervals between them. In the Test d2, on the other hand, subjects are presented with a large number of stimuli at the same time, and it presents a high load on cognitive speed. It can be assumed that the cognitive functions addressed by the respective test relate in different ways to cardiovascular autonomic control. Porges' (1992) concept is based on the assumption of decreases in sensory thresholds during periods of increased vagal tone. Such a state may indeed facilitate performance on specific attention tasks. However, one may hypothesize that a task that is executed under high time pressure demands higher energetic resources, thus performance may depend to a high degree on the activation of metabolic resources. Increased vagal tone is related to a trophotropic state and therefore may not be helpful in such a situation.

On-task RSA was inversely related to performance. One may consider that reduced cardiac vagal tone during task execution helps establish an ergotropic physiological condition, which contributes to optimizing mental functioning. This is also consistent with the inverse association between on-task BRS and all test scores. Lower BRS implies a reduced buffering effect of the baroreflex and therefore facilitates task related increases in heart rate and blood pressure and thus improvement of the energetic and metabolic supply of the organism (Duschek et al., 2008b). The inverse relationship between RPT and the number of processed stimuli suggests that higher cardiac sympathetic tone, which is also related to an ergotropic state, contributed to increased performance on the task. Regression analyses, however, indicated that on-task RSA accounted for the largest portion of test score variance among all on-task parameters. This suggests a dominant role of the parasympathetic system in the link between cardiovascular autonomic regulation and attentional functioning. Apparently, reduced cardiac inhibition is of particular importance for the establishment of a physiological condition optimal for the mental processes required by tasks of the present type.

The interpretations concerning the on-task measures certainly remain somewhat speculative. Interindividual differences in these variables may relate to some extent to the degree of effort that subjects invested in the task, which in turn may have affected performance. Even though this explanation cannot be completely ruled out, one should bare in mind that regression analyses indicated that MF power had a subordinate role in the prediction of performance. The psychophysiological counterpart of mental load was apparently not the most relevant factor in the link between autonomic control and performance. One may furthermore hypothesize that individual effort would especially influence the change in autonomic state between baseline and task execution. The present analysis, however, yielded only slight relationships between the reactivity scores and performance, and the change in MF power was unrelated to any test scores. Another restriction results from the fact that the present design allowed the exploration of attentional processing only across a limited range of autonomic tone. In an experimental situation in which individual test results are not followed by any positive or negative consequences, the highest levels of sympathetic activity are unlikely to occur. The study was therefore limited in investigating non-linear, e.g. u-shaped, relationships between autonomic parameters and attentional functioning. In particular, the hypothesis of a possible decline in performance during extreme sympathetic cardiovascular tone remains to be tested.

Baseline and on-task heart cycle duration indexed by the R–R interval, but not blood pressure, were related to attentional functioning. Given that heart cycle duration is controlled by the sympathetic, parasympathetic and baroreflex systems, its association with attentional function is consistent with the reasoning presented above. An inverted u-shaped relationship between blood pressure and cognitive performance is generally assumed (e.g. Duschek and Schandry, 2007; Waldstein et al., 2005). While the normotensive range is associated with highest functional levels, a decline in performance at both ends of the blood pressure spectrum, i.e. hypotension and hypertension, has been established (Duschek et al., 2005; Morris et al., 2002; Waldstein et al., 1991). The blood pressure range in the present sample was relatively small and widely restricted to normotension. Therefore, an association between blood pressure and cognitive performance could not be expected.

To sum up, some of the present findings are in accordance with classical psychophysiological concepts. For instance they, support the notion of a decrease in heart rate variability and inhibition of baroreflex function during mental activity, as well as that of a dependence of autonomic reactivity on resting vagal tone. However, the study also provided new information completing the current understanding of the link between cardiovascular regulation and cognition. It yielded the first evidence that the relationship between baroreflex function and performance is not restricted to tasks aiming at internal cognitive elaboration, but can be generalized to such requiring the detection and identification of external stimuli. This finding may be best explained by bottom-up modulation of general cognitive function by baroreceptor activity. Our results, furthermore, suggest that the classic assumption of an association between higher resting levels of cardiac vagal tone and improved attentional capacity does not universally hold, but depends on properties of the current task. In particular, cognitive processing under time pressure may demand a pattern of cardiovascular adjustment suitable to coping with increased metabolic needs. For this, reduction of cardiac vagal tone rather than its increase may be most adaptive. In future studies it would be promising to directly compare different types of tests of attentional capacity regarding their links to RSA and further parameters of autonomic cardiovascular control.

Acknowledgements

This study was partly financed by the German Research Foundation (Project No.: DU 447/1-1) and the Spanish Commission of Science and Technology (Project No.: SEJ 2006-09808). The cooperation between the Universities of Munich and Jaén was supported by the German Academic Exchange Service and the Spanish Ministry of Education and Science (Project No.: D/07/13368).

References

Aasman, J., Mulder, G., Mulder, L.J.M., 1987. Operator effort and the measurement of heart-rate variability. Human Factors 29, 161–170.
Althaus, M., Mulder, L.J.M., Mulder, G., van Roon, A.M., Minderaa, R.B., 1998. Influence of respiratory activity on the cardiac response pattern to mental effort. Psychophysiology 35, 420–430.
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. International Journal of Psychophysiology 16, 57–68.
Berntson, G.G., Cacioppo, J.T., Quigley, K.S., 1993. Respiratory sinus arrhythmia: autonomic origins, physiological mechanisms, and psychophysiological implications. Psychophysiology 30, 183–196.
Berntson, G.G., Bigger Jr., J.T., Eckberg, D.L., Grossman, P., Kaufmann, P.G., Malik, M., et al., 1997. Heart rate variability: origins, methods, and interpretive caveats. Psychophysiology 34, 623–648.
Boucsein, W., Backs, R.W., 2000. Engineering psychophysiology as a discipline: historical and theoretical aspects. In: Backs, R.W., Boucsein, W. (Eds.), Engineering Psychophysiology: Issues and Applications. Lawrence Erlbaum, London, pp. 3–30.
Brickenkamp, R., 1994. Test d2, Aufmerksamkeits-Belastungs-Test [Test d2, Attentional Performance Test]. Hogrefe, Göttingen.
Bruehl, S., Chung, O.Y., 2004. Interactions between the cardiovascular and pain regulatory systems: an updated review of mechanisms and possible alterations in chronic pain. Neuroscience and Biobehavioral Reviews 28, 395–414.
Cahill, L., Prins, B., Weber, M., McGaugh, J.L., 1994. Beta-adrenergic activation and memory for emotional events. Nature 371, 702–704.
Cahill, L., Alkire, M.T., 2003. Epinephrine enhancement of human memory consolidation: interaction with arousal at encoding. Neurobiology of Learning and Memory 79, 194–198.
Chmura, J., Nazar, K., Kaciuba-Uscilko, H., 1994. Choice reaction time during graded exercise in relation to blood lactate and plasma catecholamine thresholds. International Journal of Sports Medicine 15, 172–176.
Contrada, R.J., Del, B.A., Levy, L., Weiss, T., 1995. Form and magnitude of beta-sympathetic and parasympathetic influences on pulse transit time. Psychophysiology 32, 329–334.
DeGangi, G.A., DiPietro, J.A., Greenspan, S.I., Porges, S.W., 1991. Psychophysiological characteristics of the regularly disordered infant. Infant Behavior and Development 14, 37–50.
Dembowsky, K., Seller, H., 1995. Arterial baroreceptor reflexes. In: Vaitl, D., Schandry, R. (Eds.), From the Heart to the Brain: The Psychophysiology of Circulation–Brain Interaction. Europäischer Verlag der Wissenschaften, Frankfurt a.M., pp. 35–60.
Denver, J.W., Reed, S.F., Porges, S.W., 2007. Methodological issues in the quantification of respiratory sinus arrhythmia. Biological Psychology 74, 286–294.
Duschek, S., 2005. Aufmerksamkeitsleistungen, zerebrale Durchblutung und kortikale Aktivierungsprozesse bei essentieller Hypotonie [Attentional Performance, Cerebral Blood Flow and Cortical Activation in Chronic Hypotension]. Dissertation at the University of Munich.
Duschek, S., Matthias, E., Schandry, R., 2005. Essential hypotension is accompanied by deficits in attention and working memory. Behavioral Medicine 30, 149–158.
Duschek, S., Mück, I., Reyes del Paso, G.A., 2007. Relationships between baroreceptor cardiac reflex sensitivity and pain experience in normotensive individuals. International Journal of Psychophysiology 65, 193–200.
Duschek, S., Reyes del Paso, G.A., 2007. Quantification of cardiac baroreflex function at rest and during autonomic stimulation. Journal of Physiological Sciences 57, 259–268.
Duschek, S., Schandry, R., 2007. Reduced brain perfusion and cognitive performance due to essential hypotension. Clinical Autonomic Research 17, 69–76.
Duschek, S., Werner, N., Kapan, N., Reyes del Paso, G.A., 2008a. Patterns of cerebral blood flow and systemic hemodynamics during arithmetic processing. Journal of Psychophysiology 22, 81–90.
Duschek, S., Dietel, A., Schandry, R., Reyes del Paso, G.A., 2008b. Increased baroreflex sensitivity and reduced cardiovascular reactivity in chronic low blood pressure. Hypertension Research 31, 1873–1878.
Dworkin, B.R., Elbert, T., Rau, H., Birbaumer, N., Pauli, P., Droste, C., Brunia, C.H., 1994. Central effects of baroreceptor activation in humans: attenuation of skeletal reflexes and pain perception. Proceedings of the National Academy of Sciences of the United States of America 91, 6329–6333.
Furedy, J.J., Szabo, A., Péronnet, F., 1996. Effects of psychological and physiological challenges on heart rate, T-wave amplitude, and pulse-transit time. International Journal of Psychophysiology 22, 173–183.
Hansen, A.L., Johnsen, B.H., Thayer, J.F., 2003. Vagal influence on working memory and attention. International Journal of Psychophysiology 48, 263–274.
Hebb, D.O., 1955. Drives and the C.N.S. (conceptual nervous system). Psychological Reviews 62, 243–254.
Hugdahl, K., 2001. Psychophysiology: The Mind–Body Perspective. Harvard University Press, London.
Johnson, A., Proctor, R.W., 2004. Attention. Theory and Practice. Sage Publications, Thousand Oaks.
Lacey, J.I., 1967. Somatic response patterning and stress: some revisions of activation theory. In: Appley, M.H., Trumbell, R. (Eds.), Psychological Stress: Issues in Research. Academic Press, New York, pp. 4–44.
Lacey, B.C., Lacey, J.I., 1970. Some autonomic-central nervous system interrelationships. In: Black, P. (Ed.), Physiological Correlations of Emotion. Academic Press, New York, pp. 205–227.
Levy, M.N., Pappano, A.J., 2007. Cardiovascular Physiology. Mosby Elsevier, Philadelphia.
Maheu, F.S., Joober, R., Beaulieu, S., Lupien, S.J., 2004. Differential effects of adrenergic and corticosteroid hormonal systems on human short- and long-term declarative memory for emotionally arousing material. Behavioral Neuroscience 118, 420–428.
Marie, G.V., Lo, C.R., Van Jones, J., Johnston, D.W., 1984. The relationship between arterial blood pressure and pulse transit time during dynamic and static exercise. Psychophysiology 21, 521–527.
McIntyre, D., Ring, C., Hamer, M., Carroll, D., 2007. Effects of arterial and cardiopulmonary baroreceptor activation on simple and choice reaction times. Psychophysiology 44, 874–879.
Morris, M.C., Scherr, P.A., Hebert, L.E., Bennett, D.A., Wilson, R.S., Glynn, R.J., Evans, D.A., 2002. Association between blood pressure and cognitive function in a biracial community population of older persons. Neuroepidemiology 21, 123–130.
Mulder, G., Mulder, L.J.M., 1981. Task-related cardiovascular stress. In: Long, J., Baddeley, A. (Eds.), Attention and Performance IX. Lawrence Erlbaum, Hillsdale.
Mulders, H.P.G., Meijman, T.F., O'Hanlon, J.F., Mulder, G., 1982. Differential psychophysiological reactivity of city bus drivers. Ergonomics 25, 1003–1011.
Newlin, D.B., 1981. Relationships of pulse transit times to pre-ejection period and blood pressure. Psychophysiology 18, 316–321.
Niskanen, J.P., Tarvainen, M.P., Ranta-aho, P.O., Karjalainen, P.A., 2004. Software for advanced HRV analysis. Computer Methods and Programs in Biomedicine 76, 73–81.
Obrist, P.A., Webb, R.A., Sutterer, J.R., Howard, J.L., 1970. The cardiac–somatic relationship: some reformulations. Psychophysiology 6, 569–587.
Obrist, P.A., 1981. Cardiovascular Psychophysiology. Plenum Press, New York.
Oldfield, R.C., 1971. The assessment and analysis of handedness: the Edinburgh Inventory. Neuropsychologia 9, 97–113.
Parati, G., di Rienzo, M., Mancia, G., 2000. How to measure baroreflex sensitivity: from the cardiovascular laboratory to daily life. Journal of Hypertension 18, 7–19.
Parlow, J., Viale, J.P., Annat, G., Hughson, R., Quintin, L., 1995. Spontaneous cardiac baroreflex in humans: comparison with drugs-induced responses. Hypertension 25, 1058–1068.
Peyrin, L., Pequignot, J.M., Lacour, J.R., Fourcade, J., 1987. Relationship between catecholamine or 3-methoxy 4-hydroxy phenylglycol changes and the mental performance under submaximal exercise in man. Psychopharmacology 93, 188–192.

Porges, S.W., 1972. Heart rate variability and deceleration as indexes of reaction time. Journal of Experimental Psychology 92, 103–110.
Porges, S.W., 1973. Heart rate variability: an autonomic correlate of reaction time performance. Bulletin of the Psychosomatic Society 1, 270–272.
Porges, S.W., 1992. Autonomic regulation and attention. In: Campbell, B.A., Hayne, H., Richardson, R. (Eds.), Attention and Information Processing in Infants and Adults. Erlbaum, Hillsdale, pp. 201–223.
Porter, F.L., Porges, S.W., Marshall, R.E., 1988. Newborn pain cries and vagal tone: parallel changes in response to circumcision. Child Development 59, 495–505.
Posner, M.I., Rafal, R.D., 1987. Cognitive theories of attention and the rehabilitation of attentional deficits. In: Meier, M.J., Benton, A.L., Diller, L. (Eds.), Neuropsychological Rehabilitation. Churchill Livingston, Edinburgh, pp. 182–201.
Rau, H., Pauli, P., Brody, S., Elbert, T., Birbaumer, N., 1993. Baroreceptor stimulation alters cortical activity. Psychophysiology 30, 322–325.
Rau, H., Elbert, T., 2001. Psychophysiology of arterial baroreceptors and the etiology of hypertension. Biological Psychology 57, 179–201.
Reyes del Paso, G.A., 1994. A program to assess baroreceptor cardiac reflex function. Behaviour Research Methods Instruments & Computers 26, 62–64.
Reyes del Paso, G.A., Langewitz, W., Robles, H., Perez, N., 1996. A between-subjects comparison of respiratory sinus arrythmia and baroreceptor cardiac reflex sensitivity as non-invasive measures of tonic parasympathetic cardiac control. International Journal of Psychophysiology 22, 163–171.
Reyes del Paso, G.A., Gonzalez, I., Hernandez, J.A., 2004. Baroreceptor sensitivity and effectiveness varies differentially as a function of cognitive-attentional demands. Biological Psychology 67, 385–395.
Reyes del Paso, G.A., González, M.I., Hernández, J.A., Duschek, S., Gutiérrez, N. Tonic blood pressure modulated the relationships between baroreceptor cardiac reflex sensitivity and cognitive performance. Psychophysiology, in press.
Richards, J.E., 1987. Infant visual sustained attention and respiratory sinus arrhythmia. Child Development 58, 488–496.
Robbe, H., Mulder, L., Ruddel, H., Langewitz, W., Veldman, J., Mulder, G., 1987. Assessment of BRS by means of spectral analysis. Hypertension 10, 538–543.
Sleight, P., La Rovere, M.T., Mortara, A., Pinna, G., Maestri, R., Leuzzi, S., et al., 1995. Physiology and pathophysiology of heart rate and blood pressure variability in humans: Is power spectral analysis largely an index of baroreflex gain? Clinical Sciences (London) 88, 103–109.
Steptoe, A., Vögele, C., 1990. Cardiac baroreceptor reflex function during postural change assessed using non-invasive spontaneous sequence analysis in young men. Cardiovascular Research 24, 627–632.
Suess, P.E., Porges, S.W., Plude, D.J., 1994. Cardiac vagal tone and sustained attention in school-age children. Psychophysiology 31, 17–22.
Task Force of the European Society of Cardiology and the North American Society of Pacing and Electrophysiology, 1996. Heart rate variability: standards of measurement, physiological interpretation and clinical use. Circulation 93, 1043–1065.
van Roon, A.M., Mulder, L.J.M., Veldman, J.B.P., Mulder, G., 1995. Beat-to-beat blood-pressure measurements applied is studies on mental workload. Homeostasis 36, 316–324.
van Roon, A.M., Mulder, L.J.M., Althaus, M., Mulder, G., 2004. Introducing a baroreflex model for studying cardiovascular effects of mental workload. Psychophysiology 41, 961–981.
Veltman, J.A., Gaillard, A.W.K., 1993. Indices of mental workload in a complex task environment. Neuropsychobiology 28, 72–75.
Veltman, J.A., Gaillard, A.W.K., 1998. Physiological workload reactions to increasing levels of task difficulty. Ergonomics 41, 656–669.
Waldstein, S.R., Ryan, C.M., Manuck, S.B., Parkinson, D.K., Bromet, E.J., 1991. Learning and memory function in men with untreated blood pressure elevation. Journal of Consulting and Clinical Psychology 59, 513–517.
Waldstein, S.R., Giggey, P.P., Thayer, J.F., Zonderman, A.B., 2005. Nonlinear relations of blood pressure to cognitive function: the Baltimore Longitudinal Study of Aging. Hypertension 45, 374–379.
Wright, C.E., Kunz-Ebrecht, S.R., Iliffe, S., Foese, O., Steptoe, A., 2005. Physiological correlates of cognitive functioning in an elderly population. Psychoneuroendocrinology 30, 826–838.
Yagi, Y., Coburn, K.L., Estes, K.M., Arruda, J.E., 1999. Effects of aerobic exercise and gender on visual and auditory P300, reaction time, and accuracy. European Journal of Applied Physiology 80, 402–408.
Yasumasu, T., Reyes del Paso, G.A., Takahara, K., Nakashima, Y., 2006. Reduced baroreflex cardiac sensitivity predicts increased cognitive performance. Psychophysiology 43, 41–45.
Yerkes, R.M., Dodson, J.D., 1908. The relation of strength of stimulus to rapidity of habit-formation. Journal of Comparative and Neurological Psychology 18, 459–482.